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Effects of fatigue and recovery on electromechanical delay during isokinetic muscle actions

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Abstract

Objective: To examine muscle-specific differences and the effects of fatigue and recovery on electromechanical delay (EMD) during maximal isokinetic muscle actions.

Approach: Thirteen men performed maximal isokinetic knee extension muscle actions at 60° s^{-1} , pretest, posttest, and after 5 min of recovery from 25 maximal isokinetic knee extensions. The onsets of the electromyographic, mechanomyographic, and force signals were used to identify EMD measures from the vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF).

Main results: There were posttest increases in all EMD measures for all muscles that returned to pretest levels after 5 min of recovery. There were, however, no differences in EMD measures between the VL and VM. All EMD values from the RF were greater than the VL and VM.

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Significance: These findings suggested muscle-specific differences in EMD and that excitation-contraction coupling failure and increased compliance of the series elastic component occurred posttest, but subsided after 5 min of recovery.

Keywords: electromyography, mechanomyography, excitation-contraction coupling, series elastic component

1. Introduction

Electromechanical delay (EMD) measures the time delay between the onset of electrical activation of the muscle and the onset of force production (Norman and Komi 1979). Typically (Vos *et al* 1991, Zhou *et al* 1998), EMD has been operationally defined as the time period between the onset of the electromyographic (EMG) signal and the onset of force production during a muscle contraction. More recently, however, mechanomyography (MMG) has been used to identify the onset of the lateral oscillations associated with the contraction of skeletal muscle and provides additional information regarding the factors that contribute to EMD (Ce *et al* 2013, Esposito 2013, Smith *et al* 2016b). Specifically, the onset of the EMG signal identifies when an electrical impulse activates the muscle while the MMG signal reflects the initiation of movement from the activated muscle fibers (Basmajian and De Luca 1985). The time difference between the onsets of the EMG and MMG signals is a measure of the total duration of the events from the motor unit action potentials travelling along the sarcolemma to cross-bridge formation (excitation–contraction coupling) (Orizio *et al* 1997). The onset of the MMG signal to the onset of force production is a measure of the time required to take up the muscle-tendon unit slack before force transmission can occur, which has been termed the series elastic component (Orizio *et al* 1997). Thus, simultaneous assessments of EMG, MMG, and force production allow for the identification of the onset of the EMG signal to the onset of the MMG signal (EMD_{E-M}), the onset of the MMG signal to the onset of force production (EMD_{M-F}), and the onset of the EMG signal to the onset of force production (EMD_{E-F}) (Orizio *et al* 1997, Ce *et al* 2015a). Therefore, EMD_{E-M} and EMD_{M-F} can measure the relative contributions from excitation-contraction coupling and the series elastic component, respectively, to the overall time duration of EMD_{E-F} .

Muscle-specific differences in EMD measures have been controversial in recent research (Hakkinen and Komi 1983, Lieber and Friden 2000, Chan *et al* 2001, Conchola *et al* 2013, 2015). For example, Chan *et al* (2001) reported similar EMD_{E-F} for the vastus lateralis (VL) and vastus medialis (VM) during isometric muscle actions. Conchola *et al* (2013, 2015), however, reported muscle-specific differences in EMD_{E-F} from the VL and biceps femoris

during isometric muscle actions. In addition, Hakkinen and Komi (1983) reported muscle-specific differences between the VL, VM, and rectus femoris (RF) during reflex EMD measures during involuntary muscle actions. Lieber and Friden (2000) suggested that muscles within the human body consist of different muscle-tendon ratios, pennation angles, muscle architecture, contraction velocities, muscle fiber lengths, and muscle fiber-type composition which may affect EMD measurements. Thus, these anatomical and physiological differences may explain the muscle-specific differences in EMD measure. Few studies (Smith *et al* 2016b, 2017), however, have simultaneously examined EMD_{E-M} , EMD_{M-F} and EMD_{E-F} from muscles within the same muscle group before (pretest), after (posttest), as well as during recovery from the same fatiguing protocol. Therefore, simultaneously examining EMD_{E-M} , EMD_{M-F} and EMD_{E-F} from the VL, VM, and RF may explain the influences of these anatomical and physiological differences on excitation-contraction coupling (EMD_{E-M}) and the series elastic component (EMD_{M-F}) prior to and following a fatiguing task.

Fatigue-induced increases in voluntary EMD measures are thought to be influenced by a number of factors including: (1) the buildup of metabolic byproducts (Zhou *et al* 1998, Begovic *et al* 2014, de Ste Croix *et al* 2015, Ce *et al* 2015a), (2) Ca^{2+} efflux from the sarcoplasmic reticulum (Zhou *et al* 1998, Ce *et al* 2013, Begovic *et al* 2014), (3) cross-bridge cycling rate (Ce *et al* 2013, Begovic *et al* 2014), and (4) increases in muscle temperature (Zhou *et al* 1998, Ce *et al* 2013). Thus, metabolic factors related to excitation-contraction coupling as well as exercise-induced increases in the compliance of the series elastic component, lengthen EMD measures (Zhou *et al* 1998, Ce *et al* 2013). It has been suggested (Ce *et al* 2013, Smith *et al* 2016b, 2017) that fatigue-related excitation-contraction coupling failure results in an increase in EMD_{E-M} , while increases in the compliance of the series elastic component associated with muscle temperature result in increased EMD_{M-F} . The effects of fatigue on these aspects of voluntary EMD measures, however, have primarily been examined using pre-fatigue versus post-fatigue measurements (Taylor *et al* 1997, Chan *et al* 2001, Ce *et al* 2013). The few studies (Conchola *et al* 2013, 2015, Rampichini *et al* 2014) that have examined the recovery of EMD performed isometric (maximal and submaximal) or stimulated muscle actions. Stimulated muscle actions have lower EMD values than those during voluntary muscle actions and stimulated muscle actions do not reflect the motor unit control strategies used to voluntarily contract a muscle (Hopkins *et al* 2007). In addition, elongation of EMD measures and its process of recovery may be of interest to clinical and athletic setting due to its relation to fatigue, joint instability, injury risk, and recovery times (Minshull *et al* 2012, Hannah *et al* 2014, de Ste Croix *et al* 2015). For example, de Ste Croix *et al* (2015) reported that increased EMD measures are associated with increased

risk for ACL injuries in athletes. Minshull *et al* (2012) and Hannah *et al* (2014) also indicated that fatigue resulted in greater EMD measures and that during fatigue EMD measures increased, but returned to normal values during recovery. Therefore, it is likely that during the recovery EMD measures will return to normal values. In addition, it has been suggested (Howatson *et al* 2009, Lacourpaille *et al* 2013, Smith *et al* 2017) that EMD measures can be influenced by the intensity and mode (isometric versus dynamic) of a muscle action. Therefore, the purposes of the present study were to examine: (1) the effects of fatigue and recovery on EMD_{E-M} , EMD_{M-F} and EMD_{E-F} from the VL, VM, and RF muscles; and (2) the relative contributions from EMD_{E-M} and EMD_{M-F} to EMD_{E-F} from the VL, VM, and RF. It was hypothesized that there would be fatigue induced-increases in EMD_{E-M} , EMD_{M-F} and EMD_{E-F} which would recover after 5 min of rest. In addition, it was hypothesized that the relative contributions from EMD_{E-M} and EMD_{M-F} to EMD_{E-F} would remain similar during all maximal isokinetic muscle actions.

2. Methods

2.1. Participants

Thirteen men (mean \pm SD age 24 ± 3.8 years; body mass 79.8 ± 9.7 kg; height 172.8 ± 8.6 cm) volunteered to participate in this study. The participants were recreationally trained (greater than 6 months of resistance training three times per week), and free from any musculoskeletal injuries or neuromuscular disorders. This study was approved by the Institutional Review Board, and all participants signed a written informed consent and completed a health history questionnaire prior to participation. In addition, this study was performed in agreement with the ethical principles stated in the Declaration of Helsinki (WMA 2013).

2.2. Experimental approach

The study consisted of two visits, separated by at least 48 h. The first visit was a familiarization visit which consisted of maximal and submaximal isokinetic knee extension muscle actions. Emphasis was placed on contracting and relaxing as quickly as possible on command. This was performed until participants were comfortable performing these muscle actions. During both visits, participants were able to visualize their muscle activation (EMG and MMG signal) and force on a monitor placed in front of them. The visualization of the muscle actions was used to emphasize the importance of contracting and relaxing as quickly as possible.

During the testing visit (visit 2) the participants performed two pretest maximal isokinetic knee extension muscle actions at 60° s^{-1} with the dominant knee. The participants then performed 25 maximal isokinetic knee extension muscle actions at 60° s^{-1} . Immediately following the 25 fatiguing isokinetic knee extension muscle actions, each subject performed a post-test maximal isokinetic knee extension muscle action at 60° s^{-1} . After 5 min of recovery each subject performed a recovery maximal isokinetic knee extension muscle actions at 60° s^{-1} .

2.3. Protocol

A warmup consisting of five to seven isokinetic knee extension muscle actions were performed at approximately 50 to 70% of their maximal effort. Following the warmup, each subject performed two maximal isokinetic knee extension muscle actions at 60° s^{-1} with 1 min of rest between the pretest muscle actions. The highest torque value of the two trials was used for the analyses. All isokinetic muscle actions were performed on a Cybex II isokinetic dynamometer calibrated per the Cybex User's Guide (CybexII 1991). Each participant began each isokinetic knee extension at a joint angle of 90° and performed the isokinetic knee extension until their leg was fully extended, then immediately back to the starting position of 90° . A miniscule pause was performed between each knee extension where the participants were instructed to relax until force reached zero and there were no EMG or MMG activity on the monitor.

After the pretest muscle actions, participants were given 2 min of rest and then performed the fatiguing protocol consisting of 25 maximal isokinetic knee extension muscle actions at 60° s^{-1} . Immediately after the fatiguing protocol, the participants performed a maximal isokinetic knee extension muscle action at 60° s^{-1} followed by a 5 min recovery period and then another maximal isokinetic knee extension muscle action at 60° s^{-1} . Electromyography, MMG, and force were simultaneously collected from the VL, VM, and RF during each assessment. Each participant was verbally instructed by "Ready, Go!" for when to perform each knee extension throughout the maximal testing and fatiguing protocol.

2.4. Electromyographic, mechanomyographic, and force signal acquisition

Bipolar surface electrode arrangements (Ag/AgCl, AccuSensor, Lynn Medical, Wixom, MI, USA) were placed on the VL, VM, and RF of the dominant knee (based on kicking preference) with an interelectrode distance of 30 mm. The skin was dry shaven, abraded, and cleaned with isopropyl alcohol

prior to electrode placement. For the VL, the bipolar electrode arrangements were placed 66% of the distance between the anterior superior iliac spine (ASIS) and the lateral border of the patella and orientated at a 20° angle to approximate the pennation angle of the muscle fibers (Hermens *et al* 1999, Abe *et al* 2000). For the VM, the bipolar electrode arrangements were placed 80% of the distance between the ASIS and the joint space in front of the anterior border of the medial collateral ligament and orientated at a 53° angle to approximate the pennation angle of the muscle fibers (Hermens *et al* 1999, Smith *et al* 2016a). For the RF, the bipolar electrode arrangements were placed 50% the distance between the ASIS and the superior border of the patella (Hermens *et al* 1999). A reference electrode was placed over the ASIS. The EMG signals were zero-meaned and bandpass filtered (fourth-order Butterworth) at 10–500 Hz. The MMG signal was measured using a tri-axial accelerometer (EGAS-FT-10/V05, Measurement Specialties Inc., Hampton, VA) placed between the bipolar electrode arrangement on the VL, VM, and RF using double-sided adhesive foam tape. The MMG signals were zero-meaned and bandpass filtered (fourth-order Butterworth) at 5–100 Hz. Force was measured using a low-profile pancake load cell (Honeywell Model 41, Morris Plains, NJ) attached to the lever arm behind the shin-pad participants was attached and was filtered at 5 Hz. All signals were simultaneously collected through a BioPac MP150 (BioPac System Inc., Goleta, CA) at a sampling frequency of 10 000 Hz. All signal processing and EMD measurements were performed using custom programs written with LabVIEW software (Version 15.0, National Instruments, Austin TX).

2.5. Electromechanical delay

The EMD measurements were determined as the time periods from the onset of the EMG signal to the onset of force (EMD_{E-F}), onset of the MMG signal to the onset of force (EMD_{M-F}), and the onset of the EMG signal to the onset of the MMG signal (EMD_{E-M}). The onset of EMG, MMG, and force were determined by the condition of three standard deviations (SDs) from the mean baseline noise observed for each signal, determined from 10 000 Hz (Costa *et al* 2012, Begovic *et al* 2014, Stock *et al* 2015) and were selected off-line by the primary investigator (CMS) using a custom written LabVIEW program that provided interactive graphical viewing of each signal (Figure 1).

2.6. Statistical analysis

A 3 (Muscle: VL, VM, and RF) \times 3 (EMD: EMD_{E-M} , EMD_{M-F} and EMD_{E-F}) \times 3 (Time: pretest, posttest, and 5 min recovery) repeated measures ANOVA was performed. Follow-up two- and one-way repeated measures ANOVAs and

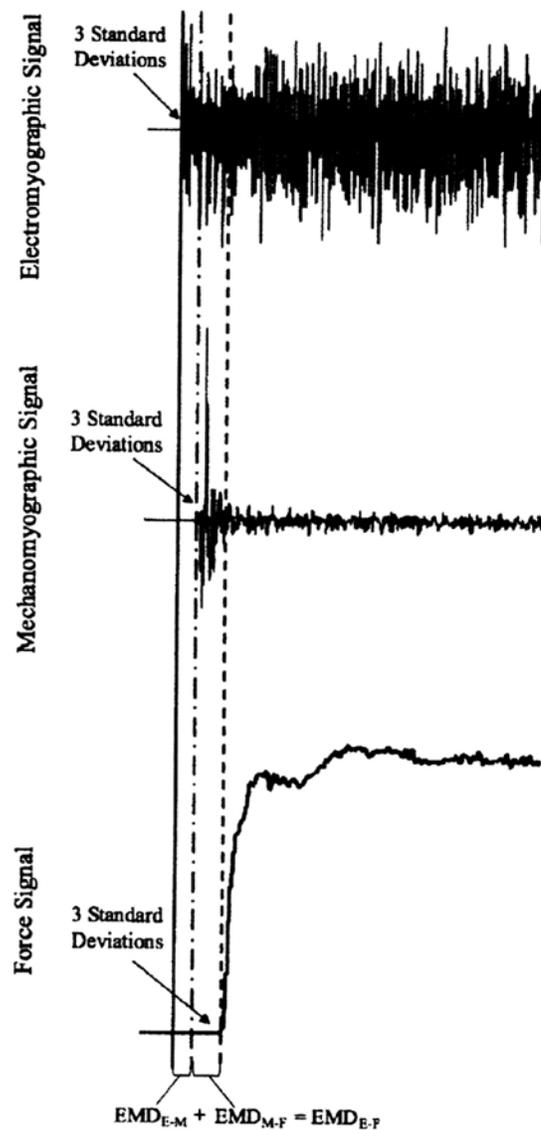


Figure 1. Graphical representation of the electromyographic, mechanomyographic, and force combination for the determinations of electromechanical delay (EMD). Together, these signals allowed for the identification of the onset of the electromyographic signal to the onset of the mechanomyographic signal (EMD_{E-M}), onset of the mechanomyographic signal to the onset of force production (EMD_{M-F}), and onset of the electromyographic signal to the onset of force production (EMD_{E-F}).

paired samples *t*-tests with Bonferonni correction were performed when appropriate. If the assumption of sphericity was violated, the Huynh–Feldt correction was used. An alpha of $p \leq 0.05$ was considered statistically significant for all ANOVAs and Bonferonni significance was based off the number of comparisons made (alpha/n) (SPSS Version 22.0, Armonk, NY).

Table 1. Electromechanical delay (EMD) measurements (mean and standard error of the mean (SE)) from the vastus lateralis, vastus medialis, and rectus femoris muscles determined from the onset of the electromyographic to mechanomyographic signal (EMD_{E-M}), onset of the mechanomyographic to force (EMD_{M-F}), and onset of the electromyographic signal to the onset of force (EMD_{E-F}) at pretest, posttest, and 5 min of recovery from the fatiguing workout during maximal isokinetic knee extension muscle actions at $60^\circ s^{-1}$. All measurements are reported in ms.

	EMD_{E-M}	EMD_{M-F}	EMD_{E-F}
Pretest			
Vastus lateralis ^a	18.71 (2.0)	29.95 (1.8)	48.66 (3.3)
Vastus medialis ^a	23.69 (2.5)	31.32 (1.9)	55.00 (4.1)
Rectus femoris ^{a,b}	33.13 (2.4)	35.86 (2.8)	68.99 (4.6)
Posttest^c			
Vastus lateralis ^a	30.65 (1.7)	41.23 (3.7)	71.88 (4.8)
Vastus medialis ^a	30.89 (3.3)	43.52 (3.9)	74.41 (7.0)
Rectus femoris ^{a,b}	42.63 (3.5)	44.43 (3.5)	87.06 (7.1)
5 min recovery			
Vastus lateralis ^a	24.29 (3.5)	32.84 (4.1)	57.13 (6.4)
Vastus medialis ^a	25.49 (3.7)	36.98 (4.3)	62.47 (7.1)
Rectus femoris ^{a,b}	33.18 (4.3)	36.98 (4.4)	70.16 (8.7)

a. $EMD_{E-M} < EMD_{M-F}$ ($p < 0.01$).

b. EMD_{E-M} , EMD_{M-F} and EMD_{E-F} are greater than those from the VL and VM collapsed across time ($p < 0.01$).

c. Posttest EMD_{E-M} , EMD_{M-F} and EMD_{E-F} are greater than pretest and 5 min recovery values for each muscle ($p < 0.01$).

3. Results

The 3 (Muscle: VL, VM, and RF) \times 3 (EMD: EMD_{E-M} , EMD_{M-F} and EMD_{E-F}) \times 3 (Time: pretest, posttest, and 5 min recovery) repeated measures ANOVA with follow-up two- and one-way ANOVAs as well as post-hoc paired samples *t*-tests indicated no differences in the responses between the VL and VM for EMD_{E-M} , EMD_{M-F} or EMD_{E-F} at each time point (pretest, posttest, and 5 min recovery). Therefore, the VL and VM responded similarly to one another during the pretest, posttest, and 5 min recovery measurements. That is, there were increases in EMD_{E-M} , EMD_{M-F} and EMD_{E-F} from pretest to posttest measurements that returned to pretest values after 5 min of recovery (Table 1; Figure 2).

All EMD values (EMD_{E-M} , EMD_{M-F} or EMD_{E-F}) from the RF were greater than those of the VL and VM at each time-point (pretest, posttest, and 5 min recovery) (Table 1; Figure 2). The RF, however, did have the same pattern of responses for each EMD measure pretest, posttest, and at 5 min recovery (Table 1; Figure 2). Specifically, there were pretest to posttest increases

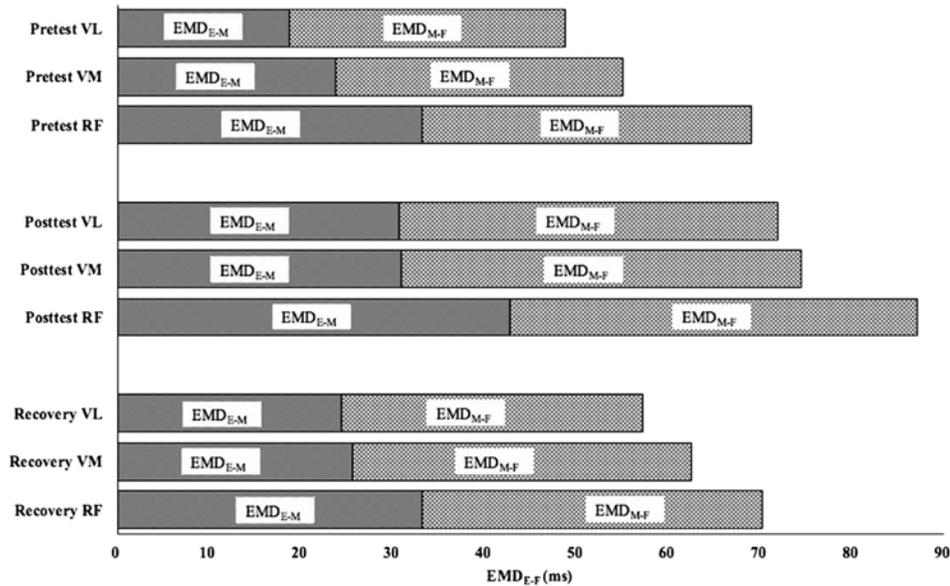


Figure 2. Electromechanical delay (EMD) from the vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF) from pretest, posttest, and 5 min of recovery measurements during maximal isokinetic knee extension muscle actions at 60° s^{-1} . The EMD measurements were determined from the onset of the electromyographic signal to the onset of the mechanomyographic signal ($\text{EMD}_{\text{E-M}}$), onset of the mechanomyographic signal to the onset of force production ($\text{EMD}_{\text{M-F}}$), and the onset of the electromyographic signal to the onset of force production ($\text{EMD}_{\text{E-F}}$).

in $\text{EMD}_{\text{E-M}}$, $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$. After 5 min of recovery $\text{EMD}_{\text{E-M}}$, $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$ returned to pretest values. In addition, at each time-point (pretest, posttest, and 5 min recovery) for all muscles (VL, VM, and RF) $\text{EMD}_{\text{E-M}}$ was less than $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$ was greater than $\text{EMD}_{\text{E-M}}$ and $\text{EMD}_{\text{M-F}}$ (Table 1; Figure 2). The following are the descriptive statistics for the strength measures indicated as peak force (mean \pm SD) during the Pretest (78.6 ± 12.3 kg), Posttest (52.9 ± 16.1 kg), and 5 min Recovery (68.2 ± 14.7 kg) measurements.

4. Discussion

The primary finding of the current study was that $\text{EMD}_{\text{E-M}}$, $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$ from the VL, VM, and RF increased from pretest to posttest, but returned to pretest values after 5 min of recovery during maximal isokinetic knee extension muscle actions (Table 1). These findings were in agreement with those of Conchola *et al* (2013) who reported a pretest to posttest increase in isometric $\text{EMD}_{\text{E-F}}$ (97–122 ms) which returned to pretest values (99 ms) after 7

min of recovery from the VL after intermittent 50% MVIC muscle actions to volitional exhaustion. In addition, Conchola *et al* (2015) reported an increase in EMD_{E-F} (91–120 ms) from the VL immediately after a fatiguing protocol at 60% MVIC which recovered to pretest values after 7 min of recovery (97 ms). It has been suggested (Ce *et al* 2013, 2014, 2015b, Smith *et al* 2016b, 2017) that increases in EMD_{E-F} reflect peripheral fatigue and can be explained by changes in EMD_{E-M} and EMD_{M-F} . Specifically, EMD_{E-M} represents excitation-contraction coupling; a fatigue-induced buildup of metabolic byproducts slows motor unit action potential conduction velocity and causes excitation-contraction coupling failure, which increases EMD_{E-M} . The EMD_{M-F} reflects the compliance of the series elastic component which increases with muscle fatigue and, thereby increases EMD_{M-F} . Thus, the current study suggested that excitation-contraction coupling failure (EMD_{E-M}) and increases in the compliance of the series elastic component (EMD_{M-F}) were evident immediately following the fatiguing, maximal isokinetic protocol. After 5 min of recovery, all EMD measures for all muscles returned to pretest values (Table 1). Therefore, there were fatigue-induced increases in EMD_{E-M} , EMD_{M-F} and EMD_{E-F} immediately after the fatiguing protocol for all muscles and 5 min of recovery was sufficient to recover to pretest values. Thus, excitation-contraction coupling failure and increases in the compliance of the series elastic component did not influence any of the EMD measures after 5 min of recovery.

In the current study, there were no significant differences between the VL and VM for the EMD_{E-M} , EMD_{M-F} or EMD_{E-F} during the pretest, posttest, or 5 min recovery measurements (Figure 2). The EMD_{E-M} , EMD_{M-F} and EMD_{E-F} from the RF, however, were greater than those recorded from the VL and VM during the pretest, posttest, and 5 min of recovery (Figure 2). The findings of the current study were in agreement with those of Chan *et al* (2001) who reported no differences in EMD_{E-F} measures between the VL (32.1–52.2 ms) and VM (31.7–48.1 ms) during MVIC muscle actions. These findings, however, were not in complete agreement with those of Vos *et al* (1991) who reported no differences in EMD_{E-F} measurements (ranging from 95 to 110 ms) from the VL, VM, and RF during 50 and 70% MVIC muscle actions. The differences in EMD measurements in the current study and those of Vos *et al* (1991) may indicate intensity- (maximal versus submaximal) and mode-specific (isokinetic versus isometric) differences in EMD measures related to the structural differences of the muscles. Specifically, the differences in muscle architecture including muscle length, pennation angle, muscle-to-tendon ratio, and articulation (VL and VM = monoarticate; RF = biarticate) may have contributed to differences in EMD values during different intensities and modes of exercise (Lieber and Friden 2000). In addition, the differences in EMD values may be related to the methodology used to identify the onset of the EMG and force signals (i.e. 3 SD above baseline or a specific

threshold) as well as EMG, MMG, and force signal conditioning. Thus, during pretest, posttest, and 5 min recovery maximal isokinetic knee extension muscle actions at 60° s^{-1} there were muscle-specific (VL and VM versus RF) differences in the $\text{EMD}_{\text{E-M}}$, $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$ which may be explained by differences in muscle architecture (Lieber and Friden 2000).

The relative contributions from $\text{EMD}_{\text{E-M}}$ and $\text{EMD}_{\text{M-F}}$ to $\text{EMD}_{\text{E-F}}$ from the VL, VM, and RF was similar during the pretest, posttest and 5 min recovery measurements, although there were changes in the absolute EMD measures (Table 1). Specifically, excitation-contraction coupling ($\text{EMD}_{\text{E-M}}$) accounted for slightly less than 50% of the total time delay between the onset of the EMG signal to the onset of force production for the VL (38–43%), VM (41–43%), and RF (47–49%) (Table 1). In addition, the time duration to take up the slack of the series elastic component ($\text{EMD}_{\text{M-F}}$) accounted for greater than 50% of $\text{EMD}_{\text{E-F}}$ for the VL (57–62%), VM (57–59%), and RF (51–53%) (Table 1). These findings were similar to those of Smith *et al* (2016b) who reported approximately equal contributions from $\text{EMD}_{\text{E-M}}$ and $\text{EMD}_{\text{M-F}}$ to $\text{EMD}_{\text{E-F}}$ during pretest and posttest MVIC muscle actions with an increase in absolute EMD after a fatiguing dynamic constant external resistance muscle actions to failure at 70% of 1-repetition maximum. Thus, the current and previous study of Smith *et al* (2016b) suggested that the fatigue-induced buildup of metabolic byproducts ($\text{EMD}_{\text{E-M}}$) and increased compliance of the series elastic component ($\text{EMD}_{\text{M-F}}$) in the VL, VM, and RF contributed equally to $\text{EMD}_{\text{E-F}}$ during dynamic muscle actions (isokinetic and dynamic constant external resistance). In addition, after 5 min of recovery the relative contributions from $\text{EMD}_{\text{E-M}}$ and $\text{EMD}_{\text{M-F}}$ to $\text{EMD}_{\text{E-F}}$ for the VL, VM, and RF remained similar to those during pretest and posttest measurements.

5. Conclusion

In summary, there were fatigue-induced increases in $\text{EMD}_{\text{E-M}}$, $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$ from the VL, VM, and RF, however, all EMD measures for all muscles returned to pretest values after 5 min of recovery. Thus, excitation-contraction coupling failure (increased $\text{EMD}_{\text{E-M}}$) and increased compliance of the series elastic component (increased $\text{EMD}_{\text{M-F}}$) were present immediately after the fatiguing protocol, but subsided after 5 min of recovery. In addition, during the pretest, posttest, and 5 min recovery maximal isokinetic knee extension muscle actions there were muscle-specific (VL and VM versus RF) differences in the $\text{EMD}_{\text{E-M}}$, $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$ measurements. That is, $\text{EMD}_{\text{E-M}}$, $\text{EMD}_{\text{M-F}}$ and $\text{EMD}_{\text{E-F}}$ were greater for the RF than the VL and VM. These muscle-specific differences may be associated with differences in muscle architecture (Lieber and Friden 2000). In the current study, there were also similar

relative contributions from EMD_{E-M} and EMD_{M-F} to EMD_{E-F} from the VL, VM, and RF during the pretest, posttest, and 5 min recovery measurements despite changes in the absolute EMD measures. Therefore, fatigue resulted in increases in EMD_{E-M} , EMD_{M-F} and EMD_{E-F} from the VL, VM, and RF, which returned to pretest values after 5 min of recovery.

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