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Repetitive Eccentric Muscle Contractions Increase Torque Unsteadiness in the Human Triceps Brachii

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A B S T R A C T

Torque steadiness and low-frequency fatigue (LFF) were examined in the human triceps brachii after concentric or eccentric fatigue protocols. Healthy young males ($n = 17$) performed either concentric or eccentric elbow extensor contractions until the eccentric maximal voluntary torque decreased to 75% of pre-fatigue for both (concentric and eccentric) protocols. The number of concentric contractions was greater than the number of eccentric contractions needed to induce the same 25% decrease in eccentric MVC torque (52.2 ± 2.9 vs. 41.5 ± 2.1 for the concentric and eccentric protocols, respectively, $p < .01$). The extent of peripheral fatigue was ~12% greater after the concentric compared to the eccentric protocol (twitch amplitude), whereas LFF (increase in double pulse torque/single pulse torque), was similar across protocols. Steadiness, or the ability for a subject to hold a submaximal isometric contraction, was ~20 % more impaired during the Ecc protocol ($p = .052$). Similarly, the EMG activity required to hold the torque steady was nearly 20% greater after the eccentric compared to concentric protocol. These findings support that task dependent eccentric contractions preferentially alter CNS control during a precision based steadiness task.

1. Introduction

Muscle fatigue is defined as "any exercise-induced loss of ability to produce force with a muscle or muscle group" (Gandevia, 2001), and can result from failure at one or more sites along the motor pathway originating from the central nervous system and ending with force loss through cross-bridge cycling. Muscle fatigue has been documented as task dependent, meaning that fatigue and its mechanisms vary depending on the task the muscle performs (Enoka and Duchateau, 2008). The cause of muscle fatigue may depend on task performance and is important to developing task specific training interventions.

During dynamic contractions, the majority of volitional force decline can be explained by fatigue-induced changes in the exercising skeletal muscles (peripheral fatigue) (Loscher and Nordlund, 2002; Baudry et al., 2007). Low-frequency fatigue (LFF) is a primary source of peripheral fatigue, and is usually defined as a preferential decrease in the force elicited with low-frequency stimulation compared to that elicited with high frequency stimulation (Jones, 1996). Many assert that LFF is attributable to impairment in excitation–contraction coupling, resulting in a decrease for calcium release from the sarcoplasmic reticulum per action potential (Bruton et al., 1998; Westerblad et al., 2000).

For instance, LFF of the biceps brachii was greater and developed and recovered faster after concentric (Con) compared to eccentric (Ecc) contractions (Smith and Newham, 2007). Dundon and colleagues recently found that when the human biceps brachii was fatigued through either Con or Ecc contractions until a similar decrease in isometric (Iso) MVC torque was achieved, the extent of LFF was similar, but the recovery was faster after Con contractions (Dundon et al., 2008). In a most recent study, LFF was evident after submaximal Con, but not after submaximal Ecc contractions in the quadriceps (Baptista et al., 2009). Even within the upper limb muscles acting on the same joint, the elbow extensors are more fatigue resistant than the elbow flexors after maximal Con–Ecc contractions (Maquet et al., 2004). These findings suggest that the fatigue mechanisms may vary between flexors and extensors of the upper extremity based on their routine patterns of use.

Eccentrically-induced fatigue in the elbow flexors has been known to impair the ability to maintain submaximal isometric contraction (increase in force fluctuation or unsteadiness) as compared to concentrically-induced fatigue (Lavender and Nosaka, 2006; Dundon et al., 2008). To our knowledge, no previous study compared the effects of Ecc and Con exercise on LFF, electromyography (EMG), and steadiness while controlling the amount of fatigue-induced eccentrically in the triceps brachii muscles.

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The purpose of this study was to compare the fatigue-related changes among contraction types (concentric, eccentric, and isometric) in human triceps brachii after either a concentric or an eccentric protocol while controlling for eccentric fatigue. Muscle activation, LFF, and steadiness (force fluctuation during an isometric) were used to compare the three contraction types. We hypothesized that steadiness and muscle activation strategies (EMG) would vary according to contraction type even though similar levels of LFF would be induced.

2. Materials and methods

2.1. Subjects and general design

A total of 17 healthy male subjects (age = 27.9 ± 5.8 (mean ± SD) year; height = 181.5 ± 6.6 cm; weight = 78.4 ± 7.8 kg) participated in this study. Only male subjects were recruited to eliminate gender differences in endurance time (Hicks et al., 2001; Wust et al., 2008). Those in the exercise group were enrolled in both Con and Ecc fatigue protocols on separate days (~1 week apart), whereas those in the control group participated in one testing session with no fatigue protocol. The order of testing was randomized. After the first testing session (Con or Ecc protocol), each subject completed the opposite protocol (Con or Ecc). The subjects were in good health without any current or previous elbow problems, injuries, and/or surgeries. All subjects were asked to refrain from any strenuous physical activity for the duration of the study, and reviewed and signed a consent form. The Human Subjects Institutional Review Board at the University of Iowa approved this study.

At the first session, all subjects were familiarized with the experimental set-up and were asked to practice non-fatiguing submaximal and maximal isokinetic Ecc and Con as well as isometric (Iso) contractions of the elbow extension muscles. On a separate day, after the familiarization session, subjects in the exercise group participated in the two exercise sessions (Con and Ecc). Ecc and Con MVCs as well as Iso MVCs were performed before and after fatigue regardless of the exercise session (Ecc or Con), and the pre- and post-fatigue MVCs were performed in the order of Ecc, Con and Iso for both (Ecc and Con) fatigue protocols and the control protocol. Subjects in the control protocol participated in one testing session on a separate day after the familiarization session. The control subjects received all testing procedures before and after quiet sitting of 20 min.

2.2. Instrumentation and experimental set-up

2.2.1. Torque recording

Subjects sat upright attached to a Kin-Com 125E+ (Chattex Corp; Chattanooga, TN) computer-controlled isokinetic dynamometer. In this study, the right arm was used for all subjects as they were all right handed. The subjects were strapped with a seat belt, shoulder and thigh straps to stabilize the trunk and the lower extremities. The wrist was placed in a splint that held the wrist in a neutral position. The joint angles in the resting position of the right arm were as follows: shoulder at 45° flexion, elbow at 35° flexion (0° = full extension), radioulnar joint in neutral with respect to supination/pronation (midpoint of supination and pronation), wrist joint in neutral (without flexion/extension and radial/ulnar deviations) and digits relaxed in flexion. The elbow joint axis was aligned with that of the Kin-Com's mechanical axis for each subject. A force transducer (Genesco Technology Corp., Comptom, CA) was positioned just proximal to the base of the fifth metacarpal to obtain maximal force generated and the output of the transducer was displayed on an oscilloscope for visual feedback. The distance from the transducer to the mechanical axis of the Kin-Com was used as a moment arm for torque calculations.

For voluntary contractions, the range of motion of 35°–75° elbow flexion was used with a work/rest velocity of $13°/7°\ s^{-1}$. During the rest $7°\ s^{-1}$ time, the limb was passively returned to the starting position. It has been shown that, at a slow velocity ($20°\ s^{-1}$), central activation levels were similar for Con and Ecc contractions (Babault et al., 2001). For both Ecc and Con contractions, subjects were asked to reach the target or maximal torque as quickly as possible once the work phase had started and to maintain the target/maximal torque throughout the work phase. For Iso volitional and elicited contractions (see below for electrical stimulation), the elbow joint was locked in 35° of flexion. During the Iso MVCs, the subjects were asked to maximally extend the elbow for 4 s. Strong verbal encouragement was given to the subjects when they were performing all MVCs.

In addition to the Iso MVCs, subjects were asked to maintain a submaximal target torque (17.8 Nm) for 30 s (Fig. 1D). This torque corresponded to 15% pre-fatigue Iso MVC.

2.2.2. Electrical stimulation

The relaxed triceps brachii was electrically stimulated to quantify the amount of LFF (by calculating a ratio of the double pulse torque (doublet) to the single pulse torque (twitch), D/S ratio, Fig. 1C), using two gel adhesive pads: one 2.5 cm × 6.0 cm was around the triceps, approximately 5 cm inferior to the axillary fold and one 3.75 cm × 3.75 cm was on the distal aspect of the triceps, approximately 8 cm superior to the elbow (VersaStim by Con-Med Corp; Utica, NY) and a custom designed stimulator (constant current; 50 μA – 200 mA range with <5% current variations; total capability 400 V). The ratio of a high frequency relative to a low-frequency is a documented method in the literature (Sargeant and Dolan, 1987; Ratkevicius et al., 1995; de Ruiter et al., 2005). We chose the double pulse vs. the single pulse ration (D/S) because it has less influence on muscle fatigue (Rassier et al., 1999), and volitional reactions to the noxious stimulation via stimulation trains may induce artifact in the torque curve. Because the twitch peak torque occurs at approximately 100 ms, the volitional reaction response will not interfere with the peak.

At the beginning of each session, a maximal stimulating intensity was determined by increasing the intensity until no further increase in the peak torque was elicited with a 500 μs single pulse. Once the maximal intensity was determined, this intensity was maintained throughout the session. The doublet was elicited by delivering two pulses separated by 6 ms (166 Hz), and these two pulses always preceded the single pulse by 1.5 s. The subjects received 16 pairs of double and single pulses for each measurement.

2.2.3. Electromyographic (EMG) recording

EMG was recorded using an active bipolar surface electrode (silver–silver chloride discs of 8 mm in diameter spaced 20 mm between centers) for the medial triceps head of the right arm. The location of the electrode was the most prominent aspect of the muscle, and was marked for the consistency between exercise protocols. The skin at the location was cleaned with sandpaper first, and then with an alcohol swab. The ground electrode was placed on the acromion of the tested side. The signal was pre-amplified (gain 35) and high-pass filtered at 15 Hz.

2.3. Procedures

2.3.1. Pre-fatigue measurements

After the skin preparation, stimulating and recording electrodes were placed on the subjects' arm. Subjects were then seated on and secured to the Kin-Com and the maximal stimulating intensity was determined as described above. The subjects performed 12 Ecc

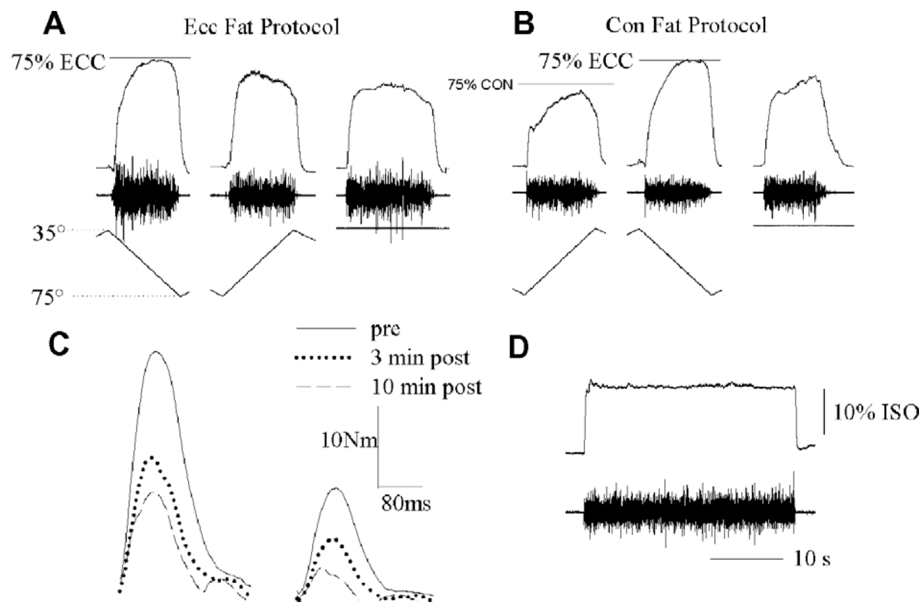

Fig. 1. Representative examples of one subject showing the fatigue protocols (A and B), doublet and single twitch elicited torque (C) and steadiness assessment (D). A and B show, from the top, the force, EMG and displacement signals associated with MVCs performed at the end of the fatigue protocols. After MVCs measurements, the relaxed muscle was stimulated with doublet (left) and single (right) pulses (C) followed by voluntary submaximal steady contraction (the force and EMG signals in D).

contractions, the first 10 of which were submaximal (less than 30% effort with 1 min rest), and the last two were maximal. Then, the subjects repeated the same procedure for Con contractions. The higher peak torque of the last two Ecc and the last two Con MVCs was used to calculate the target torque of 75% Ecc and 75% Con contractions, respectively, and the target torque was displayed on the oscilloscope. Seventy-five percent was chosen because 100% MVC would be too centrally demanding and 50% MVC would last too long and increase the likelihood of considerable central fatigue. Next, the subjects performed two Iso MVCs and received pairs of double and single pulses for the D/S ratio at rest. Finally, steadiness was measured.

2.3.2. Fatigue protocol

For the Ecc fatigue protocol (Fig. 1A), subjects performed Ecc contractions of the triceps at the target torque of the pre-fatigue 75% Ecc contraction. Similarly, for the Con fatigue protocol (Fig. 1B), subjects performed Con contractions at the target torque of the pre-fatigue 75% Con contractions. In both Ecc and Con protocols, the protocol was terminated when subjects were not able to reach the 75% of the pre-fatigue Ecc MVC torque. Therefore, for the Ecc fatigue protocol, subjects were asked to perform one Con MVC, followed by one Iso MVC, when their maximal effort in Ecc contraction resulted in 75% of the pre-fatigue Ecc MVC torque. For the Con fatigue protocol, when subjects became fatigued and were no longer able to reach their pre-fatigue 75% Con MVC torque, one Ecc MVC torque was measured. If this maximal effort in Ecc contraction resulted in at or below the pre-fatigue 75% Ecc MVC stopping criteria, the Con protocol was terminated. If the maximal effort generated a peak torque that was above the 75% Ecc MVC stopping criteria, repetitive Con contractions were resumed immediately, and then, periodically, the Ecc maximal force-generating capacity was re-tested. Rarely were more than three eccentric attempts necessary to find the stopping point during the Con protocol. Once the Ecc MVC torque that had met the stopping criteria was measured, one Iso MVC was performed immediately.

2.3.3. Post-fatigue and recovery measurements

After the Iso MVC in both protocols, the triceps was stimulated to obtain the double pulse to single pulse ratio (D/S ratio). Then subjects performed the submaximal contraction for 30 s to assess the steadiness.

After a rest of 10 min, the same battery of testing performed before the fatigue protocol was administrated. That is, the subjects were asked to perform 1 Ecc MVC, 1 Con MVC and 1 Iso MVC, followed by D/S ratio and steadiness measurements.

2.4. Data analysis

All the data were sampled at 2 kHz. For the MVCs, the highest value of the force signal was found, and then multiplied by the moment arm to obtain torque for each subject. For the Ecc and Con contractions, the first and last 5° of each contraction was discarded to ensure that the torque analyzed was generated while the cross-bridges were actually cycling/being disrupted. The last three MVCs (Ecc, Con and Iso MVCs for the Ecc protocol, and Con, Ecc and Iso MVCs for the Con protocol; Fig. 1A and B) performed in the fatigue protocols were used as endpoint MVCs. For the EMG analysis, the root mean square (RMS) amplitude and median frequency of the power spectrum were calculated from 1.5 s around the peak torque for each contraction.

Because the peak torque of the twitch and doublet in the last two (the 15th and 16th) pairs was similar ($p > .05$ for both twitch and doublet), each was averaged to obtain single and doublet twitch averages, respectively. The mean doublet peak torque was divided by the mean twitch peak torque to obtain the D/S ratio. Only the last two pairs were used for the analysis because it was fully potentiated (Kufel et al., 2002).

For the steadiness measurement, the mean torque, standard deviation, coefficient of variation (standard deviation/mean $\times$ 100) and the EMG RMS amplitude were calculated for the middle 10 s from the 30 s contraction.

2.5. Statistical analysis

Two-way analysis of variance (ANOVA) for repeated measures was used to test the effects of the fatigue protocol (Ecc vs. Con) and time (pre-fatigue vs. endpoint/3 min post-fatigue vs. 10 min post-fatigue) on the dependent variables. Independent t test was used to compare control data with those from the fatigue group at the same sampling period. A significance level was set at .05. Data are reported as mean ± standard deviation in the text and as mean ± standard error in the figures.

3. Results

3.1. Voluntary torque

Before fatigue Ecc MVC torque was greater than the Con MVC torque, which was also greater than the Iso MVC torque (144.4 ± 39.3 Nm, 132.6 ± 42.8 Nm and 122.9 ± 45.0 Nm for Ecc, Con and Iso MVCs, respectively; $p < .05$ for all comparisons). There were no differences in pre-fatigue MVC torque from the control subjects ($p = .23$).

Regardless of which protocol was used to fatigue the muscle, the fatigue protocol was terminated when Ecc MVC torque was decreased by 25% from the pre-fatigue (arrows in Fig. 2; Ecc MVC torque at endpoint = 75.2 ± 6.2% vs. 77.5 ± 5.1% for the Con and Ecc protocols, respectively; $p > .05$). The number of contractions necessary to induce the 25% decrease in Ecc MVC torque was greater in the Con protocol compared to that in the Ecc protocol (52.2 ± 2.9 vs. 41.5 ± 2.1 for the Con and Ecc protocols, respectively, $p < .01$). There were no differences in the MVC torques for the control subjects who sat quietly for 20 min. Although both Con and Iso MVC torque at endpoint was lower than that of the control subjects, there were no differences across protocols (range from ~67% for Iso MVC in Con protocol to ~78% pre-fatigue for Con MVC in Ecc protocol). At 10 min post-fatigue, MVC torque was at ~83% pre-fatigue with no differences across protocols or across MVC types.

3.2. EMG activity

Both fatigue protocols reduced the EMG RMS amplitude at endpoint with no differences in the control data. There was no difference across protocols within MVC types (Fig. 3A). However, the RMS amplitude with Iso MVC in the Con protocol was lower than that of the control after fatigue (70.4 ± 12.7% vs. 93.5 ± 4.9% for the Con and control, respectively; $p < .01$). At 10 min post-fatigue, the RMS amplitude was similar across protocols in all MVC types.

Median frequency of the EMG power spectrum was similar across protocols within MVC types before fatigue. Fatigue decreased the median frequency in all conditions, but the extent of decrease was similar across protocols (Fig. 3B). At endpoint of the Con protocol, the median frequency of the Con MVC was lower than that of the control (74.7 ± 10.9% vs. 97.8 ± 6.8% for the Con and control protocols, respectively; $p < .01$). The recovery at 10 min post-fatigue in median frequency was similar across protocols.

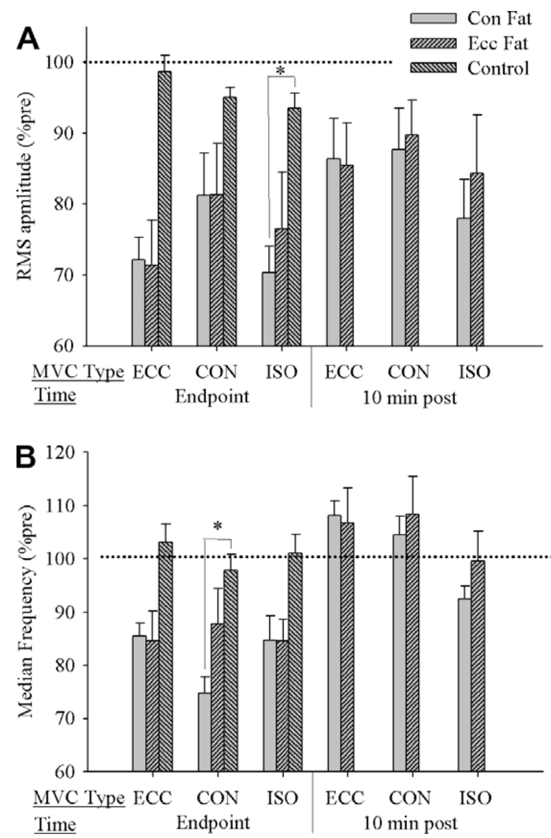

Fig. 3. Changes in the EMG root mean square (RMS) amplitude (A) and median frequency (B) of the triceps brachii with the fatigue protocols. Although both the RMS amplitude and the median frequency were decreased with fatigue, there were no differences across protocols. However, after the Con protocol, but not after the Ecc protocol, the RMS amplitude with Iso MVC and the median frequency with Con MVC were lower than those of the control at endpoint (indicated by ∗).

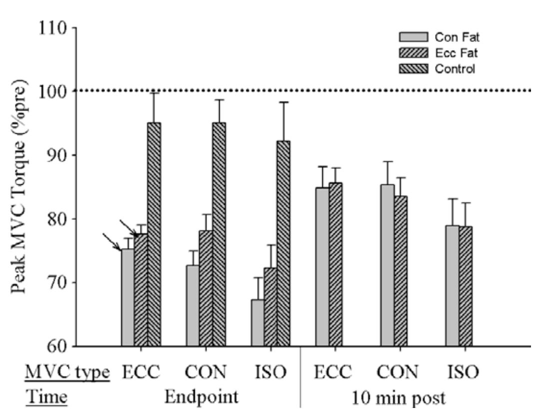

Fig. 2. Changes in volitional torque with eccentric (Ecc), concentric (Con) and isometric (Iso) maximal voluntary contractions (MVCs) at endpoint and at 10 min post-fatigue of the Ecc and Con fatigue protocols. The 25% decrease in Ecc MVC torque at endpoint was the stopping criteria, and shown with the arrows in the figure. Although both Ecc and Con protocols induced a significant decrease in the volitional torque, there were no differences across protocols.

3.3. Single twitch, doublet and D/S ratio

Before fatigue, there were no differences across protocols in the peak torque amplitude elicited with the single and with the double pulse electrical stimulation (~20.4 and ~9.5 Nm, corresponding to ~16.6% and ~7.7% pre-fatigue Iso MVC torque for doublet and single twitch, respectively). Fatigue reduced both the single twitch and doublet torque amplitude (Fig. 4A). ANOVA showed an interaction of time × protocol ($p = .029$) from pre-fatigue to 3 min post-fatigue, and paired t test indicates that the decrease in doublet peak torque in the Con protocol was greater than that in the Ecc protocol at 3 min post-fatigue (53.6 ± 18.5% pre-fatigue vs. 65.0 ± 14.2% pre-fatigue for the Con and Ecc protocols; $p = .03$) and there was a trend of the Con protocol inducing a greater decrease in the single twitch torque compared to the Ecc protocol (53.7 ± 21.0% pre-fatigue vs. 63.4 ± 14.3% pre-fatigue for the Con and Ecc protocols, respectively; $p = .056$). There was an interaction of time × stimulation type (doublet/single twitch) from 3 min post-fatigue to 10 min post-fatigue ($p < .01$), which resulted in an increase in the D/S ratio (LFF) at 10 min post-fatigue (Fig. 4B). However, the extent of LFF (mean increase of 39.2% from pre-fatigue) was similar across protocols, and the effect of protocol seen at 3 min post-fatigue was no longer present at 10 min post-fatigue for either single twitch or doublet peak torque.

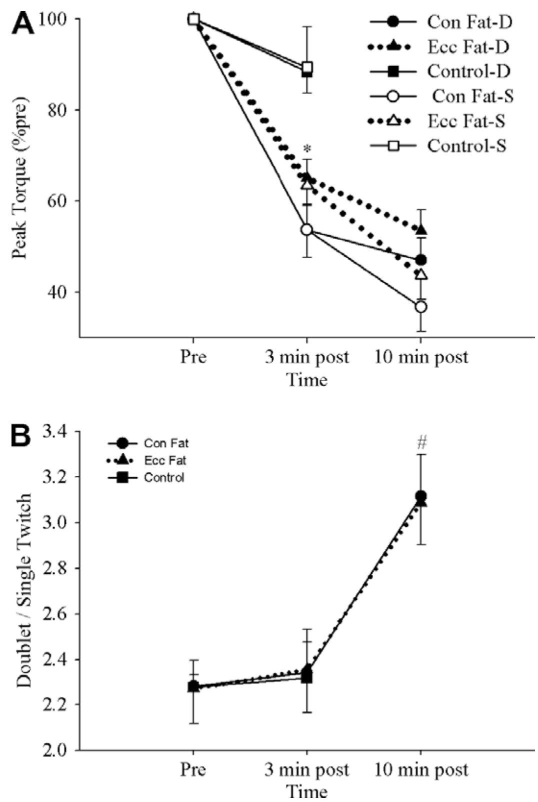

Fig. 4. Changes in the peak torque with doublet (D in the legend) and single twitch (S in the legend) (A) and the D/S ratio (B) after the fatigue protocols. The Con protocol decreased both the doublet and single twitch more than did the Ecc protocol at 3 min post-fatigue ($p = .03$ and .056 for double and single twitch, respectively, $*$ in the figure). The D/S ratio (B) increased only at 10 min post-fatigue (# in the figure) with no difference across protocols.

3.4. Torque fluctuation

The mean of the torque coefficient of variation while holding the target torque before fatigue was 1.46% with no differences across protocols. After fatigue there was a strong trend supporting that the Ecc protocol induced greater torque fluctuation compared to the Con protocol and the control (Fig. 5A; $p = .052$).

The EMG amplitude after the Ecc protocol increased whereas it did not after the Con protocol, resulting in a difference between protocols at 3 min post-fatigue (95.0 ± 49.7% of pre-fatigue vs. 118.7 ± 55.7% of pre-fatigue for the Con and Ecc protocols, respectively; $p = .049$; Fig. 5B). At 10 min post-fatigue, the amplitude was higher than pre-fatigue in both protocols, but there was no difference in the amplitude across protocols.

4. Discussion

In the present study, the triceps brachii was fatigued either eccentrically or concentrically until the same amount of Ecc MVC torque decrease was induced. The main findings of the study were (1) fatiguing eccentrically or concentrically does not differentially influence the extent of concentric or isometric MVC torque decrease, (2) fatiguing concentric contractions induced a greater change in EMG activity compared to fatiguing eccentric contractions, (3) greater peripheral fatigue was observed after concentric compared to eccentric fatiguing contractions, whereas the extent of low-frequency fatigue was similar across protocols, and (4) fatiguing with Ecc contractions increased unsteadiness and EMG during a torque holding task to a greater extent than Con contractions.

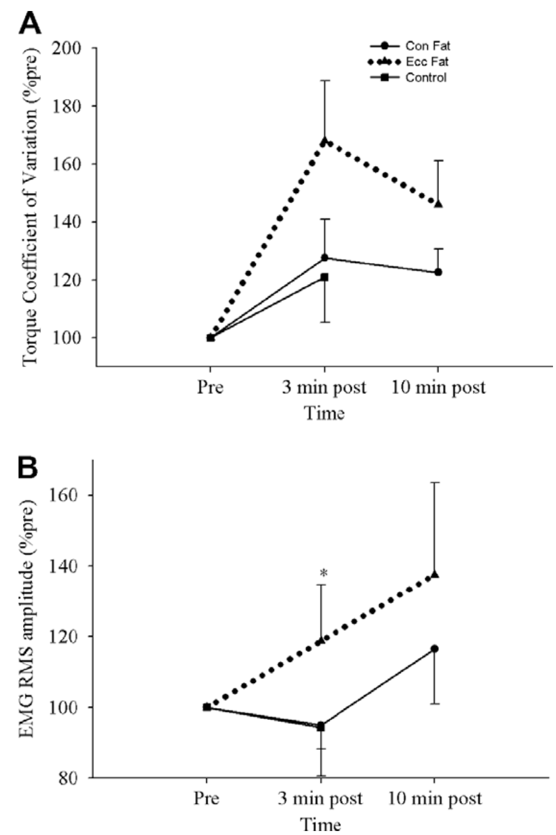

Fig. 5. Changes in torque fluctuation (A) and the EMG RMS amplitude (B) while holding a fixed submaximal target torque (17% pre-fatigue isometric MVC torque) after the fatigue protocols. Both the Ecc and Con protocols increased the torque fluctuation (A), and the Ecc showed a greater torque fluctuation than the Con and control conditions ($p = .052$). The EMG amplitude was increased only after the Ecc protocol at 3 min post-fatigue ($*$ in B for Con vs. Ecc; $p < .05$), but no difference was found at 10 min post-fatigue across protocols.

4.1. Volitional torque changes

When the triceps brachii was fatigued either eccentrically or concentrically until the 25% decrease in Ecc MVC torque was induced, how the muscle was fatigued (concentrically or eccentrically) did not have a major influence on the Con and Iso MVC torque decrease. One would expect that Con MVC torque would be decreased more after the Con protocol compared to the Ecc protocol if Ecc contractions are more fatigue resistant than Con contractions. The fatigability difference between Ecc and Con contractions, however, is likely muscle dependent. Several studies support that the decrease in torque is comparable after Ecc exercise and Con exercise in the biceps brachii (Kawakami et al., 1993; Linnamo et al., 2000; Loscher and Nordlund, 2002). It is possible that the effect of contraction type (concentric vs. eccentric) on muscle fatigue is less obvious in upper extremity muscles (e.g. triceps brachii) compared to weight-bearing, lower extremity muscles. Similar studies of the quadriceps (Tesch et al., 1990) and the tibialis anterior (Pasquet et al., 2000) support that Ecc exercise is more fatigue resistant compared to Con exercise. Recent findings from our lab support that the identical experimental protocol as performed in this study and applied to the quadriceps induces a greater decrease in the Con MVC torque after the Con protocol when compared to an Ecc protocol (78 ± 9.8% pre-fatigue vs. 64 ± 8.4% pre-fatigue for the Ecc and Con protocols, respectively. Thus, normal every day use of a muscle may influence responses to repetitive lengthening vs. shortening contractions.

4.2. EMG changes

Our data showed that the Con protocol induced greater fatigue-related changes in the EMG activity compared to the Ecc protocol. The RMS amplitude with Iso MVC was lower after the Con protocol, but not after the Ecc protocol compared to that of the control. Similarly, a fatigue-induced decrease in the median frequency with Con MVC was observed after the Con protocol. This difference in the median frequency across protocols may be attributed to the higher metabolite turnover during Con vs. Ecc contractions (Abbott et al., 1952). Consistent with this finding is that the median frequency is highly correlated with the changes in the sarcolemma conduction velocity, which decreases with a decrease in pH (increase metabolites) (Vestergaard-Poulsen et al., 1992). Alternatively, impairment in maintaining the recruitment of high-threshold, fast-conducting motor units during MVCs would also shift the EMG power spectrum to the lower frequency.

4.3. Evoked torque changes and D/S ratio

Both the single twitch and doublet peak torque decreased more after the Con compared to Ecc protocols, indicating that peripheral fatigue was greater after the Con protocol. The more pronounced fatigue-induced decrease in the median frequency after the Con protocol, is consistent with a greater energy turnover associated with Con contractions with excessive metabolites contributing to greater peripheral fatigue after Con protocol.

Increased peripheral fatigue did not influence LFF. The LFF was not evident at 3 min post-fatigue, but, consistent with the notion that LFF is delayed in onset, became significant at 10 min post-fatigue. The slow development of LFF is consistent with other reports (Binder-Macleod and Russ, 1999; Baptista et al., 2009). LFF involves an early rapidly recovering phase, likely related to metabolite build-up, and the other with a long-lasting response, which is not dependent on metabolite levels (Chin et al., 1997; Binder-Macleod and Russ, 1999). Our results were not influenced by post-activation potentiation as both the single twitch and doublet twitch peak torque reached a plateau before the final two pairs were accepted.

At 10 min post-fatigue, the majority of the fatigue-induced metabolic changes had been recovered, and therefore, the observed LFF is probably due to excitation–contraction coupling compromise. The absence of difference in LFF across protocols at 10 min post-fatigue indicates that when the amount of fatigue is appropriately controlled, the level of excitation–contraction coupling compromise is similar after Con and after Ecc exercise in this muscle. It has been shown that, in the biceps brachii, when the same extent of isometric MVC torque decrease was induced either concentrically or eccentrically, the extent of LFF was similar after Con and Ecc exercise, but the recovery of the LFF was faster after the Con exercise (Dundon et al., 2008). More frequent measurements with longer recovery follow-up are necessary to determine whether the time course of LFF recovery of the triceps brachii resembles that of the biceps brachii (Dundon et al., 2008).

Delayed onset muscle soreness, which can provide indirect information on exercise-induced muscle damage (Cheung et al., 2003), was not assessed, and therefore, it is not known whether the Ecc and Con fatigue protocols preferentially induced muscle damage. However, previous studies strongly support that repetitive Ecc contractions often result in structural muscle damage (Lieber and Friden, 1999; Takekura et al., 2001). Because the physical disruption of structures associated with excitation–contraction coupling and Ecc contractions has been reported to cause LFF (Takekura et al., 2001), the time course for these changes is not well defined. The same level of LFF observed at 10 min post-fatigue across protocols in this study suggests that the contribution of factors that cause LFF were similar. Repeated high Ca^{2+} transients and increased production of reactive oxygen species has been suggested to reduce the Ca^{2+} release from the sarcoplasmic reticulum (Westerblad and Allen, 2002). Moreover, inorganic phosphates, which increase considerably with fatigue, also reduces the Ca^{2+} release through precipitation of calcium phosphate (Allen and Westerblad, 2001). Because Con contractions have been associated with higher energy turnover compared to Ecc contractions (Abbott et al., 1952), it is likely that the contribution of these fatigue-induced chemical changes to LFF collectively contributed to both protocols.

The relative contribution of the factors contributing to LFF may be muscle type dependent. For example, lower extremity muscles, like the quadriceps, are repetitively activated during gait, and are likely adapted differently from upper extremity muscles. Recent studies support that the quadriceps LFF (Baptista et al., 2009) to various contraction types is different to the findings from this study and others examining upper extremity muscles (Dundon et al., 2008). Thus, adaptations to training or frequency of use likely influence the excitation–contraction sites associated with LFF.

4.4. Torque fluctuation

The extent of fatigue-induced increase in torque fluctuation depended on the type of contraction used to fatigue the muscle; although both fatigue protocols (Ecc and Con) had a common ending point (25% decrease in Ecc torque). This finding is consistent with recent studies of other muscles (Lavender and Nosaka, 2006; Dundon et al., 2008). More systematic studies are necessary to determine many of the factors contributing to this finding, however, it does not appear that the fatigue-induced increase in the torque fluctuation, at least at 3 min post-fatigue, is attributed to the LFF (Fig. 4B), or to peripheral fatigue, which was greater after the Con protocol (Fig. 4A). An increase in EMG activity with a submaximal contraction after fatigue is usually interpreted as a compensatory mechanism to recruit additional motor units and/or to further increase the firing rates to maintain the same force in fatigued muscle (Loscher et al., 1996). The finding that there was less peripheral fatigue after the Ecc protocol, but greater EMG with the torque steadiness task suggests that the increase in EMG activity observed in the present study is not simply to compensate for the peripheral fatigue. This is in line with the recent findings that Ecc fatiguing contractions alter the EMG–force relationship (Lavender and Nosaka, 2006; Semmler et al., 2007; Dundon et al., 2008). However, this finding does not support that LFF contributes to the increased neuronal drive and the altered EMG–force relationship during submaximal isometric contractions (Dundon et al., 2008) because both contraction types induced a similar level of LFF. Therefore, the increased EMG activity at 3 min post-fatigue after the Ecc protocol may be attributed to other mechanisms such as an increased motor unit synchronization after Ecc exercise (Dartnall et al., 2008).

A limitation of this study may be that the method used to determine LFF across protocols lacked sensitivity (D/S ratio). This question is important because others used low and high frequency stimulation to characterize LFF (Rijkelijkhuizen et al., 2003; de Ruiter et al., 2005; Dundon et al., 2008; Baptista et al., 2009). However, we have previously shown that in individuals with spinal cord injury, the doublet pulse activation is sensitive to muscle physiological properties (Dudley-Javoroski et al., 2008) and, under isometric conditions, when LFF is expected to be less, the D/S ratio increased only 8–10% (Iguchi et al., 2008), while in this study it increased over 20%. Thus, the D/S ratio appears to scale in accordance to the level of LFF induced.

It is possible that the ability to maximally drive the exercising muscle (the level of voluntary activation/central fatigue) was different across protocols. However, all the subjects had enough practice in both submaximal/maximal Con and Ecc contractions in the familiarization session. The angular velocity used in the present study ($13\ s^{-1}$) is much slower than the ones commonly used in the literature (Pasquet et al., 2000; Baudry et al., 2007; Smith and Newham, 2007), which is expected to make it easier for subjects to fully activate the muscle compared to higher velocity. Moreover, in pilot studies, interpolated twitch technique used under isometric MVCs did not show that the extent of voluntary activation/central fatigue was different across protocols before and after fatigue.

5. Conclusion

When the same amount of eccentric maximal voluntary contraction fatigue was induced in the triceps brachii through either concentric or eccentric contractions, the concentric protocol induced greater peripheral fatigue compared to the eccentric protocol. The level of fatigue-induced excitation–contraction coupling compromise was similar across protocols, but eccentrically-induced fatigue creates greater unsteadiness during a precision task. These findings suggest that low-frequency fatigue is induced to a similar extent regardless of how the fatigue is induced across different contraction types, that the CNS strategy to activate muscle for controlled tasks is influenced by the type of contraction, and that fatigue-induced via Ecc contractions selectively lead to greater unsteadiness.

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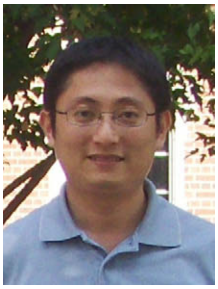

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