Muscular and Neural Contributions to Postactivation Potentiation

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Abstract

Wallace, BJ, Shapiro, R, Wallace, KL, Abel, MG, and Symons, TB. Muscular and neural contributions to postactivation potentiation. *J Strength Cond Res* 33(3): 615–625, 2019—This study's purpose was to explain the relationship between muscle factors (twitch potentiation [TP]) and neural factors (reflex potentiation) contributing to total postactivation potentiation (PAP) that couples these. The tibial nerve of 15 participants were stimulated intermittently for 20 minutes at supramaximal (Mmax) and submaximal (Hmax) intensities on separate days under 2 conditions: (a) rest (Control) and (b) after a 10-second plantarflexion maximum voluntary isometric contraction (MVIC). Isometric twitch torque and rate of force development (RFD) as well as soleus and gastrocnemius electromyographic values were analyzed. Torque and RFD TP were significantly greater 10 and 30 seconds after MVIC vs. Control. Postactivation potentiation of torque and RFD at Hmax were highest at 3 and 4.5 minutes after MVIC, respectively, with RFD significantly elevated. Electromyographic values were not different between conditions. Twitch potentiation significantly contributed to PAP at the following time points: 20 seconds, Hmax peak, and 20 minutes after MVIC (torque: $R^2 = 0.54$, 0.76, and 0.70; RFD: $R^2 = 0.46$, 0.59, and 0.53). The soleus significantly contributed to PAP torque at 20 seconds and 20 minutes after MVIC, and to PAP RFD at 20 seconds, 4.5 minutes, and 20 minutes (torque: $R^2 = 0.26$ and 0.34, $p \leq 0.05$; RFD: $R^2 = 0.65$, 0.52, and 0.41). The gastrocnemius did not significantly contribute to PAP. Both muscle and neural factors play a significant role in PAP, and neural factors may play a more prominent role in RFD potentiation than torque potentiation.

Key Words twitch potentiation, reflex potentiation, H-reflex

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Introduction

The contractile performance of skeletal muscle may be either reduced or enhanced based on its recent contractile history. Some contractions may result in muscle force, rate of force development (RFD), or both being increased in subsequent contractions through postactivation potentiation (PAP) (35). A conditioning activity, usually taking the form of a maximum voluntary isometric contraction (MVIC) or other maximal volitional exercise, is required. Studies have reported that short-duration activities (i.e., MVIC ≤10 seconds) elicit PAP, whereas long-duration (i.e., MVIC ≥60 seconds) activities elicit both PAP and fatigue (40,41). The coupling of PAP and fatigue determines the net muscle force response (38).

Central and peripheral mechanisms are responsible for muscle behavior during volitional movement (15,19). Postactivation potentiation has most often been measured as twitch potentiation (TP), defined as the force characteristics produced in response to a single muscle stimulation after a conditioning activity (13,39). However, this is a consequence of actin-myosin cross-bridge kinetics due to myosin light chain phosphorylation and possibly increased stimulus efficacy, and fails to account for the influence of the nervous system in muscle recruitment during volitional effort (17,23). The Hoffmann reflex (H-reflex) is the electromyographic (EMG) signal in response to a stimulus that elicits an H-wave. The electrical muscle response to a stimulation intensity that elicits the largest magnitude H-wave (Hmax) is widely recognized as an index of measuring peripheral nervous system motor neuron pool excitability (44). Typically, the H-wave is reported as a ratio of the EMG response to an electrical stimulation of the α-motoneuron to produce a muscle contraction (M-wave). An increase in the Hmax-to-Mmax ratio (Hmax/Mmax) after a conditioning activity has been termed reflex potentiation (RP) (11,37). A larger ratio can be attributed to more or larger motor units, or both, being recruited (15,44). Methods of recruiting more motor units may be important in performance training. Complex training, executed by performing a "complex pair" of a resistance exercise followed by plyometrics several minutes later, has been used to help achieve preferential acute and chronic

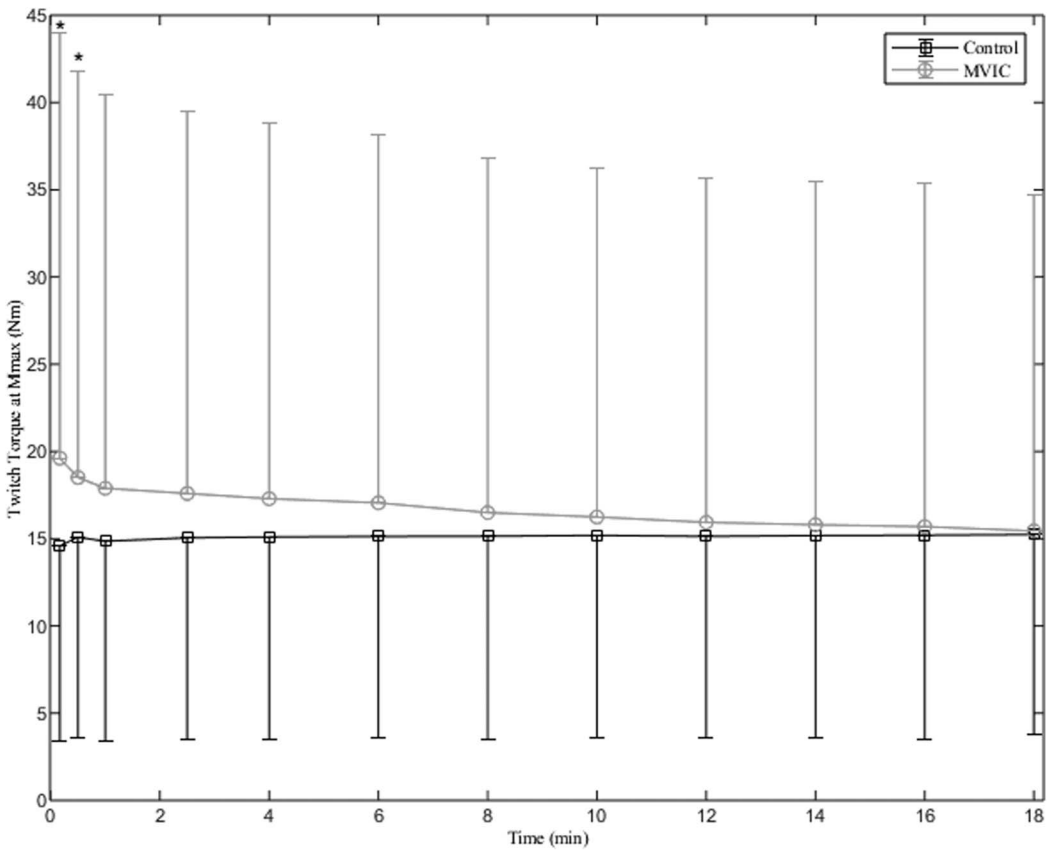

Figure 1. Isometric twitch torque at Mmax stimulations vs. time. Mean ± *SD*. *Significant difference between conditions, $p \leq 0.05$. MVIC = maximum voluntary isometric contraction.

physiological adaptations through eliciting greater force, RFD, or both, than if both exercises were not coupled (7,9). However, the PAP response is highly variable between individuals based on the amount of time since the activity and a variety of individual factors (e.g., maximum strength, training status, muscle architecture, etc.) (4,8), and also seems to be specific to velocity-related attributes rather than strength-related attributes (7,24).

Enoka et al. (10) first reported that a reduction in H-wave amplitude (postactivation depression [PAD]) occurs after muscle contractions. Three studies have investigated the time course of H-wave amplitude after a conditioning activity, each reporting PAD followed by RP 3-plus minutes after the conditioning activity (11,15,37). In contrast to TP which is highest immediately after the conditioning activity (40) and quickly subsides due to myosin regulatory light chain dephosphorylation (20), the timing of the neural response better relates temporally to when PAP has been reported with volitional movements (43). This indicates that neural factors may play an important role in force and RFD production during volitional muscle activation designed to induce PAP. Torque and RFD responses to a twitch at Hmax intensity have been previously described as a method of measuring the coupled muscle and neural influences to PAP (11). No previous studies have investigated the relative contributions of muscle and neural factors responsible for PAP in the triceps surae nor RFD in any muscle. Therefore, the purpose of this study was to test the contribution of muscle and neural factors to PAP in the triceps surae muscles. We hypothesized that: (a) both TP and RP would significantly contribute to PAP, and (b) the gastrocnemius would contribute more than the soleus.

Methods

Experimental Approach to the Problem

A repeated-measures design was used. Participants performed 2 testing sessions separated by at least 96 hours: Control and MVIC (experimental). On the Control day, the force and EMG responses to stimulations at supramaximal (i.e., 120% of the stimulation intensity determined to result in Mmax) and submaximal (i.e., Hmax) intensities were recorded at select time points over a 20-minute period to

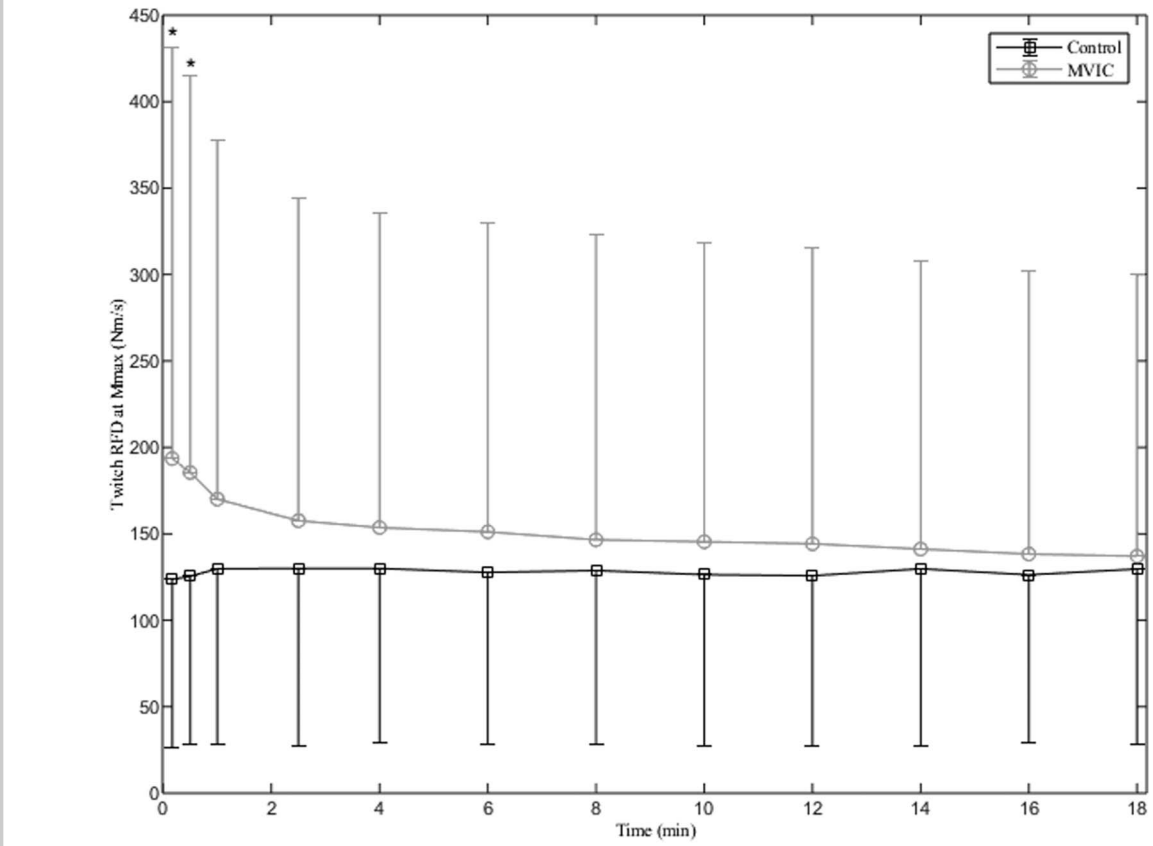

Figure 2. Isometric twitch RFD at Mmax stimulations vs. time. Mean ± *SD*. *Significant difference between conditions, $p \leq 0.05$. MVIC = maximum voluntary isometric contraction; RFD = rate of force development.

establish a baseline. The MVIC condition was similar, except it examined the muscle responses after a 10-second plantarflexion MVIC. Testing was conducted at approximately the same time of day in a quiet laboratory.

Subjects

Eleven men (mean ± *SD*: age 24.2 ± 2.9 years, range 21-29 years, height 182.2 ± 9.3 cm, body mass 94.2 ± 14.3 kg) and 4 women (age 28.0 ± 4.1 years, range 24-32 years, height 164.5 ± 13.0 cm, body mass 61.2 ± 12.6 kg) participated, excluding 3 participants who did not complete the study and whose data were not analyzed. Height, mass, and age variability presented as standard deviation. A minimum of 14 participants were required as determined by an a priori power analysis. All participants were healthy resistance-trained volunteers between 18 and 35 years of age, and were engaged in a whole-body resistance training program at least 3 times weekly for at least the previous 1 year. Men verbally asserted that they could maximally back squat a weight ≥1.5 times their bodyweight, and women ≥1.0 times their bodyweight (42). Participants were excluded if they had any history of neurological disorder or major lower-extremity neuromuscular injury as determined by a health history questionnaire and Par-Q. Participants were asked to refrain from strenuous exercise and avoid alcohol and caffeine consumption for at least 24 hours before testing. Institutional review board (IRB) approval was obtained for this investigation at the University of Kentucky. Participants provided written informed consent on an IRB approved form before taking part in any study procedures.

Procedures

On both testing days, the stimulating and EMG electrodes were applied before participants were being positioned on the Biodex dynamometer. Once positioned, they sat passively for 20 minutes to remove any lingering potentiation (22). Several single stimulations of the tibial nerve were evoked at progressively greater intensities to acclimate participants (10,22). Thereafter, Hmax and Mmax stimulus response curves were determined by a series of single electrical stimuli of increasing intensity to the tibial nerve. Stimuli were delivered from 2 to 60 mA in 2 mA increments, temporally separated by 10 seconds. Immediately thereafter, the principal investigator manually identified Mmax and Hmax intensities from the data recordings. Five minutes

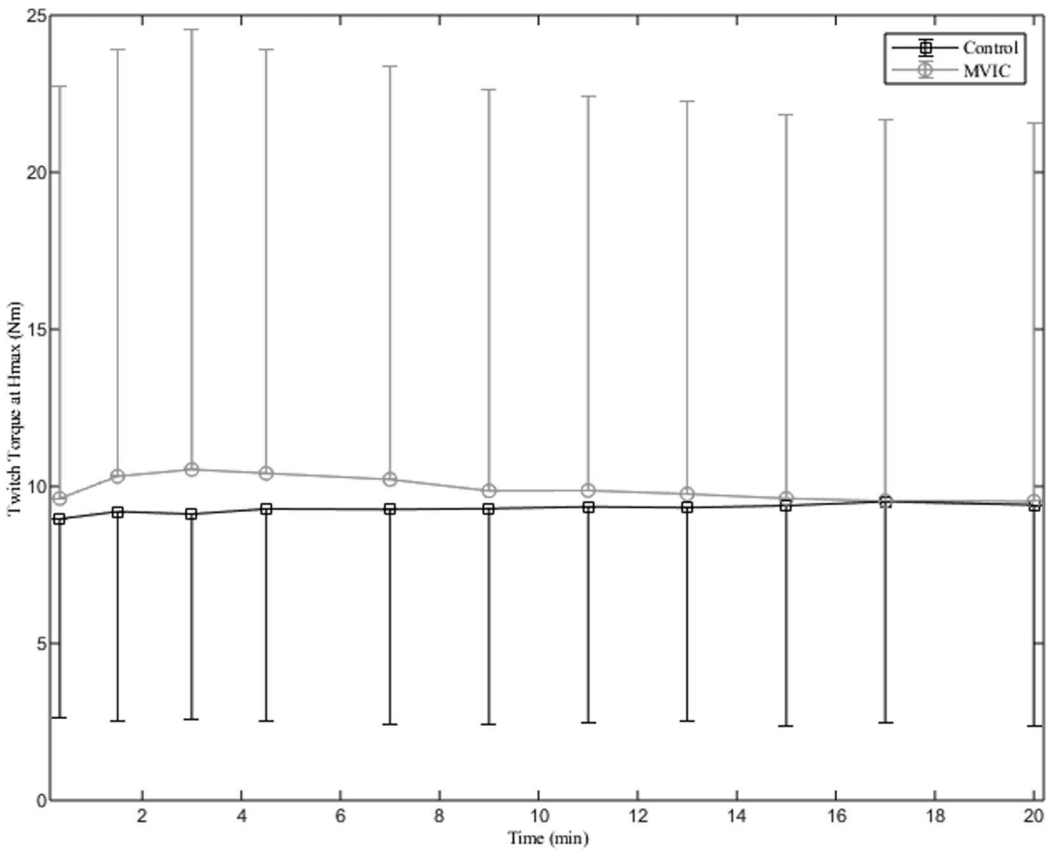

Figure 3. Isometric twitch torque at Hmax stimulations vs. time. Mean ± *SD*. No significant differences. MVIC = maximum voluntary isometric contraction.

thereafter, the 5 intensities in the region of Hmax were repeated to verify the previous maximum value (11). In the rare instances where the stimulation intensity required to elicit Hmax was not consistent, the higher intensity was used for that session's subsequent procedures. This difference did not exceed one increment (2 mA) for any subject.

During the Control condition, EMG and torque values for stimulations at Mmax and Hmax were established 10 minutes after Hmax and Mmax were determined (3). Mmax stimuli were elicited at: 10 and 30 seconds, and 1, 2.5, 4, 6, 8, 10, 12, 14, 16, and 18 minutes, and Hmax twitches at: 20 seconds, 1.5, 3, 4.5, 7, 9, 11, 13, 15, 17, and 20 minutes. Five minutes after baseline values were established, subjects performed 3–5 10-second familiarization MVICs, separated by 1 minute.

During the MVIC condition, participants rested passively on the Biodex dynamometer for 20 minutes, after which Hmax and Mmax were determined as described below. Five minutes thereafter, participants performed a 10-second max onset MVIC. Immediately after the MVIC, stimulations at Hmax and Mmax intensities were evoked, and the corresponding EMG and torque values were recorded, as described for the Control condition.

Experimental Setup. Participants were positioned on a Biodex Quick-Set System 4 isokinetic dynamometer (Rev. 1; Biodex Medical Systems, Shirley, NY, USA) for testing. The dominant leg, described as the preferred one used to kick a ball, of each participant was used. All participants were right-leg dominant. The dynamometer's isometric mode measured torque produced from MVICs and electrical stimulations. Participants were positioned in the dynamometer to a relative anterior hip flexion angle of 100°, relative posterior knee flexion angle of 120°, and relative ankle angle of 90° (2,17,18,27,30,32–34). The lateral malleolus was aligned with the dynamometer's armature axis of rotation. Two straps secured the foot to the foot plate, which was wrapped using a heel-lock technique to prevent the heel from coming off of the foot plate during isometric plantarflexions (Ank-L Wrap; Cramer Products, Inc., Gardner, KS, USA). The Biodex settings associated with subject positioning were recorded to ensure consistency between testing days. Participants were instructed to keep their lower-extremity musculature relaxed during testing, except while performing the MVIC.

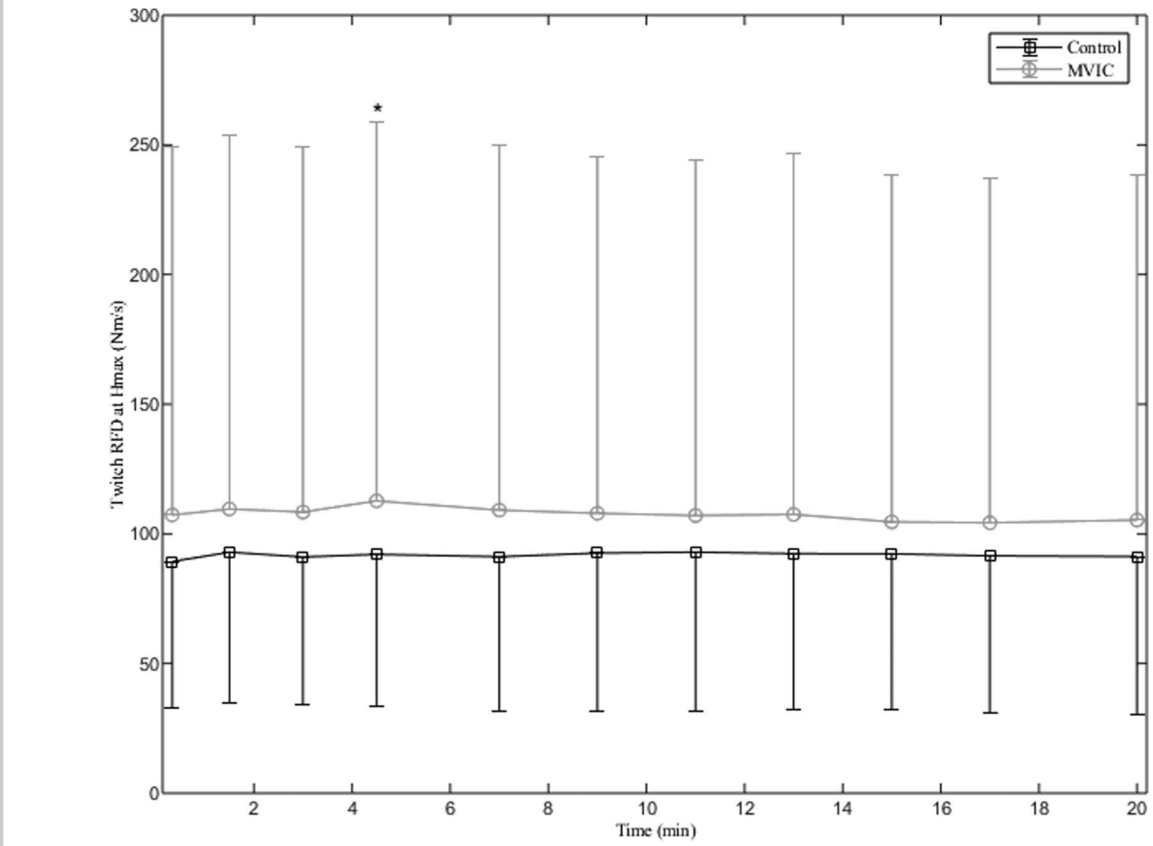

Figure 4. Isometric twitch RFD at Hmax stimulations vs. time. Mean ± *SD*. *Significant difference between conditions, $p \leq 0.05$. MVIC = maximum voluntary isometric contraction; RFD = rate of force development.

Stimulation and Electromyogram Recording. To reduce impedance, the skin was shaved, abraded with a gauze pad, and cleaned with isopropyl alcohol before the stimulating or EMG electrodes were placed on the skin. The lateral gastrocnemius and soleus were evoked by surface stimulation of the tibial nerve delivered by square-wave impulses through a constant current stimulator (DS7AH; Digitimer Ltd., Welwyn Garden City, United Kingdom) using 2 custom-sized 2 × 3 cm reusable rubber electrodes. The cathode (positive lead) was placed on the skin over the tibial nerve in the popliteal fossa as determined by palpation, whereas the anode (negative lead) was placed over the midportion of the thigh approximately 2 cm proximal to the superior border of the patella (17,27). Conductor gel was placed on the stimulating electrodes before them being placed and taped on the skin using surgical tape. Pulse durations were 1 ms for all stimulations (22). All stimulations were controlled using custom-written Matlab code (Mathworks, Inc., Natick, MA, USA).

A Delsys Bagnoli-8 EMG system (Delsys, Inc., Boston, MA, USA) was used to record EMG signals. Model DE-2.1 single differential surface electrodes (Delsys, Inc.) with a bipolar configuration recorded action potentials. The Ag electrode sensors on the electrodes were 1 mm wide with an intersensor distance of 1 cm. The electrode housing was internally shielded and contained a preamplifier. The EMG electrodes were placed over the longitudinal axis of the soleus muscle belly approximately 4 cm below the inferior margin of the gastrocnemius (22), and over the muscle belly of the lateral gastrocnemius at 1/3 the distance from the fibular head to the calcaneus (37). The ground electrode was placed on the ipsilateral patella. Stimulating and EMG electrode placements were marked with a marker to ensure consistency for both testing sessions. Electromyographic signals were amplified (×1,000) and band-pass filtered (20–450 Hz).

Data Measurements and Analysis. Torque values were recorded from the analog output of the dynamometer. Analog torque and EMG data were collected through a 16-bit AD board (model USB-2659 BNC; National Instruments, Austin, TX, USA) connected to a personal computer. Data were sampled at 4 kHz using commercial software (EMGWorks, version 4.0; Delsys, Inc.). Torque and EMG responses to all

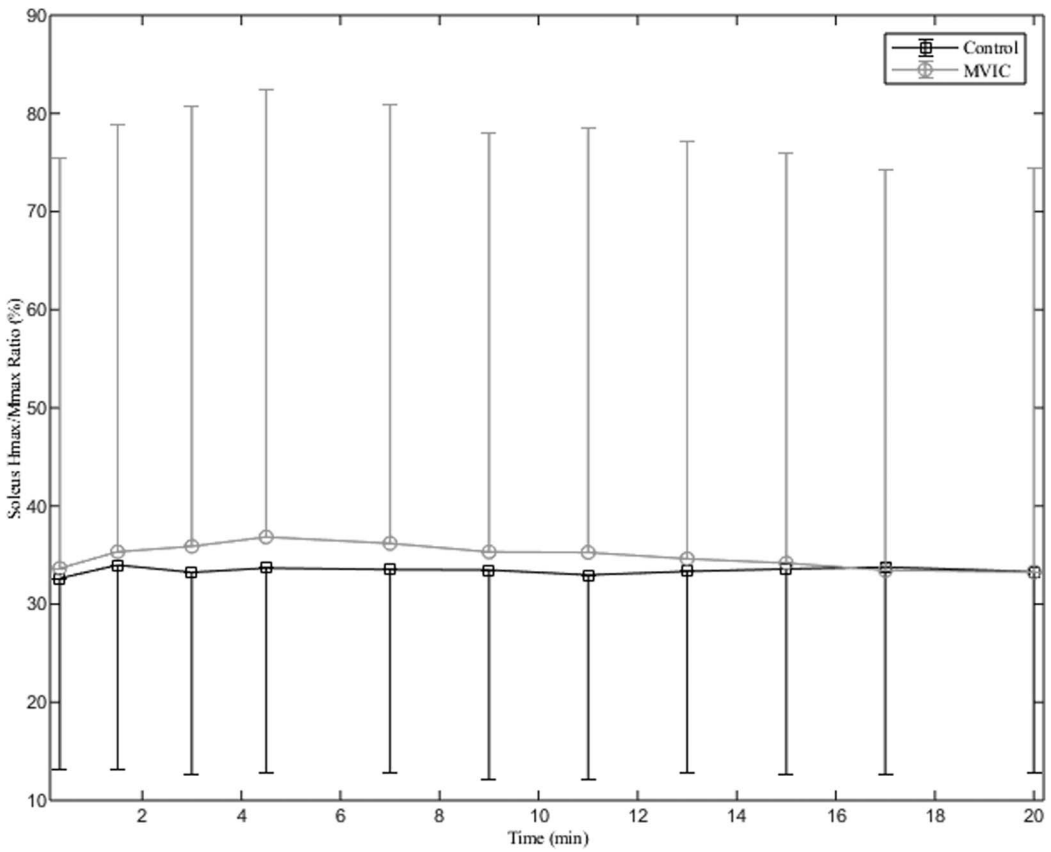

Figure 5. Soleus Hmax/Mmax ratio vs. time. Mean ± *SD*. Electromyography was measured as peak-to-peak amplitude. No significant differences. MVIC = maximum voluntary isometric contraction.

stimulations were recorded. Peak twitch torque, average RFD, and peak-to-peak EMG of the gastrocnemius and soleus were calculated. Average RFD for each twitch response was calculated using time and force values from between when the signal crossed 20% of the difference between the start and peak of the signal, and the peak force of each response. To attenuate signal noise, torque data were filtered using a low-pass fourth-order zero-lag Butterworth filter, with a cutoff frequency of 24 Hz as determined by a residual analysis. Data were analyzed and compiled using standard functions and custom-written code (EMGWorks, version 4.0; Delsys, Inc.; Excel 2013; Microsoft Corporation, Redmond, WA, USA; Matlab, version R2012b; Mathworks, Inc.).

Statistical Analyses

Data are reported as mean ± *SD*. The Hmax and Mmax EMG amplitudes from stimulations at Hmax intensity were normalized to the temporally nearest Mmax EMG value to determine Hmax/Mmax ratios. In situations where Hmax was elicited at the temporal midpoint between 2 Mmax stimulations, Hmax was normalized to the preceding Mmax stimulation. Two-way repeated-measures analyses of variance (condition × time) were performed to determine significant differences between the MVIC and Control conditions. Specifically, torque, RFD, and EMG values in response to stimulations at Mmax were analyzed at 12 time points between 10 seconds and 18 minutes. Torque and RFD values for stimulations at Hmax were analyzed at 11 time points between 20 seconds and 20 minutes.

Linear regression analyses were performed on the MVIC condition to calculate coefficients of determination (e.g., R^2 values) and the significance of the regression coefficients at select time points corresponding with when Hmax torque and RFD were greatest. The variance of PAP (e.g., Hmax torque and RFD) accounted for by TP and RP was computed for: Hmax torque vs. Mmax torque, and Hmax torque vs. Hmax/Mmax ratios for the gastrocnemius and soleus; and for Hmax RFD vs. Mmax RFD, and Hmax RFD vs. Hmax/Mmax ratios for the gastrocnemius and soleus. Because Hmax and Mmax stimulations were elicited at different time points, Hmax comparisons with Mmax were made using the temporally closest time point. All statistical analyses were performed using the Statistical Package for the

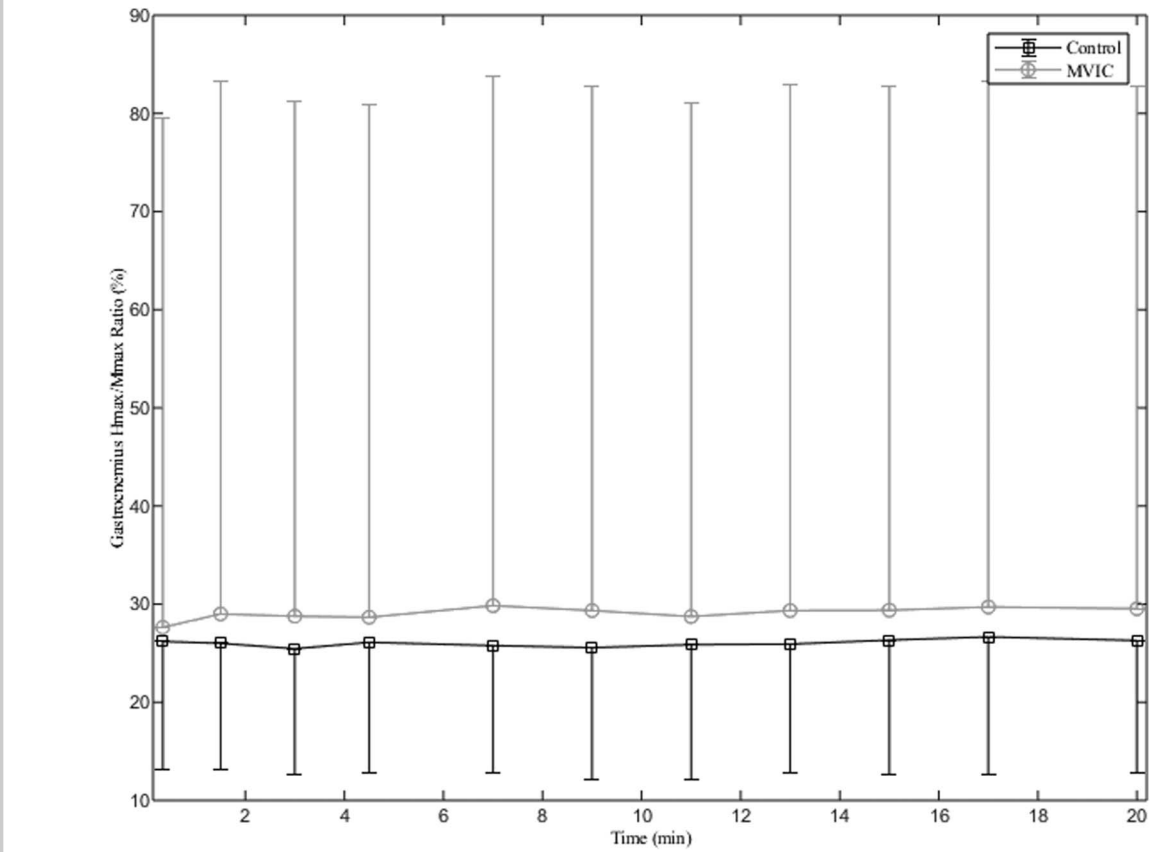

Figure 6. Gastrocnemius Hmax/Mmax ratio vs. time. Mean ± *SD*. Electromyography was measured as peak-to-peak amplitude. No significant differences. MVIC = maximum voluntary isometric contraction.

Social Sciences (SPSS, version 22; IBM Corporation, Armonk, NY, USA). The level of significance was set a priori at $\alpha\ p \leq 0.05$.

Results

Twitch and Reflex Responses

There was a significant interaction (condition × time) effect for TP (i.e., the Mmax stimulations) for torque and RFD ($p < 0.001$). The experimental condition showed significant TP vs. the Control condition for both torque (Figure 1; $p < 0.001$, $p = 0.027$ at 10 and 30 seconds after MVIC) and RFD (Figure 2, $p < 0.001$, $p = 0.007$ at 10 and 30 seconds after MVIC). There were no significant differences in either torque or RFD TP responses between the Control and MVIC conditions from the 30-second post-MVIC time point to the 18-minute time point.

Temporally, torque at Hmax was highest at 3 minutes after MVIC (Figure 3) and Hmax RFD was highest at 4.5 minutes (Figure 4). There were no significant differences between conditions for Hmax torque throughout the 20-minute measurement period ($p > 0.05$). Rate of force development at Hmax was significantly greater in the MVIC condition than the Control condition at 4.5 minutes after MVIC ($p = 0.03$).

Reflex potentiation was not observed in this study (Figures 5 and 6). There were no statistically significant differences in the Hmax/Mmax ratio for the gastrocnemius or soleus between conditions at any of the time points analyzed ($p > 0.05$).

Coefficients of Determination

Coefficients of determination that were calculated for the 2 measures of PAP (torque and RFD at Hmax) at initial (20 seconds), Hmax peak (3 minutes for torque and 4.5 minutes for RFD), and end time points (20 minutes) after MVIC are shown in Table 1. Mmax torque and RFD significantly contributed to Hmax torque and RFD at all time points analyzed (torque: $R^2 = 0.54$, 0.76, and 0.70 at 20 seconds, 3 minutes, and 20 minutes, $p \leq 0.05$; RFD: $R^2 = 0.46$, 0.59, and 0.53 at 20 seconds, 4.5 minutes, and 20 minutes, $p \leq 0.05$). The soleus' EMG ratio significantly contributed to Hmax torque variance at 20 seconds and 20 minutes after MVIC ($R^2 = 0.26$ and 0.34, $p \leq 0.05$). It also significantly

Table 1. Coefficients of determination for EMG Hmax/Mmax ratio, and Mmax torque and RFD, contributions to Hmax torque and Hmax RFD at initial, Hmax peak, and end time points in MVIC condition.*†

	Hmax torque		
	20 s	3 min	20 min
Gastrocnemius	5.8E-05	3.00E-04	0.02
Soleus	0.26‡	0.22	0.34‡
Mmax	0.54‡	0.76‡	0.70‡
	Hmax RFD		
	20 s	4.5 min	20 min
Gastrocnemius	3.00E-03	0.02	0.07
Soleus	0.65‡	0.52‡	0.41‡
Mmax	0.46‡	0.59‡	0.53‡

*EMG = electromyography; RFD = rate of force development; MVIC = maximum voluntary isometric contraction.

†Values reported as R^2. Comparisons with Mmax were made using temporally closest time point.

‡Denotes significance ($p \leq 0.05$).

contributed to Hmax RFD at 20-second, 4.5-minute, and 20-minute time points ($R^2 = 0.65, 0.52, 0.41, p \leq 0.05$). The gastrocnemius EMG did not significantly contribute to the variation in Hmax torque or RFD at any time point.

Discussion

Our most novel findings are the contributions of the muscle and reflex mechanisms to peak torque and average RFD in response to stimulations at Hmax, and the timing of these contributions. Muscle mechanisms (TP) significantly accounted for between 54 and 76% of the variance in Hmax torque, increasing between the first and last time points. Neural mechanisms (RP) accounted for 22–34% of the variance in Hmax torque in the soleus. It has previously been inferred that torque PAP is closely related to TP soon after an MVIC, and closely related to RP starting approximately 3 minutes after (11). In our study, TP accounted for approximately 50% of the variance in Hmax RFD throughout the 20 minutes of post-MVIC testing. This was a smaller portion than with torque, especially as more time elapsed after the MVIC. Supramaximal stimulation muscle responses have been shown to be related to volitional performance in both the quadriceps (27) and plantarflexors (28) for up to 4 minutes after a conditioning activity, suggesting inferences of volitional performance may be made from supramaximal stimulation muscle responses during this period. In addition, H-reflex amplitude has been reported to be closely related to force for up to 11 minutes after MVICs (15). Therefore, it was unexpected that the contribution of RP to PAP and relative values of RP either did not increase or only marginally increased as time progressed after MVIC. Possible reasons for the discrepancy between the aforementioned and present investigations are the nature of the conditioning activities and muscles assessed.

Our results suggest that neural factors play a more prominent role with RFD production than with torque production, particularly soon after a conditioning activity. The soleus' mean Hmax/Mmax R^2 value relative to Hmax RFD declined consistently from 0.65 to 0.41 between the 20-second and 20-minute time points. These values are considerably higher than those for Hmax torque, where muscle factors were more responsible. There may be 2 contributing causes responsible for this finding. First, conditioning activities result in phosphorylation of the myosin light chains (29), which has been shown to increase calcium sensitivity (26) by moving the myosin head closer to the thin filament (31,36). Increased calcium sensitivity would lead to a greater Hmax/Mmax ratio due to a greater number of myosin-actin attachments. However, although proximity increases the probability of attachment, it does not increase the rate of attachment. Thus, the second factor is likely related to the acute reflexive contribution to neural drive (19). A clearer understanding of the mechanisms responsible for these findings requires further research.

Alterations in twitch torque at Hmax intensity did not reach statistical significance in the experimental condition compared with Control, being enhanced by approximately 7% at 20 seconds after MVIC. Two previous studies reported conflicting results in this area. Gullich and Schmidtbleicher (15) tested subjects for dynamic voluntary isometric force of the plantarflexors after MVICs. They reported that voluntary force was significantly depressed by approximately 12% for the first 2 minutes of recovery before being potentiated starting at 4 minutes. A more recent study measured torque at Hmax, similar to the methods used in the present investigation (11). The authors reported similar results as our study, although the percent change in their study reached up to approximately 20%. This difference may be due to the fact that we tested the plantarflexors vs. their testing of the quadriceps. The dissimilar results of these 3 studies may be due to the conditioning activities used. Although we and Folland et al. (11) used a 10-second MVIC, Gullich and Schmidtbleicher (15) used five, 5-second MVICs. The 25 seconds of MVICs could have elicited peripheral fatigue that the 10-second MVICs did not. However, peak twitch torque after 10- and 30-second plantarflexion MVICs has been reported to be similar (40), suggesting similar peripheral conditions. It may be that PAD was elicited as a result of the longer conditioning activity. This is substantiated by the authors reporting that H-wave amplitude was depressed by approximately 20% during the period where reduced voluntary plantarflexion force was observed (15).

Our study was the first to investigate RFD in response to stimulations at Hmax as a measure of PAP. The increase in RFD at Hmax reached statistical significance at its peak value, which occurred 4.5 minutes after MVIC. Previous studies have reported equivocal results for potentiation of RFD after a conditioning activity. In mammalian models, RFD is increased in response to a supramaximal stimulation (39) and tetanic stimulation (1). In humans, voluntary knee extension velocity was not increased after a 10-second MVIC (13). An increase in velocity would have been indicative of an enhanced RFD. However, increased velocity has been shown in the mouse extensor digitorum longus (14). In addition, Baudry and Duchateau (3) reported increased RFD in thumb adductors during maximum-effort contractions for the 5 minutes after a 6-second MVIC. The conflicting results during knee extension (13) vs. the aforementioned investigations could be due to the low velocity associated with maximum-effort contractions of the quadriceps because the relative effect of PAP is more pronounced at lower stimulation frequencies (3). These results, combined with the results of our investigation, suggest that RFD may be enhanced during high-velocity movements 4 to 5 minutes after a conditioning activity.

Twitch torque and RFD at Mmax were both significantly higher in the experimental condition vs. Control immediately after the MVIC. Twitch torque potentiation of approximately 38–50% in the plantarflexors has been reported previously (16). This corresponds with the results of this study. In the quadriceps, twitch torque potentiation after a conditioning activity has been shown to vary between 10.7% (27) and 66.6% (11,13). Not surprisingly, the 10-second MVIC used in this study showed significant TP of approximately 60% immediately after the conditioning activity. By 18 minutes after MVIC, both torque and RFD returned to near baseline. One study reported twitch torque potentiation to last for up to 18 minutes after a conditioning activity (11), whereas others have taken measurements for only up to 10 minutes (20,29). The mechanism for the increased torque and RFD at Mmax are both likely myosin light chain phosphorylation, mentioned previously (3,35). The number of cross-bridge attachments at a given calcium concentration increases because the probability of myosin attaching to actin increases as their separation distance decreases (25). More cross-bridges would result in both more force and force being produced more quickly, enhancing both twitch torque and RFD.

The gastrocnemius' contribution to Hmax torque or RFD was only significant at 4.5 minutes after MVIC for RFD. The gastrocnemius is composed of mostly type II fibers (21), which experience PAP to a greater degree than slow-twitch fibers (17). Like previous studies that used similar knee (10,15) and ankle (10,15,37) angles, we successfully elicited M- and H-waves in the gastrocnemius. The Hmax/Mmax ratios for the soleus and gastrocnemius were similar (Figures 5 and 6). However, as knee flexion increases from 180° (i.e., a straight-leg position) to 120°, the contribution of the gastrocnemius to isometric plantarflexion torque decreases (5). A recent investigation reported slightly, but significantly, higher-twitch torque and RFD in the medial gastrocnemius with an extended knee position vs. with a relative knee angle of 90° (12). It is possible that a greater contribution of the gastrocnemius to overall potentiation would have been observed if a more extended knee position was used, as was done in one other study (37).

Short-term depression of the H-reflex occurs in response to conditioning activities comprised of electrical stimulations (6). Other studies have found PAD in the triceps surae after volitional muscle contractions (10,15,37), followed by RP several minutes thereafter. Although in our study neural factors significantly contributed to the kinetic responses at Hmax, there were no significant differences between the experimental and Control conditions for either the gastrocnemius or soleus Hmax/Mmax ratios at any of the time points analyzed. This may largely explain why, generally, significance between conditions for measures of PAP was not found. Trimble and Harp (37) reported PAD of the soleus and gastrocnemius for the first several minutes after dynamic plantarflexions and dorsiflexions. However, they observed equivocal results regarding RP of the gastrocnemius and soleus, with some subjects showing RP in one muscle and not the other, starting at 3 minutes after the conditioning activity. Enoka et al. (10) also reported a lack of RP in the soleus after isometric plantarflexions. By contrast, other authors have reported that the soleus H-reflex is highly related to torque depression and subsequent potentiation after tetanic nerve stimulation (23) or volitional force (15) using lower-extremity joint angles similar to those used in this study. Because of the gastrocnemius' lack of contribution to overall PAP, shown in Table 1, any possible RP would be due to the soleus. As shown in Figure 5, RP of the soleus was not statistically significant. However, it was highest at 4.5 minutes after MVIC, helping to explain why we observed significant PAP for RFD at Hmax at this time point.

There are some limitations to the current investigation that should be noted. The most notable is the inherently high intersubject variability in these neurophysiological measures, which has also been shown in applied studies relating to PAP (4). The study design used was necessary to measure the dependent variables required to answer the research question, but the isometric nature of the recorded kinetic values in this study is dissimilar to the dynamic nature of volitional training movements. However, the timing and application of our findings relate to applied investigations that used volitional movements (43), and further help explain the neuromuscular factors responsible for the results of those other investigations. In addition, as mentioned previously, a more extended relative knee angle may have led to a better indication of the gastrocnemius' contribution to PAP in our study while also providing a knee

position more similar to what is experienced during the propulsive phase of in vivo dynamic movements such as jumping. Future studies should directly measure myosin light chain phosphorylation to gain a further understanding of the physiology involved with PAP as defined in this investigation and by Folland et al. (11). Finally, although our findings do relate to applied investigations, the relationship between the measures of isometric PAP and dynamic PAP requires further study (13).

Practical Applications

This study was the first to statistically quantify the effects of TP and RP on PAP in vivo. Both TP and RP were significantly related to torque and RFD PAP factors for the duration of testing. In addition, neural factors were more highly related to RFD potentiation than to torque potentiation, with the opposite being true for muscle factors. Considering the relationship found between RP and RFD, persons who would benefit from increasing or maintaining high amounts of RFD, such as athletes or the elderly, may benefit from exercise methodologies designed to increase neural drive. Exercise methods that use a conditioning activity, such as complex training, may be especially helpful in this regard.

For the practitioner, the timing of using PAP seems important. The net muscle response may be most important to practitioners looking to enhance performance. Force PAP was not statistically enhanced at any time point, but was highest 3 minutes after MVIC, whereas RFD PAP was statistically elevated at 4.5 minutes after MVIC. Therefore, the TP response may not be important because of reduced neural efficiency right after a conditioning activity negating the effect of increased calcium sensitivity in the muscle. The timing of PAP in our investigation matches closely with when PAP has been detected in the previously mentioned studies which measured it during volitional movement, including that suggested in a recent meta-analysis (8). Sustained use of complex training may induce RFD-related variables such as velocity during dynamic power-oriented tasks (7), but not strength tasks (24). However, the phenomenon is a highly individual response (4) that is dependent on timing and a number of individual's attributes (8).

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