POSTACTIVATION POTENTIATION AND MUSCULAR ENDURANCE TRAINING

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Accepted 27 September 2011

ABSTRACT: *Introduction*: The aim of this study was to investigate muscle twitch force potentiation after voluntary conditioning contractions (CC) of various intensities and the CC duration necessary to achieve maximal potentiation before and after muscular endurance training. *Methods*: Fourteen healthy men and women (23.6 ± 0.96 years of age) performed repeated CCs of 25%, 50%, and 100% maximal voluntary contraction of the adductor pollicis muscle until maximal potentiation. CCs were followed by electrically evoked twitches. The training group performed a fatigue task and endurance trained for 8 weeks. *Results*: Endurance time increased by 79.8 ± 22.5% post-training. Potentiation occurred after all CC intensities and was greater after training. The CC duration needed to achieve maximal potentiation decreased as CC intensity increased. Potentiation was greater during the fatigue task after compared to before training and was correlated with endurance time. *Conclusion*: An increase in muscle force potentiation may function as a mechanism to prolong muscular endurance.

Muscle Nerve **45:** 416–425, 2012

The contractile history of a muscle has two opposing effects on muscular force output: potentiation and fatigue. Postactivation potentiation is the enhancement of muscular twitch force after voluntary contractile activity. Potentiation after electrically elicited contractions is typically referred to as staircase[1] or posttetanic potentiation.[1,2] Twitch force potentiation of evoked contractions is most commonly induced experimentally using maximal voluntary contractions (MVCs).[3–9] Most activities of daily living and athletic performance, however, utilize submaximal intensity muscle contractions. Twitch force has been shown to increase after submaximal contractions,[9–13] yet there has been little investigation into methods to optimize potentiation of evoked contractions after submaximal contractions.[9] Several studies, however, have reported potentiation of functional performance (i.e., vertical jump, sprint speed, and bench press throws) after maximal[14,15] and submaximal muscular efforts.[16–29] Other studies have failed to induce potentiation of functional performance after 100% MVC knee extensions,[30,31] and after submaximal squat[32–38] and bench press[39,40] conditioning contractions. Decreased jump performance has also been observed after submaximal squat conditioning contractions.[33] Muscular fatigue has been found to influence muscle function by limiting the ability of the muscle to maintain a given level of force output. Potentiation and fatigue coexist, and the net effect can be observed in the twitch force amplitude.[41,42]

Potentiation is present in both fiber types, but it is more prevalent in fast- than slow-twitch muscle fibers.[9,15,43,44] Individuals with a greater percentage of fast-twitch fibers have greater potentiation,[46] and the anterior tibialis muscle, which is composed of about 27% fast-twitch muscle fibers,[47] exhibits greater potentiation compared with the soleus muscle, which is composed of about 11% fast-twitch muscle fibers.[9,47] This suggests that greater potentiation may occur after higher intensity contractions in which more fast-twitch muscle fibers are activated compared with lower intensity contractions.

During submaximal contractions in untrained individuals, Vandervoort and colleagues[9] observed little to no potentiation after contractions of <75% MVC. A 10-s MVC produced the greatest potentiation for contractions of 100% MVC[7,9]; however, the optimal contraction duration to potentiate the muscle during submaximal intensity contractions is unknown. In this study, we chose to use the predominantly slow-twitch adductor pollicis (AdP) muscle to minimize the effects of fatigue on potentiation during repeated contractions.

In electrically evoked contractions, potentiation magnitude is dependent on the number of pulses delivered.[43,48] During voluntary contractions, fewer motor units are recruited during low- vs. high-intensity contractions[49–51] and the firing rates of those motor units are lower compared with higher intensity contractions[49,52]; hence, a longer contraction time would be needed to accrue an equal number of action potentials during low- vs. high-intensity contractions. The conditioning contraction (CC) duration required to produce maximal potentiation may therefore be specific to the CC intensity. Specific activation parameters such as CC intensity and CC duration, which may influence maximal postactivation potentiation, are not well established.

Cross-sectional studies showed that endurance athletes have greater twitch potentiation after a

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Abbreviations: AdP, adductor pollicis; ANOVA, analysis of variance; CC, conditioning contraction; EMG, electromyography; FTI, force–time integral; MVC, maximal voluntary contraction; RLC, regulatory light chain; RMS, room mean square; TR, training group

Key words: endurance training, fatigue, skeletal muscle, submaximal contraction, twitch

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DOI 10.1002/mus.22313

100% MVC compared with untrained individuals,[5] and that twitch amplitudes remain above resting levels for a longer duration during an intermittent submaximal fatigue task in endurance-trained compared with power-trained athletes.[13] The effects of muscular endurance training on potentiation magnitude have not been investigated in a longitudinal study. Endurance training may improve postactivation potentiation capacity and function as a mechanism to enhance muscular endurance.

We conducted a systematic investigation of postactivation potentiation to determine the best strategy to achieve maximal potentiation in response to voluntary contractions of maximal and submaximal intensities of various durations before and after muscular endurance training. We hypothesized that: (1) twitch force would increase after maximal and submaximal CCs; (2) maximal twitch force potentiation would increase as CC intensity increased; (3) the CC duration needed to achieve maximal potentiation would decrease as CC intensity increased; and (4) maximal potentiation would be greater after muscular endurance training than before training.

METHODS

Participants. Fourteen young, healthy men ($N = 6$) and women ($N = 8$) participated in this study. Participants were assigned to groups based on recruitment order with a 2:1 ratio for the training ($N = 9$) and control ($N = 5$) groups. The training group consisted of 4 men and 5 women, with a mean age of 24.3 ± 1.4 years. The control group consisted of 2 men and 3 women, with a mean age of 22.4 ± 1.0 years. All participants were healthy and had no history of neuromuscular disorder or injury to the nondominant hand. Musicians and athletes with a highly trained nondominant hand were excluded from the study, and participants were asked to refrain from caffeine consumption on experimental testing days. All procedures were in accordance with the Helsinki Declaration and were approved by the institutional review board of University of Texas at Austin. All individuals signed an informed consent form prior to participating in the study.

Experimental Procedures. Participants attended an initial orientation session and were familiarized with the experimental setup, equipment, and protocol. They practiced performing MVCs and three to five 5-s CCs at each contraction intensity (25%, 50%, and 100% MVC). Two experimental test days were performed before and after 8 weeks of muscular endurance training of the thumb in the training group and no training in the control group. We tested the AdP muscle, which is innervated by the easily accessible ulnar nerve, because of its importance in gripping and grasping tasks. This muscle also has a unique motor unit recruitment pattern in which a majority of motor units are recruited by 20% MVC and all motor units are recruited by 50% MVC.[53]

For all experimental sessions, participants were seated, with the nondominant forearm in a supinated position and supported in a splint. The thumb was abducted and positioned against a metal strain-gauge force transducer. A pair of pregelled adhesive Ag/AgCl disposable surface electromyography (EMG) electrodes (Danlee Products, Inc., Syracuse, New York) were placed on the palmar surface of the hand, over the AdP muscle. A ground electrode was placed on the ulnar styloid process of the wrist. A stimulating electrode was secured with a strap over the unlar nerve at the wrist. A visual display of the force and EMG was provided on a computer screen positioned in front of the individual.

Test Day 1. The purpose of test day 1 was to measure the number of contractions required to reach maximal potentiation during repeated intermittent voluntary CCs of 25%, 50%, and 100% MVC, and to compare potentiation after single CCs of matched force–time integral (FTI). We also administered the standard electrically elicited Burke fatigue protocol for 3 min[54] in order to correlate muscle fatigability with twitch force potentiation magnitude.

First, the maximal M-wave amplitude was found by stimulating the ulnar nerve with single pulses (100-μs duration), slowly increasing the stimulation current (DS7A; Digitimer, Garden City, UK) until the peak-to-peak M-wave amplitude did not increase with further increase of the current. All further stimulation was supramaximal (i.e., at a stimulation intensity 10% higher than that required to evoke the maximal M-wave). A 10-min rest interval preceded the five unpotentiated single twitches, which were evoked with single-pulse surface stimulation. Participants then performed three 5-s MVCs of the AdP muscle. For all MVCs, participants adducted the thumb against the metal bar as fast and forcefully as possible. Verbal encouragement was provided. A single pulse was delivered during each MVC to ensure that participants were maximally contracting the muscle.[55] The largest of the three MVCs was used to determine the target forces for the remaining contractions.

Potentiating protocols for test day 1 are shown in Figure 1. First, five unpotentiated single twitches were evoked prior to each CC test. These served as the control twitches. Five postactivation potentiation CC tests were performed: 5-s repeated 25%;

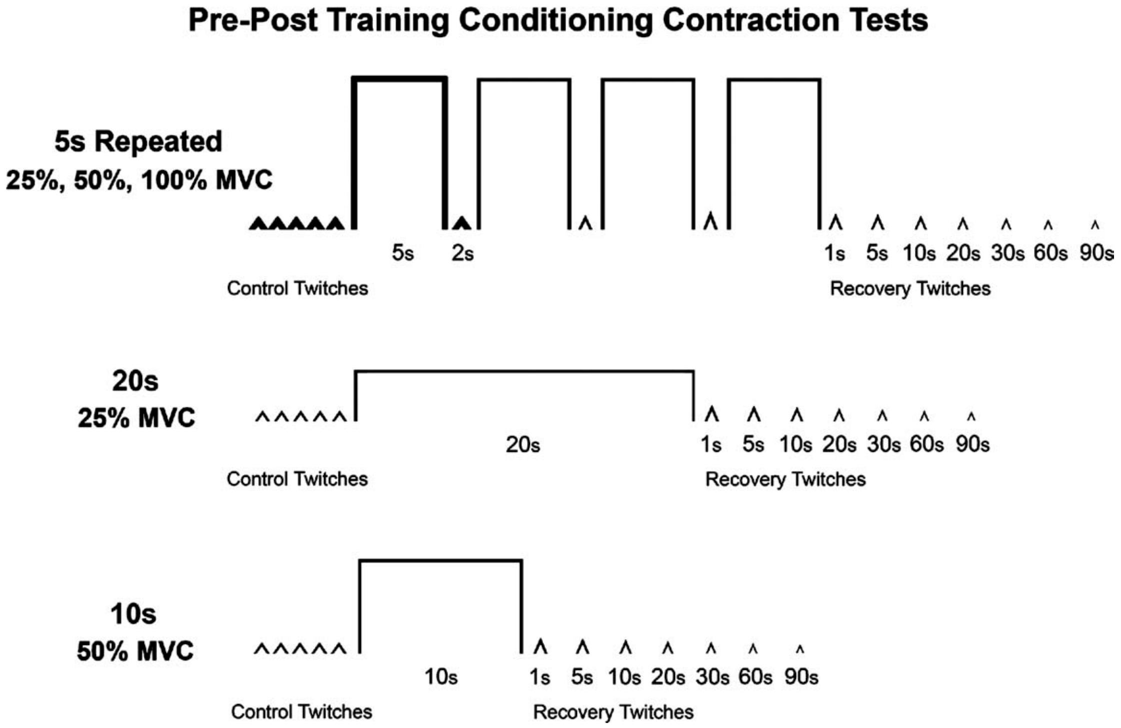

FIGURE 1. Schematic representation of conditioning contractions (CC) performed on test day 1. CCs were performed in random order across participants. The 5-s repeated CC was repeated until the twitch force after the CC decreased for the first time or when the highest level of twitch force was maintained after three consecutive CCs. Recovery twitches were elicited at 1, 5, 10, 20, and 30 s after the last CC and every 30 s thereafter until twitch force returned to baseline. The 5-s 100% MVC CC is indicated by the bold section of the 5-s repeated 100% CC.

5-s repeated 50%; 5-s repeated 100% MVC; and pt?>single CC tests matched for FTI of 20-s 25% and 10-s 50% MVC. The FTI-matched CC tests were performed to determine whether the degree of potentiation would be comparable after CCs of similar FTIs but of different contraction intensities. All tests were performed in random order. Participants followed a template on a computer monitor that displayed the contraction and rest interval pattern. To ensure the muscle was not potentiated prior to the CC, a rest interval of approximately 10 min preceded each CC test, and the peak forces of the single twitches were measured before each CC. The repeated CC tests consisted of a 5-s contraction followed by a 2-s rest interval, and this pattern was repeated until the twitch force that followed the CC decreased for the first time or when the highest level of twitch force was twitch force was maintained after three consecutive CCs. Recovery twitches were elicited at 1, 5, 10, 20, and 30 s after the last CC and every 30 s thereafter until twitch force returned to baseline. For most participants, twitch force returned to baseline within 10 min; however, if the twitch force remained elevated after 10 min, single pulses were delivered every 30 s until force returned to baseline. After a 10-min rest period and/or the twitch force returned to the control value, the same procedures were repeated for each CC level.

After the CC tests, the modified Burke fatigue protocol was administered. It consisted of a 3-min application of repetitive intermittent surface electrical stimulation (40 Hz) of the ulnar nerve with trains of 13 stimuli repeated each second[54] with each train lasting 330 ms followed by 660 ms of no stimulation.

Test Day 2. The purpose of test day 2 was to perform a voluntary fatigue task of 25% MVC. This served as a measure of voluntary muscular endurance before and after training. Five single twitches were elicited followed by three 5-s MVCs with interpolated twitches. To ensure the muscle had returned to an unpotentiated state, a 10-min rest interval followed the MVCs. Five single control twitches were again elicited prior to the fatigue task. Next, the fatigue task, which consisted of repeated 25% MVC isometric contractions of 20 s on with 2 s off until the endurance limit was reached, was performed. A single twitch was delivered between each contraction to measure the time course of changes in twitch force amplitude during the fatigue task. The criterion for endurance time was met when the force was at or below 20% MVC for at least 1 s. Verbal encouragement was given to participants during the fatigue task.

The same experimental protocols were used for both the pre- and posttest days. The posttest day 1 protocol was performed approximately 48 hours after the final training session, and approximately 48 hours separated the 2 days of posttesting. Participants in the control group performed pre- and posttests for day 1 approximately 8 weeks apart and did not undergo training.

Muscular Endurance Training Protocol. Training group participants trained the AdP muscle of the nondominant hand every other day for 8 weeks (28 training sessions). Endurance training was performed using a portable, custom-designed and built, thumb training device, which isolates thumb adduction (University of Texas at Austin). The endurance training protocol consisted of performing three sets of six 1-min isometric, sustained thumb adduction contractions at 25% MVC. Each repetition was followed by a 5-s rest, and each set was followed by a 2-min rest interval. To provide continued overload to the muscle, the training volume was increased by 3 min every fourth training day (training volume was not changed on training day 28). By the end of the training period, participants performed six sets of six 1-min contractions. Participants were provided with visual feedback of the force they were exerting via a gauge on the training device, which allowed them to maintain the target force level throughout the contraction. The first and every fourth training session were conducted in the laboratory under the supervision of the experimenter to ensure that training was performed correctly and to adjust the training volume. To increase training compliance, participants had the option of completing the remaining training sessions at home or in the laboratory, and they were provided with a training device, stopwatch, and a training log on which to record their training sessions.

Data Analysis. Surface EMG was high-pass filtered at 13 Hz, gain 100 (Coulbourn Instruments, Allentown, Pennsylvania), and digitized at 2000 Hz [Cambridge Electronic Design (CED), Cambridge, UK]. The force signal was high-pass filtered at 13 Hz with a gain of 100 (World Precision Instruments, Sarasota, Florida) and digitized at a sampling rate of 1000 Hz (Micro 1401; CED). All data were analyzed offline using Spike2 software (version 5) for Windows (CED).

The mean peak twitch force from the five single pulses was measured before each potentiation protocol (control twitch). For the single CCs, twitch force recorded immediately after the single CC was used for the potentiated twitch force. For the 5-s repeated CCs, the twitch force after the CC that produced the greatest twitch force was used as the maximal potentiated twitch. Potentiation is expressed as the percent change in twitch force of the potentiated twitch compared with the control twitch force for each condition. EMG during the 5-s repeated CC tests was measured for the first and maximally potentiated contractions. The mean root mean square (RMS) EMG amplitude was normalized to mean RMS EMG amplitude during the peak MVC. The fatigue index for the modified Burke fatigue task was calculated as the ratio of peak twitch force at 3 min of the fatigue task to the initial twitch force of the fatigue task.[54]

Statistical Analysis. A one-way repeated-measures analysis of variance (ANOVA) was used to test pre- vs. posttraining differences in endurance time in the training group. MVC (group × training), RMS EMG amplitude during the fatigue task (training × contraction number), and twitch potentiation during the voluntary fatigue task [fatigue time (twitch force after the first six 20-s contractions) × training] were compared using two-way repeated-measures ANOVA. One participant's endurance time and fatigue task data were excluded due to technical error during data collection.

A three-way repeated-measures ANOVA [twitch time (control and maximally potentiated twitch force) × CC (5 s repeated 25%, 5 s repeated 50%, 5 s repeated 100%, and 20 s 25%, 10 s 50%, and 5 s 100% MVC) × training] was used to compare control twitch force across all trains and pre- vs. posttraining and to compare control with maximally potentiated twitch forces to determine whether potentiation was significant for each CC test.

Three-way repeated-measures ANOVAs [CC (5 s repeated 25%, 5 s repeated 50%, 5 s repeated 100%, and 20 s 25%, 10 s 50% and 5 s 100% MVC) × training × group] were used to compare maximal potentiation magnitude (percent change control to potentiated twitch), EMG RMS of the 5-s CCs to maximal potentiation, and CC duration needed to elicit maximal potentiation. Potentiation did not occur after one or more of the CC tests for 2 training group participants; therefore, there was not a CC duration that elicited maximal potentiation, and these participants were excluded from the statistical analysis for the CC duration needed to elicit maximal potentiation. These participants were included in all other statistical analyses even if potentiation was equal to zero. Recovery twitch forces were also compared with a three-way repeated-measures ANOVA [group × training × recovery time (5 s, and 1, 5, and 10 min)].

The Pearson product moment correlation test was used to the determine the correlation coefficient of the fatigue index at 3 min of the Burke fatigue test and maximal potentiation of the 5-s repeated 25%, 50%, and 100% MVC CC tests pre-

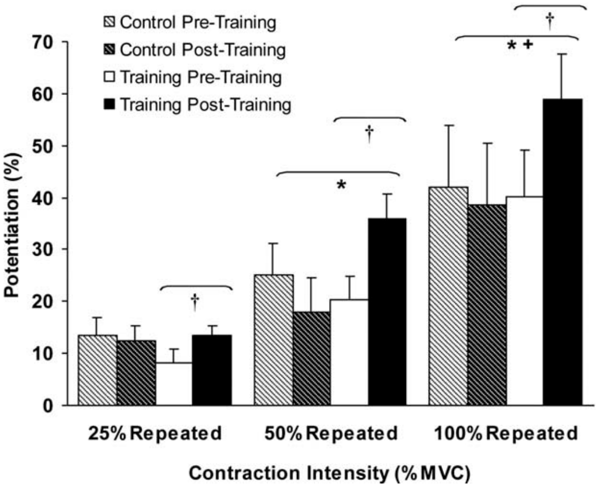

FIGURE 2. Maximal potentiation expressed as percent increase from baseline to maximally potentiated twitch force after each 5-s repeated CC intensity for each group pre- and posttest. *Significantly greater potentiation than the 25% MVC CC. +Significantly greater potentiation than the 50% MVC CC. †Significant group × training interaction. Training group: $N = 9$; control group: $N = 5$. Data presented as group mean ± standard error.

and posttraining for the training and control groups. The relationship between the change in endurance time and change in maximal potentiation after the 5-s repeated CC tests pre-and posttraining was also calculated using the Pearson product moment correlation analysis. Potentiation was calculated as the maximal potentiation produced from the 5-s repeated CC tests, and change in endurance time was the difference between endurance time posttraining and endurance time pretraining.

All data are presented as group mean ± standard error. The Bonferroni correction was used for *post hoc* analysis of multiple comparisons. Normality was tested using skewness and kurtosis statistics and was within the acceptable range (-3 to $+3$) for all tests performed. The Greenhouse–Geisser correction was used if the Mauchly test of sphericity was violated. $P \leq 0.05$ was considered statistically significant.

RESULTS

Endurance Time and MVC. Muscular endurance training resulted in a 79.8 ± 22.5% increase in endurance time of the fatigue task (450.0 ± 91.7 s and 707.5 ± 76.2 s, $P = 0.005$, pre- and posttraining, respectively, power = 0.93). There were no pre- vs. posttest differences in MVC for the training (59.9 ± 5.8 vs. 66.4 ± 7.4 N) or control (59.1 ± 8.1 vs. 58.6 ± 7.4 N) groups and no differences between groups before or after the 8 weeks. Interpolated twitches were not present during the MVCs, indicating 100% voluntary muscle activation. Training compliance was 100% for all training group participants.

Conditioning Contraction Intensity and Maximal Twitch Potentiation. Twitch force potentiated significantly for all CC tests pre- and posttraining in both groups ($P < 0.05$), except for the pre- and posttraining 5-s 100% MVC CC.

The training × group interaction was significant for maximal potentiation of the 5-s repeated CCs ($P = 0.002$, power = 0.96). *Post hoc* results showed that maximal potentiation magnitude was significantly greater after endurance training compared with before training for the training group ($P < 0.001$). There was no change in the control group from pre- to posttest (Fig. 2), and pretest maximal potentiation was no different between groups. The main effect for CC intensity for maximal twitch potentiation magnitude was also significant ($P > 0.001$, power = 1.0). *Post hoc* analysis revealed that maximal potentiation of the repeated 5-s CCs for the 50% MVC was significantly greater than the 25% MVC ($P = 0.004$). The 100% MVC was significantly greater than the 25% ($P = 0.001$) and the 50% MVC ($P = 0.002$) (Fig. 2).

Force–Time Integral Matched Conditioning Contractions. The three-way repeated-measures ANOVA showed no significant differences in potentiation magnitude between single CCs matched for FTI between groups or with training (Fig. 3).

The control twitch force did not change significantly across CC tests, indicating that the twitch force returned to resting values prior to the initiation of each test protocol (7.89 ± 0.30 N and 7.51 ± 0.36 N for training and control groups, respectively, $P > 0.05$), and the control twitch force was not significantly different between groups or for pre- vs. posttesting for either group. The coefficient of variation (CV) of the control twitches was calculated to test for variability of the twitch force. Mean CVs for the control twitches were as follows:

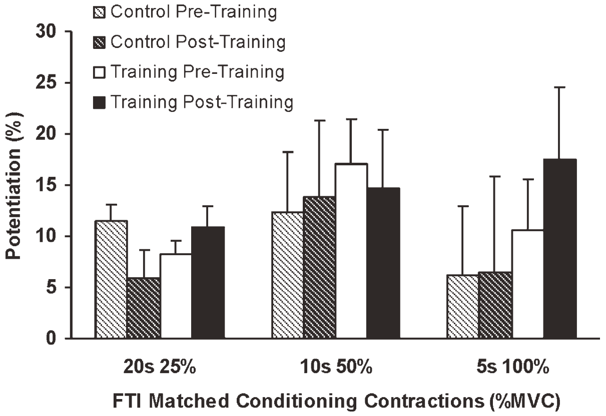

FIGURE 3. Potentiation after single CCs matched for force–time integral (FTI). There were no significant differences in potentiation magnitude between CC intensity or with training. Data presented as group mean ± standard error.

Table 1. M-wave amplitudes for control and potentiated twitches.

	Control group ($n = 5$)		Training group ($n = 9$)	
CC test	Control twitch	Potentiated twitch	Control twitch	Potentiated twitch
5 s repeated 25% pre	5.1 ± 0.1	5.1 ± 0.1	5.4 ± 0.1	5.5 ± 0.1
5 s repeated 50% pre	5.6 ± 0.1	5.1 ± 0.1	5.2 ± 0.1	5.8 ± 0.1
5 s repeated 100% pre	5.6 ± 0.1	6.4 ± 0.1	5.4 ± 0.1	6.3 ± 0.1
20 s 25% pre	5.3 ± 0.1	5.6 ± 0.1	5.1 ± 0.1	5.2 ± 0.1
10 s 50% pre	5.6 ± 0.1	6.0 ± 0.1	5.1 ± 0.1	5.9 ± 0.1
5 s 100% pre	5.6 ± 0.1	6.0 ± 0.1	5.4 ± 0.1	6.1 ± 0.1
5 s repeated 25% post	4.5 ± 0.1	5.1 ± 0.1	5.0 ± 0.1	5.2 ± 0.1
5 s repeated 50% post	4.7 ± 0.1	5.6 ± 0.1	5.4 ± 0.1	5.9 ± 0.1
5 s repeated 100% post	4.5 ± 0.1	5.6 ± 0.1	5.3 ± 0.1	6.0 ± 0.1
20 s 25% post	4.6 ± 0.1	5.0 ± 0.1	4.9 ± 0.1	5.0 ± 0.1
10s 50% post	5.6 ± 0.1	5.8 ± 0.1	5.0 ± 0.1	5.5 ± 0.1
5s 100% post	4.5 ± 0.1	6.3 ± 0.1	5.3 ± 0.1	5.9 ± 0.1

No significant difference between control twitch M-wave and potentiated twitch M-wave or across protocols on a test day. Data presented as mean ± SE.

training group, pretraining = 0.028, posttraining = 0.026; and control group, pretraining = 0.022, posttraining = 0.022. M-wave amplitudes did not change from control to potentiated twitch for either group pre- or posttraining ($P > 0.05$; Table 1).

Contraction Duration to Elicit Maximal Potentiation. There was a significant main effect for CC intensity ($P = 0.012$, power = 0.80) such that the CC duration of the 5-s repeated contractions required to elicit maximal potentiation decreased as contraction intensity increased. *Post hoc* analysis revealed that the 100% MVC CC reached maximal potentiation with a shorter contraction duration compared with the 25% CC ($P = 0.049$), and there was no change with training (Fig. 4). Normalized RMS EMG amplitude of the repeated 25%, 50%, and 100% MVC CC tests did not change between the first CC and the maximally potentiated CC ($P = 0.202$), indicating that the muscle was not fatigued during the repeated CC testing.

Fatigue Task and Potentiation. Muscular endurance training resulted in greater twitch potentiation during the first 2 min of the 25% MVC fatigue task compared with before training (training main effect: $P = 0.044$, power = 0.48; Fig. 5). Pre- vs. posttraining change in endurance time was significantly correlated with the pre- vs. posttraining change in maximal potentiation of the 5-s repeated 100% CC: $r = 0.71$, $P = 0.049$. There was no significant correlation for the 50% CC ($r = 0.25$, $P = 0.549$) and the 25% CC ($r = 0.28$, $P = 0.508$) (Fig. 6).

Burke Fatigue Task. Maximal potentiation after the repeated 100% CCs correlated significantly with the fatigue index after 3 min of the Burke fatigue task: $r = 0.49$, $P = 0.008$, $y = 100.74x + 13.989$. At the 50% and 25% CC levels, the common variance was not statistically significant (50% CC: $r = 0.35$, $P = 0.07$, $y = 40.891\times + 12.625$; 25% CC: $r = 0.21$, $P = 0.29$, $y\ 11.252x + 7.994$).

Recovery Twitch Force. The recovery twitch forces for the repeated 100% CCs are displayed in Figure 7. There were no differences pre- vs. posttraining and no differences between groups. Twitch force decreased significantly over time ($P < 0.001$, power = 1.0), and *post hoc* analysis revealed that twitch force decreased with recovery [5 s > 5 min ($P =$

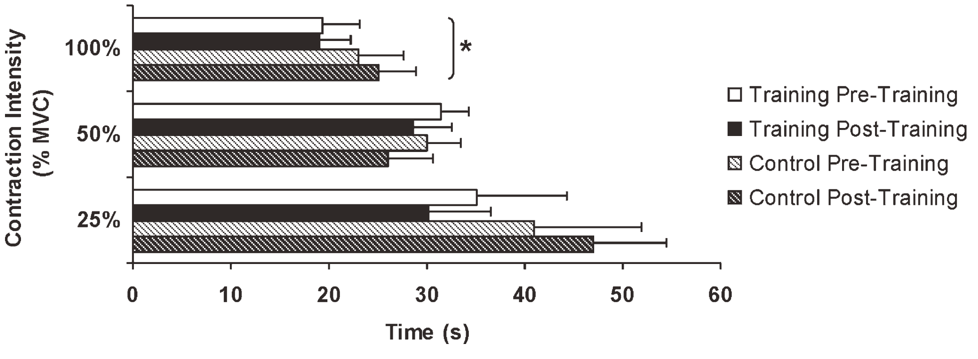

FIGURE 4. CC duration to achieve maximal potentiation for each CC intensity. Asterisk indicates significantly fewer contractions than 25% MVC CC. Data presented as group mean ± standard error.

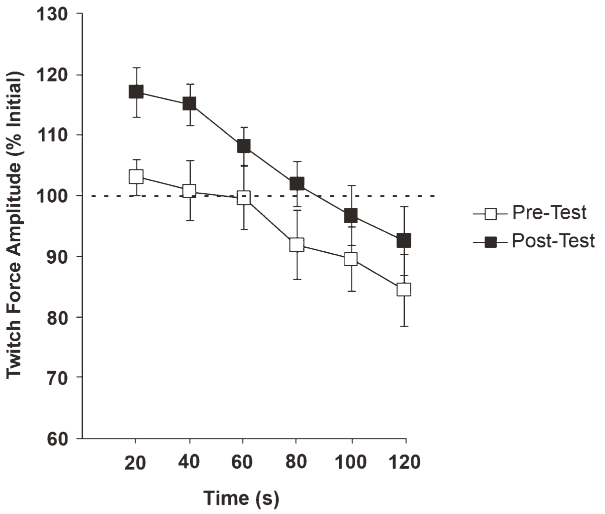

FIGURE 5. Mean twitch force potentiation during the first 2 min of the voluntary intermittent 25% MVC fatigue task. There was significantly greater potentiation posttraining compared with pretraining during the first 2 min of the fatigue task. Data presented as group mean ± standard error.

0.003) and 10 min ($P < 0.001$), 1 min > 5 min ($P = 0.016$) and 10 min ($P < 0.001$), and 5 min > 10 min ($P < 0.001$)].

DISCUSSION

We found that maximal potentiation magnitude increased after 8 weeks of muscular endurance training of the AdP muscle. Endurance training produced greater twitch force potentiation during the initial phase of a voluntary fatigue task, indicating that potentiation may have contributed to the increase in endurance time with training. The magnitude of potentiation increased as contraction intensity increased. Our study has also demonstrated that CCs of different intensities require CCs of different durations to develop maximal potentiation, and the duration required for a given intensity did not change with training. We also found that potentiation can be utilized to augment muscle force after submaximal muscle contractions as low as 25% MVC.

Contraction Intensity and Potentiation Magnitude. Maximal twitch force increased significantly after CCs of 25%, 50%, and 100% MVC, and greater potentiation occurred as contraction intensity increased. One study compared potentiation of evoked twitch forces after maximal and submaximal contractions.[9] In that study, Vandervoort and colleagues[9] observed little or no potentiation after contractions of <75% MVC, but only 2 subjects were tested. That study may have failed to show potentiation at lower contraction intensities, because only a 10-s duration CC was used to potentiate the muscle at 25%, 50%, 75%, and 100% MVC. We did, however, observe maximal potentiation after a mean CC duration of 36 s at 25% MVC and 29 s at 50% MVC. Other investigators have also reported potentiation after 30% and 75% MVC[11] in untrained individuals and 50% MVC CCs in elite athletes.[13]

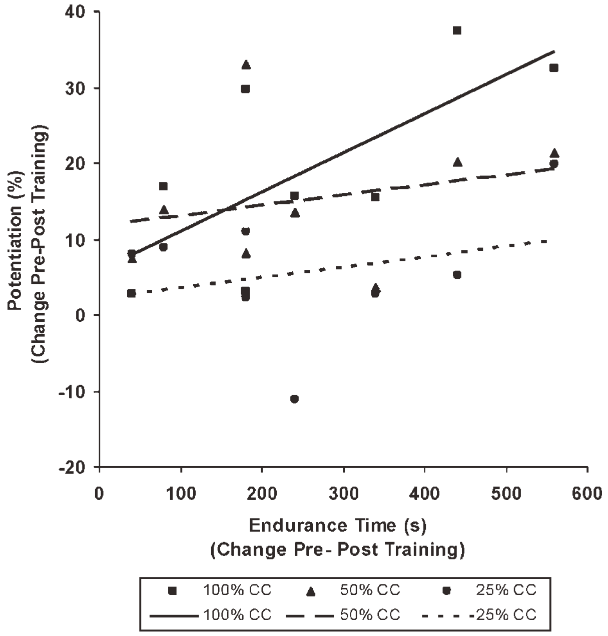

FIGURE 6. Positive correlation between the pre- vs. posttraining difference in endurance time and the pre- vs. posttraining difference in maximal potentiation of the repeated 100% MVC CC: $r = 0.71$, $P = 0.049$, $y = 0.0515x + 5.89$, $R^2 = 0.50$. No correlation for the repeated 50% MVC CC: $r = 0.25$, $P = 0.549$, $y = 0.0133x + 11.751$, $R^2 = 0.06$ and 25% MVC CC: $r = 0.28$, $P = 0.508$, $y = 0.0137x + 2.3121$, $R^2 = 0.08$. Each data point represents data of 1 training group participant ($N = 8$).

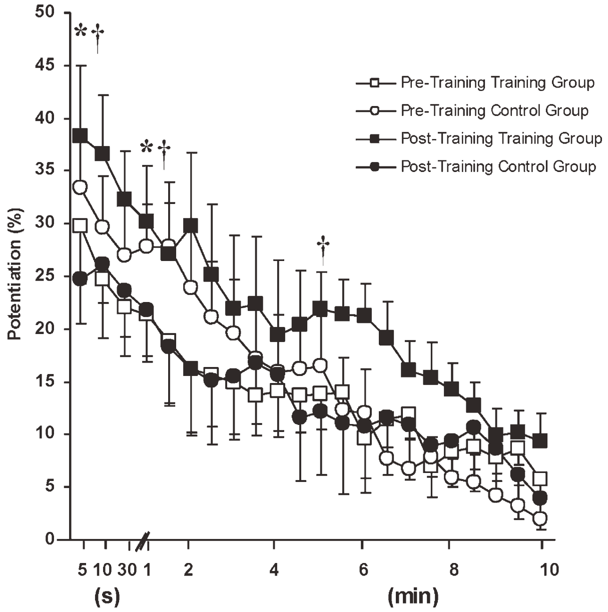

FIGURE 7. Mean recovery twitch force after the repeated 100% CCs. Data are expressed as percent increase compared with control twitch force. *Significantly > 5 min. †Significantly > 10 min. Data presented as group mean ± standard error.

In our study, it is likely that greater potentiation occurred after higher intensity CCs, because more fast-twitch muscle fibers were activated at higher CC intensities. Vandervoort et al.[9] noted that greater potentiation magnitude occurred after MVC in the fast-twitch human tibialis anterior muscle than in the slow-twitch soleus muscle,[47] regardless of CC duration. Potentiation is more prevalent in fast-twitch than in slow-twitch muscles in animals, but it is present in both fiber types.[44,45,56] After a 10-s MVC in the human quadriceps muscle, a higher percentage of fast-twitch fibers was related to greater potentiation[46]; however, Stuart and colleagues[57] observed no differences in potentiation based on fiber type composition of the quadriceps muscle.

In the AdP muscle, which is predominately slow twitch,[47,58] it was found that a majority (18 of 29) of motor units were recruited by 20% MVC, and no additional motor units were recruited after 50% MVC.[53] In our study, the difference in potentiation between the 25% and 50% CC may be related to the type of muscle fibers activated, because the 25% CC likely recruited more slow-twitch fibers that may have potentiated less than fibers recruited at 50% MVC. The 50% MVC contraction may have recruited all muscle fibers, including the fast-twitch fibers, and to increase force to 100% MVC, the firing rate of the motor units increased. Greater potentiation after the 100% MVC CC vs. the 50% MVC CC may therefore be attributed to the changes in motor unit firing rate or the total number of action potentials and not differences in the activated muscle fiber type. Potentiation is related to pulse number[48] and stimulation frequency[59] during evoked contractions of the human AdP muscle.

Contraction Duration and Potentiation. Testing a single muscle at various contraction intensities revealed that lower intensity CCs required a longer contraction duration to obtain maximum potentiation compared with higher intensity contractions. Vandervoort and colleagues[9] studied potentiation magnitude after MVC CCs of various durations (1 s, 3 s, 10 s, 30 s, and 60 s) in the human tibialis anterior and soleus muscles and found that the tibialis anterior muscle required a shorter contraction duration to achieve maximal twitch potentiation compared with the slow-twitch soleus muscle. Potentiation in the soleus muscle was greatest after 100% MVC CCs of both 10 and 30 s, but potentiation of the tibialis anterior muscle was greatest after the 10-s 100% MVC CC and decreased after the 30-s CC,[9] demonstrating that the coexistence of fatigue and potentiation[42,60] may be influenced by fiber type of the activated muscles.

The total number of action potentials produced during an evoked contraction has been shown to be related to the degree of potentiation.[43,48,61] More motor units fire at faster frequencies during higher intensity contractions. This may explain why, in this study, the higher intensity contraction reached maximal potentiation with shorter contraction times than with lower intensity contractions. This could also explain why the FTI-matched CC tests did not differ in the amount of potentiation produced, as our previous work has shown that potentiation of evoked contractions is correlated with the FTI of the CC.[48]

Muscular Endurance Training and Potentiation. We found that 8 weeks of muscular endurance training increased maximal force potentiation after maximal and submaximal CCs compared with untrained muscle. An earlier cross-sectional study showed that endurance- and strength-trained athletes have greater twitch force potentiation compared with untrained individuals after MVC CCs.[5] The results may, however, be genetically influenced, as individuals who undergo greater potentiation may find success in sports. However, Hamada et al.[5] found that distance runners who trained only the lower body had greater potentiation in the lower body muscles but not in the muscles of the upper body, and those who endurance- or strength-trained their upper and lower body had more potentiation in both muscle groups compared with sedentary individuals. Potentiation was greater in endurance athletes compared with power athletes when a submaximal CC (50% MVC) was used to induce potentiation.[13] Furthermore, endurance athletes maintained potentiation throughout a 10-min fatigue task, whereas twitch force dropped below baseline at 4.5 min in power athletes.[13]

Endurance time increased as a result of our muscular endurance training program, and twitch force potentiation was significantly greater during the fatigue task post-training compared with pre-training. During fatigue, Ca^{2+} release from the sarcoplasmic reticulum per action potential is reduced.[62,63] The process of potentiation may offset the fatigue process. Regulatory light chain (RLC) phosphorylation plays a prominent role in muscle force potentiation of rat fast-twitch type IIb muscle fibers.[64] However, in type IIa and type I fibers, increased phosphorylation did not result in potentiation of these fibers in rat muscle when contraction was induced via electrical stimulation.[64] It is possible that an alternative mechanism may induce potentiation in human slow-twitch fibers. RLC phosyphorylation moves the myosin head closer to the thin filament to enhance binding.[65] The small interfilament spacing of type I and IIa fibers and osmotic changes during muscle contraction may decrease the lattice space between the myosin and actin filaments, which can cause a shift of the force–pCa curve similar to that occurring during RLC phosphorylation.[66] RLC phosphorylation increases sensitivity to Ca^{2+} and produces a leftward shift of the force–pCa curve. This allows a given force level to be maintained at lower Ca^{2+} concentrations, and thus less adenosine triphosphate is utilized to pump Ca^{2+}.[67] In turn, this increases neuromuscular efficiency, which may be a crucial factor in fatigue prevention. Thus, greater muscle force potentiation may contribute to the increased endurance time. The balance between force enhancement due to potentiation and force attenuation due to fatigue is observed in the twitch force.[1] However, the coexistence of potentiation and fatigue make it difficult to determine the point at which potentiating processes decline and/or cease, and fatigue processes begin.[41,42] These processes are also significantly influenced by the recovery time between the conditioning contraction and the subsequent evoked twitch or functional performance test.[48,59] Fatigue results in decreased twitch force and increased contraction and half-relaxation times. Further, potentiation and fatigue processes are thought to be concurrent when the twitch force is enhanced and the contraction time and half-relaxation time are longer.[41,68] Thus, the factors of potentiation and fatigue can influence assessments of muscle contractile properties utilized during studies of outcome measures after interventions in clinical populations.

There was a significant positive correlation between the increase in endurance time and the increase in potentiation after training with repeated 100% MVC CCs. These findings suggest that muscle force potentiation, along with the training-related changes in aerobic metabolic properties and increased lactate tolerance and removal,[69] may augment muscular endurance. The fatigue index during the electrically evoked fatigue task correlated positively with the magnitude of potentiation after the repeated 100% MVC CCs, but not after the repeated 50% and 25% MVC CC tests. This may be because the electrically induced fatigue task and the 100% MVC are more similar in terms of activating all muscle fibers, whereas the submaximal CCs recruit only a portion of the motor unit pool. In this study, muscular endurance training significantly increased postactivation potentiation capacity, which was apparent in the greater maximal potentiation produced by each CC intensity and during performance of the fatigue tasks.

Potentiation results obtained in the AdP muscle may not generalize to all muscles. The AdP muscle provides a unique model of motor unit recruitment and is crucial for grasping tasks. Future study is needed to examine potentiation responses of larger muscles of the lower and upper extremities and of different fiber type composition. In human muscle, it is not clear whether potentiation magnitude is based on fiber type.[46,57] It is likely, however, that muscles with greater mass and greater fast-twitch fiber composition undergo greater potentiation and reach maximal potentiation with a different CC duration than the AdP muscle, and they may also respond differently to muscular endurance training.

In conclusion, we have demonstrated that muscular endurance training resulted in increased maximal potentiation after submaximal and maximal voluntary CCs. Potentiation was also greater during performance of a 25% MVC fatigue task after training, and the change in endurance time correlated with the change in twitch force potentiation. Our findings suggest that potentiation may serve as a mechanism that contributes to muscular endurance. We also found that the amount of potentiation increased as contraction intensity increased, that the contraction duration required to achieve maximal potentiation was longer for lower than for higher intensity contractions, and that potentiation occurred after submaximal contractions as low as 25% MVC.

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