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ORIGINAL ARTICLE

What are the stimulation parameters that affect the extent of twitch force potentiation in the adductor pollicis muscle?

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Abstract Muscle force potentiation affects force output during electrical stimulation. Few studies have examined stimulation train parameters that influence potentiation such as pulse number, stimulation frequency, train duration, and force–time integral and peak force produced during the train. Pulse-matched trains (100 pulses) at 7.5, 15, 25, 30, 50, and 100 Hz, and trains of varying pulse number (50, 100, and 200 pulses) at 30 and 50 Hz were delivered to the ulnar nerve of 10 (5 male, 5 female; 23.4 ± 0.9 years), healthy individuals in random order. Single twitches of the adductor pollicis muscle were elicited before and after each train with a rest interval of at least 5 min between each train. No differences in potentiation occurred across the pulse-matched trains at frequencies of 15–50 Hz (38.9 ± 5.4–44.6 ± 5.5%). Twitch force potentiation following the highest (100 Hz) and lowest (7.5 Hz) frequency trains were not significantly different and were lower than the other 100 pulse-matched trains. As pulse number increased, potentiation increased for both the 30 and 50-Hz trains. There was a significant positive correlation between force potentiation and force–time integral produced by the stimulation train, $r = 0.70$. The results indicate that potentiation magnitude is dependent on the force–time integral produced during the test train and the number of pulses delivered, independent of stimulation frequency.

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Introduction

The skeletal muscle is affected by its contractile history, which can enhance or degrade muscular performance. Muscle force potentiation, also termed post-activation potentiation or post-tetanic potentiation, is defined as an enhancement in muscle twitch force following contractile activity (Brown and von Euler 1938; Krarup 1981). Twitch force potentiation occurs in response to phosphorylation of the regulatory myosin light chains (RLC), which strengthens and moves the myosin head closer to the actin filament (Borovikov and Levitsky 1989; Greenberg et al. 2009) and increases the rate of the cross-bridge cycle (Uyeda et al. 1996). The ability to potentiate the muscle is of particular importance to the use of electrical stimulation paradigms to control muscle force in individuals with neuromuscular impairment. Identifying the factors that influence potentiation will assist in the design of electrical stimulation programs geared to enhance force production by potentiating force and, thereby, may prolong muscular force output in these systems that are severely plagued by fatigue. However, there has been little investigation on how various stimulation parameters (frequency, pulse number, train duration, and the force–time integral (FTI) produced by the potentiating stimulation train) might affect muscle force potentiation, and there are discrepancies among the few studies that have been done.

Close and Hoh (1968) and Krarup (1981) found that with constant frequency electrical stimulation, increases in pulse number increased twitch force potentiation. Krarup (1981) did not compare potentiation across frequencies of

pulse-matched trains. Close and Hoh (1968) determined that potentiation was greater following low (20 Hz) compared to high (300 Hz) frequencies of stimulation when matched for pulse number. Conversely, Small and Stokes (1992) found that potentiation was greater with increases in stimulation frequency (5–50 Hz), but they did not control for pulse number during the test train. MacIntosh and Willis (2000) and Binder-Macleod et al. (2002) found that potentiation during repetitive train stimulation did not differ across frequencies when the trains were matched for pulse number. Binder-Macleod et al. (2002) also reported that although potentiation was not different following these pulse-matched trains, the trains produced different mean FTIs; however, the correlation between potentiation and FTI was not studied. During maximal voluntary contractions (MVC), twitch force potentiation increased with increases in MVC duration up to 30 s (Vandervoort et al. 1983). This indicates that the FTI, and/or the number of stimuli produced during the contraction, may have influenced the degree of potentiation. FTI of the stimulation train may be an important stimulation parameter to consider in the design of electrical stimulation programs that utilize potentiation to maximize total force production over time.

The purpose of the present study was to systematically determine how stimulation frequency, pulse number, and train duration influence muscular twitch force potentiation following trains with frequencies ranging from 7.5 to 100 Hz and train durations of 1–13.34 s. Post hoc analyses of the effect of FTI and peak force produced during the stimulation train on potentiation were also examined. We tested twitch force potentiation of the adductor pollicis (AdP) muscle following stimulation trains of equal pulse number at various frequencies (7.5, 15, 25, 30, 50, 100 Hz) and trains of 30 and 50 Hz with different pulse numbers (50, 100, 200). We hypothesized that: (1) twitch force potentiation would not be significantly different following trains of different frequencies when the total number of pulses delivered was constant; (2) increasing the total number of pulses delivered at a given frequency of stimulation would increase twitch force potentiation magnitude; and (3) the FTI produced during the test train would be correlated to the degree of potentiation.

Methods

Participants

Ten individuals (5 male, 5 female) of age 23.4 ± 0.9 years participated in this study. Study volunteers had no history of injury to the non-dominant hand and no neurological or metabolic disorders. Participants had no history of hand or thumb training. All attended an orientation session and signed an informed consent form prior to beginning the experiment. All procedures were approved by The University of Texas at Austin Internal Review Board and were in accordance with the Helsinki Declaration.

Experimental arrangement

Participants were seated with the non-dominant forearm supported in a splint. The wrist was placed in a supinated position and the thumb was abducted and positioned against a metal strain-gauge force transducer. A pair of pre-gelled, adhesive, Ag/AgCl disposable surface electromyography (EMG) electrodes (Danlee Products, Inc., Syracuse, NY, USA) were placed on the palmar surface of the hand, over the AdP muscle. A ground surface electrode was placed on the ulnar styloid process of the wrist. A surface stimulating electrode was secured with a strap over the ulnar nerve at the wrist. A graphic of the experimental arrangement is shown in Fig. 1.

First, the maximal M-wave amplitude was found by stimulating with single pulses (100 μs duration) and slowly increasing the stimulation current (Model DS7A; Digitimer Ltd, Garden City, England) until increasing the current did not increase peak-to-peak M-wave amplitude. Once the maximal M-wave amplitude was found, five single pulses were delivered. Pulse-matched stimulation trains of 100 pulses were then randomly administered at the following frequencies: 7.5, 15, 25, 30, 50, and 100 Hz (duration of 13.34, 6.67, 4, 3.33, 2, and 1 s, respectively). Four additional trains matched for frequency, but not pulse number, of 30 Hz [50 (1.67 s) and 200 (6.67 s) pulses] and 50 Hz [50 (1 s) and 200 (4 s) pulses] were also included in the random sequence. The test trains were pre-programmed to

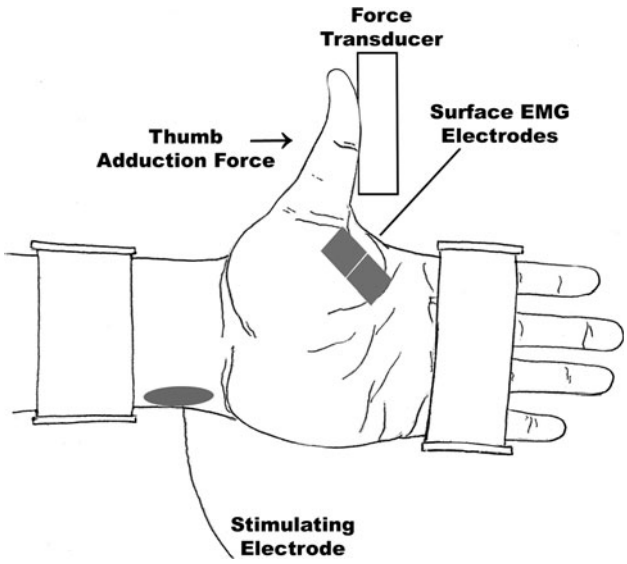

Fig. 1 Experimental arrangement

deliver the specified number of pulses at each test frequency. The train duration varied with the time required to deliver a specific number of pulses at a given frequency. To ensure reliability of the twitch force, five single pulses were delivered at 1 Hz before and approximately 1 s following each train. The coefficient of variation (CV) of the control twitches was calculated to test for variability of the twitch force. Mean CV for the control twitches was 0.025. The twitch forces from these pulses were used to determine potentiation. Two single pulses at 1 Hz were delivered at 10, 30 s, and 1, 3, 4, and 5 min after each train. If the twitches did not return to baseline within the 5-min rest interval, single twitches were evoked at approximately 30-s intervals until they returned to baseline. Figure 2 depicts the stimulation protocol.

Data analysis

Surface EMG was high pass filtered at 13 Hz, gain 100 (Coulbourn Instruments, Allentown, PA, USA), and digitized at 2,000 Hz (Micro 1401; Cambridge Electronics Design (CED), Cambridge, England). The force signal was high pass filtered at 13 Hz with a gain of 100 (Model 74030 Bridge 8 Amplifier System; World Precision Instruments, Sarasota, FL, USA) and digitized at a sampling rate of 1,000 Hz (Micro 1401; CED, Cambridge, England). All data were analyzed off-line using Spike2 for Windows (version 5.14; CED, Cambridge, England) software package.

Unpotentiated and potentiated twitch force were calculated as the mean of the five single maximal twitch forces evoked before and after the test train. Potentiation is expressed as the percent change in twitch force post-stimulation train compared to twitch force pre-stimulation train. The FTI was calculated during each stimulation train as the area under the force–time curve from the instant the force trace left the baseline until it returned to baseline. Fatigue during the stimulation train was calculated as the difference between the peak force during the stimulation train (which included any force potentiation that developed during the train) and the force when the last electrical pulse was elicited.

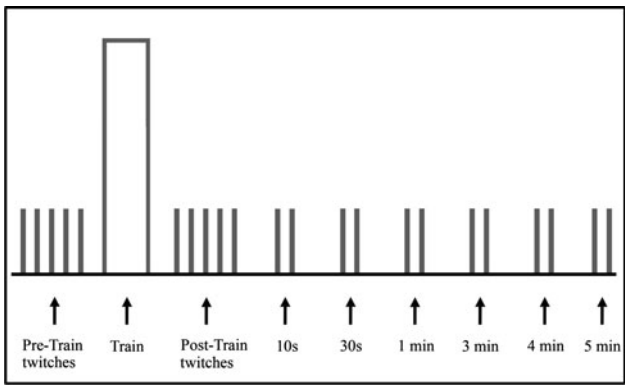

Fig. 2 Schematic representation of the experimental protocol

Statistical analysis

Twitch potentiation following all test stimulation trains, and peak force and fatigue during the stimulation train (peak force–end force) were compared using a one-way repeated measures ANOVA. A two-way repeated measures ANOVA was used to compare pre-train twitch force across all trains and to compare pre- to post-test train twitch forces. Bonferroni adjustments were 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 ANOVA tests. Potentiation during recovery did not meet the assumption of normality; therefore, potentiation across protocols was compared at each time of recovery with a Friedman's ANOVA test. Spearman's rho test was used to test the relationship between potentiation and force–time integral and potentiation and peak force during the stimulation trains. All data are presented as group mean ± standard error. An alpha level of $p \leq 0.05$ was accepted as the level of statistical significance.

Results

Trains matched for 100 pulses

Potentiation was significant following all test trains ($p < 0.001$). A representative force trace of one individual's data is shown in Fig. 3. No significant differences in potentiation were found among stimulation test trains matched for 100 pulses at the following frequencies: 15, 25, 30, and 50 Hz (for all pairwise comparisons, $p = 1.0$). The mean percent potentiation was 44.59 ± 5.47, 42.93 ± 4.72, 43.41 ± 5.16, and 38.90 ± 5.41% for these trains, respectively.

Percentages of changes in twitch force are shown in Fig. 4. Potentiation was significantly lower for the lowest and highest frequencies tested compared to most of the 100-pulse trains 7.5 Hz < 15 Hz ($p = 0.015$) and 30 Hz ($p = 0.040$), but not different than 25 Hz ($p = 0.059$) and 50 Hz ($p = 1.0$); 100 Hz < 15, 25, 30 and 50 Hz ($p < 0.001$), but were not significantly different from each other. Pre-test train twitch force was not different across trains, indicating that the twitch force returned to resting values prior to the initiation of each test train (1 s 100 Hz vs. 1 s 50 Hz, $p = 0.77$; all other pairwise comparisons, $p = 1.0$).

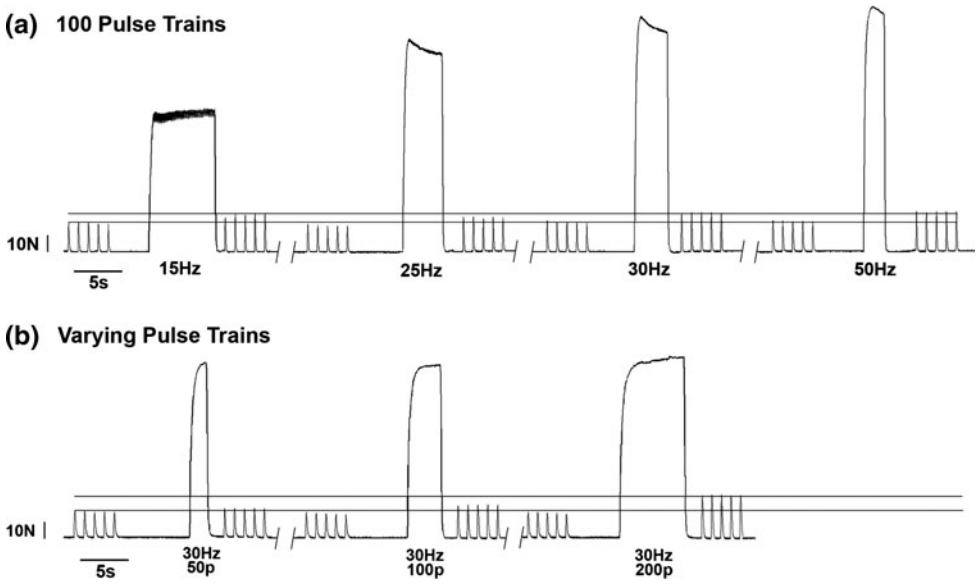

Fig. 3 **a** Force data from one participant demonstrating no difference in potentiation between stimulation trains matched for 100 pulses at 15, 25, 30, and 50 Hz. **b** Force data from one participant demonstrating increasing potentiation as train pulse number increases (50, 100, 200 pulses) with all trains at the same frequency of stimulation (30 Hz). All trains were delivered in random order for all subjects

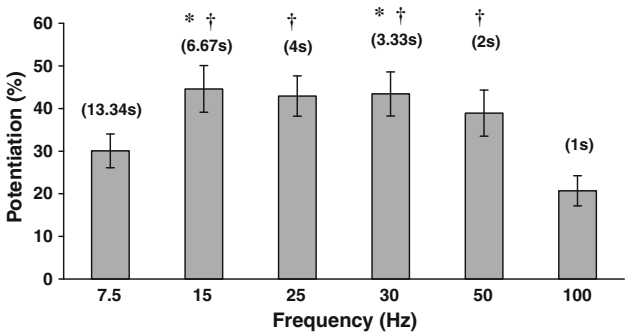

Fig. 4 Post-activation potentiation expressed as percent change in twitch force following stimulation trains matched for 100 pulses at various stimulation frequencies. *Significantly greater potentiation than 7.5-Hz train. †Significantly greater potentiation than 100-Hz train

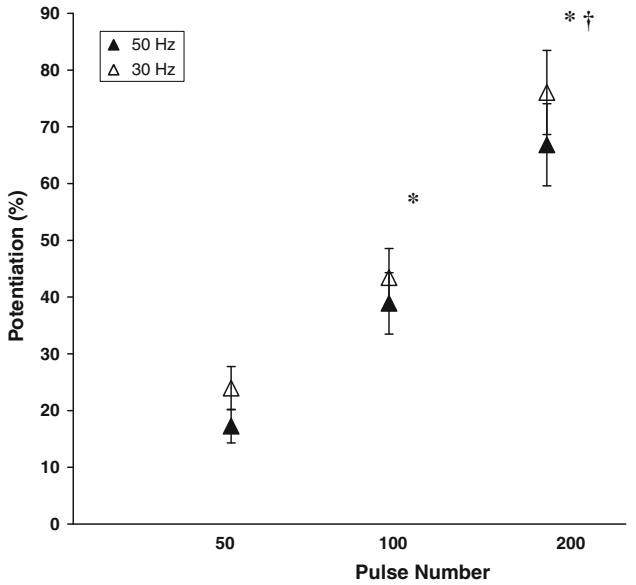

Fig. 5 Percentage of twitch force potentiation following stimulation trains of increasing pulse number at 30 and 50 Hz. *Significantly greater than at 50 pulses. †Significantly greater than at 100 pulses ($p < 0.001$)

Trains of increasing pulse number

Potentiation increased significantly when the stimulation frequency remained constant and the number of pulses of the stimulation train was increased. For the 30-Hz trains of varying pulse number, post hoc analysis showed significantly greater potentiation as pulse number increased (50, 100, and 200 pulses) ($p < 0.001$) (23.95 ± 3.80, 43.41 ± 5.16, and 76.06 ± 7.42%, respectively) (Fig. 5). At 50 Hz, post hoc analysis also revealed significantly greater potentiation as pulse number increased (50, 100, and 200 pulses) ($p < 0.001$) (17.25 ± 2.96, 38.90 ± 5.41, and 66.84 ± 7.23%, respectively) (Fig. 5). When pulse number remained constant (i.e., 50, 100, and 200 pulses), there were no significant differences in potentiation between stimulation frequencies of 30 or 50 Hz (Fig. 5).

Potentiation of trains matched for time duration, but not for stimulation frequency or pulse number (6.67 s: 15 Hz 100 pulses and 30 Hz 200 pulses; 4 s: 25 Hz 100 pulses and 50 Hz 200 pulses), resulted in significantly greater potentiation for trains of higher frequency and thus greater pulse number (Fig. 6).

Recovery twitches

There were significant differences in potentiation between test trains at each time of recovery ($p < 0.001$). Recovery twitches are displayed in Fig. 7. The decline in twitch force for all trains was greatest during the first 3 min of recovery and then remained relatively stable. At all times of recovery,

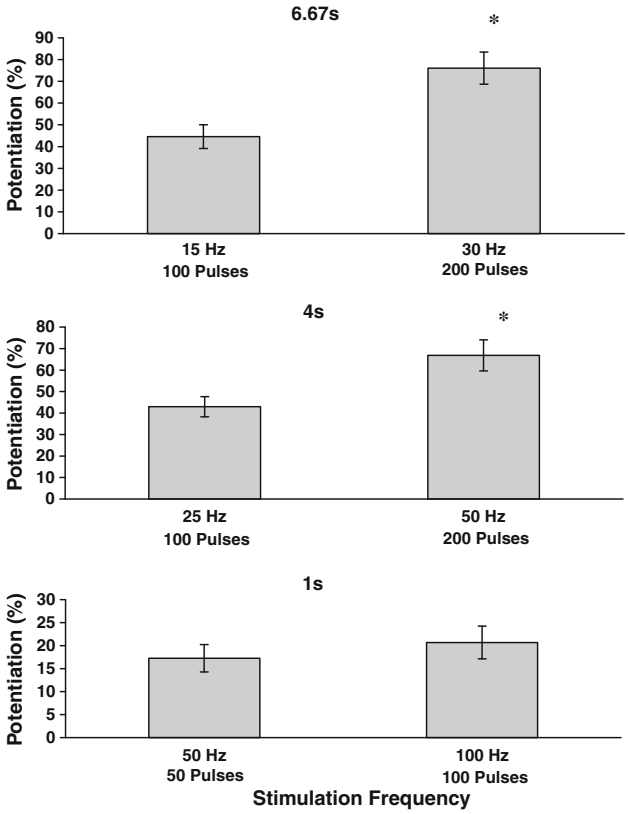

Fig. 6 Twitch force potentiation following time-matched trains with different number of pulses and various stimulation frequencies. *Significantly greater than the other train ($p < 0.001$)

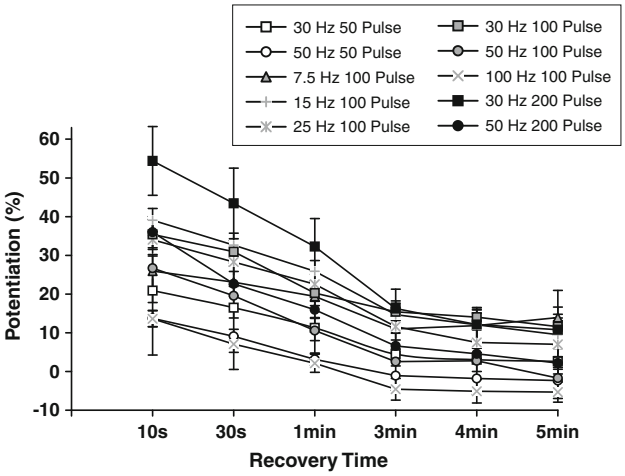

Fig. 7 Twitch force potentiation for all test trains during the recovery period

twitches were not significantly different between the 50-pulse trains or between the 200-pulse trains. For the 100-pulse trains, potentiation was significantly less for the 100-Hz train compared to the 15, 25 and 30-Hz trains at 10s, 30s and 1 min; <7.5 Hz at 1 and 4 min; less than 15 and 30 Hz at 3 and 4 min and <15 Hz at 5 min of recovery. There was no difference in potentiation across all other 100-pulse trains throughout the 5-min recovery period, except that 30 Hz was >50 Hz at 3 min. The 100-Hz, 100-pulse train generated the shortest time in the potentiated state and neared control value at 1 min of recovery. After 5 min of recovery, twitch force remained potentiated following the 30-Hz 50-pulse train, 7.5, 15, 25, and 30-Hz 100-pulse trains, and the 30 and 50-Hz 200-pulse trains (range 2.2–13.9%) (Fig. 7).

Force–time integral and potentiation

For all test trains, there was a significant positive correlation between the FTI produced during the stimulation train and twitch force potentiation, $r_s = 0.70$, ($p < 0.001$) (Fig. 8a). The FTI of the stimulation train and twitch force potentiation were also positively correlated for trains of 100 pulses, $r_s = 0.43$, ($p < 0.001$) (Fig. 8b). Table 1 displays the mean potentiation, FTI, and peak force for each train. No correlation was found between potentiation and peak force during the stimulation train, $r_s = 0.07$.

During the stimulation train, force decreased significantly from the peak force of the train to the force at the end of the trains in the following test trains: 50 pulse, 30 Hz ($p = 0.019$); 100 pulse, 25 Hz ($p = 0.002$), 30 Hz ($p = 0.004$), and 50 Hz ($p = 0.009$); 200 pulse, 30 Hz ($p = 0.003$) and 50 Hz ($p = 0.002$).

There was a significant difference in peak force produced during the stimulation train across the 100-pulse trains ($p < 0.001$). Pairwise comparisons showed that peak force increased significantly as stimulation frequency increased, except that there was no difference in peak force between 25 and 30 Hz ($p = 1.0$), 25 and 50 Hz ($p = 0.197$), 30 and 50 Hz ($p = 0.840$), and 50 and 100 Hz ($p = 1.0$) trains. The force–frequency curve for the 100-pulse trains is shown in Fig. 9.

M-wave amplitude

Pre- and post-train M-wave amplitudes were not different for stimulation trains across all protocols (8.43 ± 0.06 and 8.33 ± 0.05 mV, respectively, $p > 0.05$), indicating that the stimulating electrode position did not change.

Discussion

This study is the first to demonstrate that potentiation is correlated to the force–time integral produced during electrical stimulation. We also clearly show across frequencies ranging from 15 to 50 Hz that potentiation is dependent on pulse number and not stimulation frequency. The lowest (7.5 Hz) and highest (100 Hz) frequency trains tested

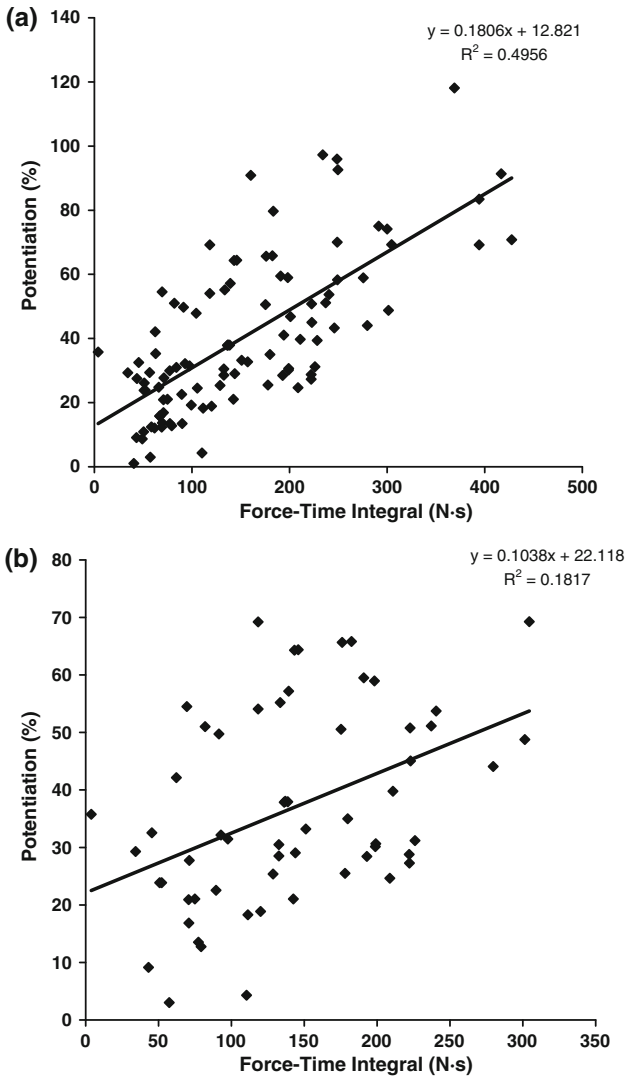

Fig. 8 **a** Twitch force potentiation is plotted against FTI for all the stimulation trains ($r_s = 0.70$). **b** Twitch force potentiation is plotted against FTI for all 100-pulse trains ($r_s = 0.43$)

produced less potentiation compared to most other pulse-matched trains. Twitch force potentiated following all test trains. Long rest periods were incorporated between each train and all twitch forces returned to baseline prior to each test train. Future work should investigate the relationship between potentiation and fatigue during prolonged repetitive stimulation.

Potentiation was observed following stimulation trains of all frequencies tested. Others have also shown potentiation across a similar range of frequencies (5–100 Hz) (Small and Stokes 1992; MacIntosh and Willis 2000; Binder-Macleod et al. 2002). Greater potentiation with greater pulse number independent of stimulation frequency indicates that the enzyme, Ca^{2+}/calmodulin-dependent RLC kinase, which phosphorylates the RLC, may be activated to a greater degree with a higher number of pulses and, therefore, RLC phosphorylation may also be pulse dependent. RLC phosphorylation, however, was not measured in the present study. By eliciting an equal number of pulses at each stimulation frequency, the Ca^{2+} released from the sarcoplasmic reticulum was likely equal for each train; and therefore, the amount of available Ca^{2+} for myosin light chain kinase activation and cross-bridge cycling would have been equal. This would explain the similar magnitudes of potentiation produced for stimulation frequencies ranging from 15 to 50 Hz following trains of equal pulse number.

Force–time integral and potentiation

Although intracellular calcium levels were not measured in the present study, the correlation between twitch force potentiation and the overall FTI of the test train for trains of matched pulse number indicates that prolonged exposure to intracellular calcium may affect potentiation independently

Table 1 Force–time integral during stimulation train and potentiation

Frequency (Hz)	Pulse number	Duration (s)	Peak force (N)	FTI (N s)	Potentiation (%)
30	50	1.67	54.5 ± 3.1	82.3 ± 5.3	24.0 ± 3.8
50	50	1.00	57.3 ± 3.2	55.0 ± 3.1	17.3 ± 3.0
7.5	100	13.34	12.3 ± 1.1	99.9 ± 18.7	30.1 ± 4.0
15	100	6.67	36.7 ± 2.9	222.2 ± 20.1	44.6 ± 5.5
25	100	4.00	51.6 ± 2.7	190.2 ± 10.9	42.9 ± 4.7
30	100	3.33	53.0 ± 3.3	164.7 ± 10.9	43.4 ± 5.5
50	100	2.00	57.8 ± 3.5	109.4 ± 7.5	38.9 ± 5.4
100	100	1.00	61.2 ± 3.5	60.5 ± 4.0	20.7 ± 3.6
30	200	6.67	56.3 ± 3.3	331.6 ± 24.3	76.5 ± 7.4
50	200	4.00	57.9 ± 3.3	215.3 ± 13.1	66.8 ± 7.2

This table displays values for the peak force and force–time integral produced during each stimulation train and the potentiation for each test train expressed as percent increase in twitch force pre- to post-stimulation train. Data are presented as mean ± SE

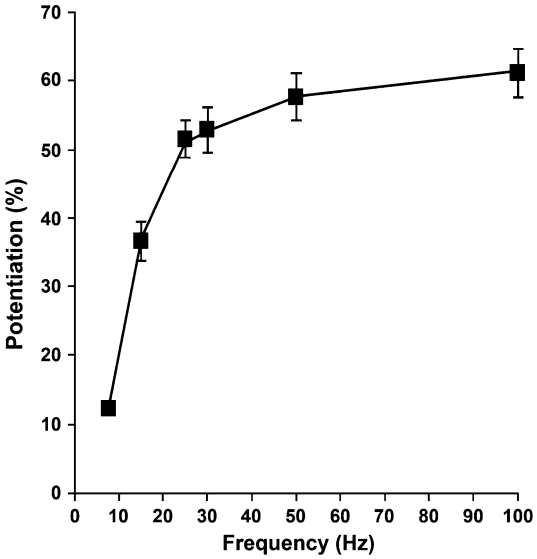

Fig. 9 Force–frequency curve for 100-pulse trains in the adductor pollicis muscle. At 7.5 Hz, no *error bars* are shown because they are within the symbol

of stimulation frequency. Using submaximal stimulation of the quadriceps muscle, Binder-Macleod et al. (2002) found no significant difference in twitch force potentiation across test trains of matched pulse number, but the FTIs during the test trains were different. In that study, mean FTIs were compared across stimulation trains; however, the relationship between FTI and potentiation was not examined (Binder-Macleod et al. 2002). Also, they measured FTI during only the first of repeated, intermittent trains; and therefore, this analysis did not include the effects of potentiation or fatigue that occurred during the entire test train sequence which may have influenced the FTI produced. Although the intent of the present study was not to investigate the relationship between potentiation and fatigue, force during the stimulation train did decrease from peak force to force at the end of the train in several of the test trains. However, in the present study, we incorporated long rest periods between test trains to allow for recovery between trains and to ensure that twitch force returned to control values prior to initiating the next train.

In the present study there was no relationship between peak force during the conditioning train and twitch force potentiation. This is supported by the findings of MacIntosh and Willis (2000) and Binder-Macleod et al. (2002) who also found that peak force during a stimulation train did not affect potentiation at a given stimulation frequency. The lack of difference in peak force during the 50 and 100-Hz trains may be explained by the saturation effect of Ca^{2+} at high stimulation frequencies (Blinks et al. 1978). During voluntary muscle activation, however, higher peak force generated during muscle contraction resulted in greater potentiation (Vandervoort et al. 1983). The differences in potentiation following voluntary and evoked contractions may be explained in the way voluntary contractions and evoked contractions are produced. Voluntary muscle force is increased by the recruitment of higher-threshold motor units and faster twitch muscle fibers, which are more susceptible to potentiation (Hamada et al. 2000; Houston et al. 1985; Moore and Stull 1984; Sweeney et al. 1993), and by increasing the firing rate of the active motor units. Thus, lower force levels would recruit fewer high threshold motor units and produce lower motor unit firing rates; whereas, maximal intensity stimulation recruits all motor units simultaneously with each pulse.

Low-frequency stimulation and potentiation

In the present study, the 7.5-Hz stimulation train produced less potentiation than pulse-matched trains of higher frequencies. Although there was not a significant difference between the 7.5 and 25-Hz trains, it neared statistical significance with a p value of 0.059. Binder-Macleod et al. (2002) also found that low-frequency trains of 5 Hz in the human quadriceps muscle produced less potentiation than trains of higher frequencies. The very low stimulation frequencies of 5 and 7.5 Hz may have produced less potentiation compared to the higher frequencies of stimulation, because there is relatively low twitch force fusion at these frequencies (Gibson et al. 1988). Stimulation trains that produce unfused force are less efficient than fused contractions (Loiselle and Walmsley 1982). The low stimulation frequencies of 5 and 7.5 Hz may also have produced less potentiation compared to the higher frequencies, because potentiation may have dissipated over time and not allowed for the same degree of temporal summation of phosphorylation and potentiation as might occur with a higher frequency over a shorter duration.

High-frequency stimulation and potentiation

In the present study, the 100 pulse, 100-Hz train resulted in less potentiation compared to the other 100-pulse trains (15, 25, 30, and 50 Hz). Twitch force potentiation also recovered faster following the high-frequency (50 and 100 Hz) than following the low-frequency (7.5, 15, 25, 30 Hz) trains. Similarly, Close and Hoh (1968) found that 20 Hz of stimulation produced greater potentiation than 300 Hz of stimulation for trains $\leq$200 pulses. Elevated Ca^{2+} concentrations increase potentiation when the troponin C is not already saturated with Ca^{2+}, causing a leftward shift of the force–pCa curve resulting in increased sensitivity to Ca^{2+} and greater force production at a given Ca^{2+} concentration. In skinned rabbit psoas fibers, RLC phosphorylation resulted in greater force at a given pCa; however, at

high pCa RLC phosphorylation had little effect on force (Persechini et al. 1985). If the potentiated state results in increased Ca^{2+} sensitivity, this would only increase twitch force until Ca^{2+} is saturated. Ca^{2+} is saturated at high frequencies of stimulation. In the present study, the force–frequency curve of the AdP muscle revealed that force did not significantly increase from 50 to 100 Hz, indicating Ca^{2+} saturation. It is possible the muscle could not utilize all the Ca^{2+} released with stimulation at 100 Hz.

The findings of this study demonstrate that the FTI produced during the test trains and the number of pulses delivered, rather than the stimulation frequency, determine potentiation magnitude. Pulse number may determine potentiation for a mid-range of stimulation frequencies (15–50 Hz), but a better indicator of potentiation over a larger range of train frequencies, pulse numbers and durations may be the FTI produced during the stimulation train. The AdP muscle is approximately 80% slow twitch (Johnson et al. 1973; Round et al. 1984). Thus, further study is needed to examine potentiation in other muscle groups of various size and fiber-type to determine the generalizability of these findings. Further work is also needed to determine the limits of the FTI in terms of optimizing potentiation while offsetting the effects of fatigue.

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Conflict of interest The authors declare that they have no conflict of interest.

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