



# What are the best isometric exercises of muscle potentiation?

Albertas Skurvydas<sup>1</sup> · Giedre Jurgelaitiene<sup>1</sup> · Sigitas Kamandulis<sup>1</sup> · Dalia Mickeviciene<sup>1</sup> · Marius Brazaitis<sup>1</sup> · Dovile Valanciene<sup>1</sup> · Diana Karanauskiene<sup>1</sup> · Mantas Mickevicius<sup>1</sup> · Gediminas Mamkus<sup>1</sup>

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## Abstract

**Purpose** The aim of this study was to follow post-activation potentiation (PAP), low-frequency fatigue (LFF), metabolic-induced fatigue and post-contraction depression (PCD) in response to different isometric muscle contraction modalities.

**Methods** Young healthy men ( $N=120$ ) were randomly assigned to one of ten exercise modality groups which differed in contraction duration (5–60 s), activation pattern (intermittent or continuous contractions), activation mode (voluntary or stimulated), and intensity [maximal or submaximal (50%)]. Isometric maximal voluntary contraction (MVC), and electrically induced knee extension torque were measured at baseline and at regular intervals for 60 min after exercise.

**Results** Muscle contraction modalities involving 5 s MVC were the most effective for PAP, whereas the lowest PAP effectiveness was found after the 12×5-MVC modality. After all of the 5–15 s MVC and 6×5-MVC protocols, the potentiation of the twitch rate was significantly higher than that recorded after continuous 30–60 s protocols ( $P<0.001$ ). Tetanic maximal torque (100 Hz) potentiation occurred 5 min after 15–30 s repetitive MVC modalities and after modality involving 15 electrical stimuli ( $P<0.05$ ).

**Conclusions** The findings demonstrate that post-activation potentiation was most effective after brief duration continuous and repetitive MVC protocols. To understand the resultant warm-up of motor performance, it is necessary to recognize the coexistence of muscle PAP, tetanic maximal force potentiation, rapid recovery of metabolic muscle, and central muscle activation processes, as well as prolonged LFF and prolonged PCD.

**Keywords** Post-activation potentiation · Tetanic maximal force potentiation · Low-frequency fatigue · Metabolic-related fatigue · Post-contraction depression · Electrostimulation

## Abbreviations

ANOVA	Analysis of variance
CT	Contraction time
ES	Electrical stimulation
LFF	Low-frequency fatigue
MC	Muscle conditioning protocol
MVC	Maximal voluntary contraction
P100	100 Hz electrically induced peak torque
P20	20 Hz electrically induced peak torque
PAP	Post-activation potentiation
PCD	Post-contraction depression
Pt	Electrically induced twitch peak torque

Pt/CT	Twitch contraction rate
Pt/RT $\frac{1}{2}$	Twitch half-relaxation rate
RT $\frac{1}{2}$	Half-relaxation time

## Introduction

The muscle force after series of muscle contractions may be increased as a result of post-activation potentiation (PAP) (Bruton et al. 1997; Skurvydas et al. 2016; Vandenoorn 2016; Gittings et al. 2017). Dominance of PAP or fatigue greatly depends on exercise parameters, e.g., contraction mode, intensity, duration, and rest intervals (Skurvydas et al. 2016). For instance, after high-frequency electrostimulation the force may be decreased, representing post-contraction depression (PCD) (Westerblad and Lännergren 1986; Skurvydas and Zachovajevs 1998) and after maximal voluntary contractions force may decrease as a consequence of peripheral or central fatigue (Kent-Braun 1999; Allen

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✉ Sigitas Kamandulis  
sigitas.kamandulis@lsu.lt

<sup>1</sup> Institute of Sports Science and Innovation, Lithuanian Sports University, Sporto 6, 44221 Kaunas, Lithuania

et al. 2008). In addition, greater reduction in force at low frequency (e.g., 10–20 Hz) than at high frequency (e.g., 50–100 Hz) of electrical stimulation is referred to as low-frequency fatigue (LFF, Jones 1996; Skurvydas and Zachovajevas 1998; Kamandulis et al. 2010). In fact, the effects of both potentiation and fatigue can coexist, and the net effect depends on the parameters of muscle contractile function tested (Skurvydas et al. 2016).

It is generally accepted that PAP is more pronounced at lower muscle stimulation frequencies (e.g., 1–10 Hz, Rassier and Macintosh 2000; Requena et al. 2008; Skurvydas et al. 2016; Cheng et al. 2017), although there is evidence that tetanic force is potentiated in animal muscles (Bruton et al. 1997). The PAP is induced by a voluntary conditioning contraction, which is performed typically at a maximal or near-maximal intensity, and has consistently been shown to increase both peak force and the rate of force development during subsequent twitch contractions. The proposed mechanisms underlying PAP are associated with the phosphorylation of myosin regulatory light chains (Stull et al. 2011; Vandenoorn 2016; Gittings et al. 2017), increased recruitment of higher-order motor units (Tillin and Bishop 2009; Sasaki et al. 2012). Classic studies have established that the magnitude and duration of potentiation depend on several factors, including muscle fiber type, species, temperature, sarcomere length, and stimulation paradigm (Vandenoorn et al. 2013).

The PAP phenomenon is quite common in sports in which the warmed-up muscles are prepared for the development of the greatest contractile force and rate during the competition (Macintosh et al. 2012; Gouvêa et al. 2013; Wilson et al. 2013; Nibali et al. 2015; Andrews et al. 2016; Seitz and Haff 2016). Because of the abundance of the above-mentioned activating and suppressing mechanisms/factors, many warm-up protocols have been developed that yield an increase in muscle force or power (Kilduff et al. 2011; Esformes et al. 2011; Macintosh et al. 2012; Miyamoto et al. 2013; Thomas et al. 2017). Most of them show that, after a brief near-maximal muscle isometric contraction, a certain amount of time has to pass for fatigue to disappear (1–10 min) and for the development of an effect of muscle contraction force or power potentiation (Macintosh et al. 2012; Gouvêa et al. 2013; Wilson et al. 2013; Bogdanis et al. 2014; Xenofondos et al. 2018).

Despite the above-mentioned research results, many questions about the dependence of muscle contractile resultant/net force on activating (potentiation) and suppressing (fatigue) factors during recovery remain unanswered; i.e., it is unclear whether brief muscle activation can cause post-contractile maximal tetanic force depression or tetanic maximal force potentiation as well as LFF. Moreover, it is not clear how the coexistence of muscle contraction activation and suppression mechanisms depends on continuous vs intermittent muscle activation at the same total intensity

and duration. When analyzing changes in resultant/net contraction force after a conditioning stimulus, it is important to note how they depend on the total isometric contraction impulse. It would be useful to identify the most effective muscle potentiation, i.e., increase in contraction and relaxation rates normalized to the muscle isometric contraction impulse.

Our research aim was to determine how twitch and tetanic maximal force activation phenomena, as well as LFF, PCD, and metabolic-related fatigue, depend on contraction duration (5–60 s), intensity (maximal and submaximal), activation pattern (intermittent or continuous contractions) and activation mode (voluntary and stimulated) protocols, and how they affect result/net force change dynamics during 60 min recovery periods. The rationale behind using these variations in exercise protocols is that it allowed us to impose various degrees of metabolic stress and activation failure on muscles. We hypothesized that the pattern of PAP changes during the brief recovery period after different types of contractile activity would reveal the role of muscle contraction activation and suppression mechanisms. This information will help to design the most effective strategy to augment muscle performance. To avoid the effect of the specificity of muscle contraction type on potentiation and fatigue (Skurvydas et al. 2016), we chose isometric muscle contraction as the muscle conditioning (MC) stimulus and we registered potentiation under the conditions of isometric maximal voluntary contraction (MVC) and electrostimulation of 1, 20, and 100 Hz-induced activation.

## Materials and methods

### Subjects

Young healthy men ( $N = 120$ , age range: 18–22 years, mass range: 66–94 kg, height range: 167–193 cm) were randomly assigned to one of ten exercise modality groups, 12 individuals in each of them. Every subject performed only one of the MC protocols described below to avoid the potential impact of previous exercise on the results. All subjects were physically active and participated in recreational activities 2–3 times per week. They were asked to refrain from any exercise for 1 week prior to the experiment. Informed consent was obtained from all individual participants included in the study. The study was approved by the Kaunas Regional Ethics Committee and is consistent with the principles outlined in the Declaration of Helsinki.

### Muscle conditioning (MC) protocols

Ten MC protocols were used that differed in contraction duration (5–10–15–30–60 s), activation pattern (intermittent

or continuous contractions), activation mode (voluntary or stimulated), and intensity (maximal or submaximal (50%)) (See Table 1 for specific protocols). Subjects were seated upright in the dynamometer chair (System 3; Biodex Medical Systems, Shiley, New York, USA) with shank, trunk, and shoulders stabilized by belts. MC protocols were performed with right-leg knee extensor muscles isometrically at knee joint angle of 60° (0°—full knee extension). The subjects were verbally encouraged to exert and maintain maximal force during maximal voluntary contractions. One of the protocols involved contractions performed at 50% maximal isometric voluntary force for 60 s (0.5-MVC-60 s). During this protocol, subjects could see a line representing the target force on the screen and were asked to match the line. We also studied electrically induced isometric 100-Hz contractions that lasted for 1 s (15-ES). The quadriceps contraction torque-time integral was calculated during each protocol, i.e., the average force developed over each protocol during MVC was multiplied by the muscle isometric contraction time.

### Torque measurements

The electrically evoked and MVC peak isometric torque of the right-leg knee extensor muscles was measured using the same equipment and position as described above. Direct electrical muscle stimulation was applied using two carbonized rubber electrodes covered with a thin layer of electrode gel (ECG–EEG Gel; Medigel, Modi'in, Israel). One of the electrodes (6 cm × 11 cm) was placed transversely across the width of the proximal portion of the quadriceps muscle, next to the inguinal ligament; the other electrode (6 cm × 20 cm) covered the distal portion of the

muscle, above the patella. An electrical stimulator (MG 440; Medicor, Budapest, Hungary) delivered square-wave pulses with a duration of 1 ms. Each subject was familiarized with the experimental procedures and electrical stimulation on a separate occasion, before the actual testing. The amplitude of the square-wave current pulses required to obtain maximum force was determined by gradually increasing the voltage until no increment in force response was elicited by a 10% voltage increase. Subjects with poor compliance were excluded from the study.

Electrically evoked and MVC peak torques were measured before, immediately after, 5, 10, 30, and 60 min after each MC protocol. Electrically evoked muscle contraction was induced by single stimuli (twitch, Pt), 20 Hz or 100 Hz 1-s trains of stimuli. Each electrical stimulus was applied once and separated by 5-s intervals. Before exercise, MVC was developed twice every 60 s and the best MVC value was included in the analysis. The MVC values immediately after the contraction protocol was given as the highest value in the last 2 s during the MVC-5 s, MVC-10 s, MVC-30 s, MVC-60 s, and MVC-12 × 5 s protocols or last repetition peak value of MVC in the 5-MVC, 15-MVC, and 6 × 5-MVC protocols. During the recovery assessment (5, 10, 30, and 60 min after MC protocol) and immediately after 15-ES and 0.5-MVC-60 s, MVC was developed once. We calculated the contraction time (CT) and half-relaxation time (RT<sub>1/2</sub>) during Pt. We also calculated Pt/CT (twitch contraction rate) and Pt/RT<sub>1/2</sub> (twitch half-relaxation rate). Moreover, quadriceps muscle twitch contraction (Pt/CT) and half-relaxation (Pt/RT<sub>1/2</sub>) rate potentiation and effectiveness (potentiation rate/torque-time integral) after MC protocols were also assessed.

**Table 1** Characteristics of the muscle conditioning protocols

Protocols	Exercise strategies	Resting time between series, s	Average force, Nm	Torque-time integral, kNm × s
<b>LOAD 5–15 s</b>				
5-MVC	Five repeated MVC for 1 s	1	262.8 (14.4)	1.3 (0.1)
MVC-5s	Maximal isometric contraction for 5 s	0	260.8 (13.1)	1.2 (0.1)
15-MVC	Fifteen repeated MVC for 1 s	1	257.2 (15.8)	3.8 (0.2)
MVC-10s	Maximal isometric contraction for 10 s	0	254.8 (13.3)	2.5 (0.2)
15-ES	Fifteen repeated electrostimulation induced force contraction at 100 Hz for 1 s	1	160.1 (11.1)	2.4 (0.1)
<b>LOAD 30–60 s</b>				
6 × 5-MVC	Six series of five repeated maximal isometric contraction in each series	60	259.5 (12.8)	7.8 (0.6)
MVC-30s	Maximal isometric contraction for 30 s	0	218.5 (15.8)	6.5 (0.5)
0.5-MVC-60 s	50% MVC for 60 s	0	133.2 (14.9)	8.0 (0.9)
MVC-60 s	Maximal isometric contraction for 60 s	0	162.5 (14.5)	9.8 (0.8)
MVC-12 × 5 s	Twelve series of maximal isometric contraction for 5 s	180	227.2 (15.9)	12.3 (1.0)

Values are given as means. Standard deviations are given in parentheses

## Statistical analysis

The data were tested for normal distribution using the Kolmogorov–Smirnov test, and all data were found to be normally distributed. The data are presented as mean and standard deviation (SD). Differences in baseline values of electrically induced torques of the quadriceps muscle and MVCs between the ten research groups (Table 1) were analyzed via one-way analysis of variance. A two-way mixed analysis ANOVA (general linear model) was used to determine the effects of the within-factor time (six levels: before, immediately after, 5, 10, 30, and 60 min after exercise) and between-factor group (10 MC protocols) for electrically and voluntary induced torque and contractile properties. If significant effects were found, Tukey's post hoc tests were performed to locate significant differences. Comparisons between groups at a single time-point were analyzed using independent-sample *t* tests. Pairwise comparisons using Sidak's adjustment were used by pairing each set of sequential periods for each separate MC protocol. Statistical significance was defined as  $P < 0.05$  and  $P < 0.001$ . Statistical analyses were performed using IBM SPSS Statistics software (v. 22, IBM Corp., Armonk, NY).

## Results

There was no significant difference ( $P > 0.05$ ) between initial mean values of electrically induced contractile properties of quadriceps muscle and MVC of 10 research groups.

Immediately after all MC protocols, with the exception of MVC-60 s and 0.5-MVC-60 s, Pt increased significantly ( $P < 0.001$ ) (Table 2). Immediately after all 5–15 s MC

protocols, Pt increased to greater extent than it did after the MC protocols of 30–60 s ( $P < 0.001$ ), with the exception of 6 × 5-MVC. There was no significant difference in Pt potentiation after all 5–15 s MC and 6 × 5-MVC protocols ( $P > 0.05$ ). After 5–15 s MC protocols, Pt decreased significantly during the 5 min recovery ( $P < 0.001$  compared with that observed immediately after MC). Interestingly, after the MVC-30 s, MVC-60 s, and 0.5-MVC-60 s MC protocols, delayed potentiation was prominent, i.e., 5–10 min after MVC-30 s and 0.5-MVC-60 s, Pt was significantly greater than it was immediately after MC ( $P < 0.001$ ). Exclusively after the MVC-12 × 5 s MC, Pt decreased significantly ( $P < 0.001$ ) within 5–60 min compared with that observed immediately after MC.

CT decreased significantly (potentiated) after the repeated MVC contraction protocols: 5-MVC ( $P < 0.001$ ), 15-MVC ( $P < 0.05$ ), and 6 × 5-MVC ( $P < 0.001$ ) (Table 3). CT also decreased after a continuous MVC-60 s ( $P < 0.001$ ). Half-relaxation time ( $RT_{1/2}$ ) decreased (potentiated) after the 15-MVC ( $P < 0.001$ ), 6 × 5-MVC ( $P < 0.05$ ), and MVC-12 × 5 s ( $P < 0.05$ ) (Table 3). There was a significant increase in  $RT_{1/2}$  after MVC-30 s ( $P < 0.05$ ), MVC-60 s ( $P < 0.05$ ), and 0.5-MVC-60 s ( $P < 0.001$ ) protocols.

The Pt contraction and relaxation rate potentiation were significantly increased immediately after all MC protocols, except for the case in which potentiation occurred only 5 min after the end of MC following the MVC-60 s and 0.5-MVC-60 s MC protocols (Fig. 1A–D). After all of the 5–15 s MC (Fig. 1A, C) and 6 × 5-MVC (Fig. 1B, D) protocols, the potentiation of the Pt rate was significantly higher than that recorded after all 30–60 s MC protocols ( $P < 0.001$ ).

The enhancement of Pt contraction and relaxation rate potentiation after the 5–15 s MC protocols was significantly

**Table 2** Changes of electrically induced twitch torque after different muscle conditioning protocols

Protocols	Before	After 0 min	5 min	10 min	30 min	60 min
LOAD 5–15 s						
5-MVC	100	251.9** (44.2)	125.5* (34.5)	110.2 (14.5)	97.5 (8.8)	100.4 (7.8)
MVC-5 s	100	260.9** (49.9)	145.8** (37.9)	115.5* (20.1)	103.4 (13.1)	104.5 (10.9)
15-MVC	100	238.9** (47.2)	129.4** (35.1)	123.4* (31.4)	103.2 (17.5)	100.1 (14.2)
MVC-10 s	100	278.9** (49.9)	155.8** (47.7)	120.5* (20.7)	102.4 (15.4)	100.5 (10.2)
15-ES	100	237.9** (15.2)	148.9** (12.1)	122.8** (8.8)	98.9 (8.2)	97.6 (7.9)
LOAD 30–60 s						
6 × 5-MVC	100	245.7** (45.9)	134.5** (21.1)	110.1* (10.5)	101.4 (13.5)	103.2 (15.2)
MVC-30 s	100	151.6** (35.7)	166.8** (35.7)	155.4** (37.4)	96.1 (19.4)	99.3 (17.2)
0.5-MVC-60 s	100	104.2 (7.8)	159.8** (11.9)	136.5** (14.2)	96.5 (8.8)	96.8 (11.4)
MVC-60 s	100	48.5** (7.5)	146.8** (15.5)	123.5* (12.2)	94.8 (14.2)	102.5 (12.5)
MVC-12 × 5 s	100	116.5* (10.5)	78.5** (9.5)	63.5** (7.8)	58.9** (6.9)	62.1** (7.9)

Values are given as means in per cent compared to before conditioning protocol. Standard deviations are given in parentheses

MVC maximal voluntary isometric quadriceps muscle contraction, ES electrical stimulation

\* $P < 0.05$ , \*\* $P < 0.001$  compared with before muscle conditioning protocols

**Table 3** Changes of electrically induced twitch contraction time and half-relaxation time after different muscle conditioning protocols

Protocols	Before	After 0 min	5 min	10 min	30 min	60 min
<b>Contraction time</b>						
LOAD 5–15 s						
5-MVC	100	75.2** (7.9)	94.2 (8.2)	98.8 (8.8)	96.4 (9.1)	97.8 (8.4)
MVC-5 s	100	94.5 (12.9)	96.8 (8.9)	98.8 (9.4)	96.8 (10.6)	102.9 (9.1)
15-MVC	100	86.5* (8.2)	99.2 (10.1)	102.9 (8.4)	100.1 (10.2)	104.2 (9.9)
MVC-10 s	100	103.5 (10.9)	98.8 (7.9)	99.2 (8.4)	95.6 (10.1)	97.9 (9.8)
15-ES	100	97.2 (8.1)	100.1 (8.2)	99.2 (8.8)	95.8 (8.9)	96.8 (9.2)
LOAD 30–60 s						
6×5MVC	100	71.6** (8.6)	85.9** (9.5)	88.4* (11.2)	95.6 (10.8)	99.9 (10.1)
MVC-30 s	100	97.2 (12.8)	94.2 (11.4)	94.8 (10.9)	93.5 (11.5)	97.8 (9.9)
0.5-MVC-60 s	100	103.5 (10.1)	99.5 (8.9)	97.8 (9.6)	96.1 (10.1)	98.8 (8.9)
MVC-60 s	100	83.2** (9.2)	100.5 (14.5)	96.9 (13.3)	103.8 (11.8)	104.2 (14.2)
MVC-12×5 s	100	97.2 (8.8)	92.4* (8.1)	81.1** (10.4)	82.7** (8.6)	84.2** (9.3)
<b>Half-relaxation time</b>						
LOAD 5–15 s						
5-MVC	100	100.5 (10.1)	97.8 (9.8)	96.8 (8.4)	97.8 (9.1)	99.3 (11.2)
MVC-5 s	100	94.7 (10.1)	95.2 (10.9)	104.3 (9.1)	98.8 (10.8)	101.9 (10.8)
15-MVC	100	84.3** (9.5)	96.7 (12.4)	97.8 (10.4)	96.8 (8.9)	102.4 (8.1)
MVC-10 s	100	96.9 (9.1)	99.2 (9.1)	102.3 (8.9)	97.5 (11.2)	104.2 (12.1)
15-ES	100	104.5 (7.8)	93.5 (10.2)	95.5 (9.5)	93.8 (9.9)	94.8 (8.9)
LOAD 30–60 s						
6×5-MVC	100	90.7* (8.1)	101.6 (9.6)	91.1 (9.2)	94.8 (8.7)	96.9 (8.8)
MVC-30 s	100	115.2** (10.7)	97.2 (9.8)	95.2 (10.1)	90.2* (8.3)	91.2* (8.1)
0.5-MVC-60 s	100	140.5** (15.8)	99.5 (12.2)	96.5 (12.5)	96.5 (14.2)	92.8 (16.1)
MVC-60 s	100	110.8* (11.1)	119.9** (10.8)	96.8 (8.4)	90.1* (8.4)	88.5* (8.4)
MVC-12×5 s	100	91.1* (8.1)	91.5* (9.2)	79.5** (9.1)	75.2** (8.6)	71.9** (9.8)

Values are given as means in per cent compared to before conditioning protocol. Standard deviations are given in parentheses

MVC maximal voluntary isometric quadriceps muscle contraction, ES electrical stimulation

\* $P < 0.05$ , \*\* $P < 0.001$  compared with before muscle conditioning protocols

greater than that observed after the 30–60 s MC protocols ( $P < 0.001$ ); however, it was greater after the 5 s MC protocols ( $P < 0.001$ ) than that observed for the 10–15 s MC protocols (Fig. 2).

A significantly greater 20 Hz torque potentiation was recorded after all 5–15 s MC protocols, as well as after the 6×5-MVC protocols ( $P < 0.05$ ) (Table 4). Five minutes after MC 20 Hz torque, potentiation disappeared. Immediately after all 30–60 s MC protocols (with the exception of the one after 6×5-MVC), the 20 Hz torque decreased significantly ( $P < 0.001$ ). It is interesting to note that, within 30–60 min after the end of the 30–60 s MC protocols, with the exception of 6×5-MVC, torque at 20 Hz was significantly lower than that observed before MC.

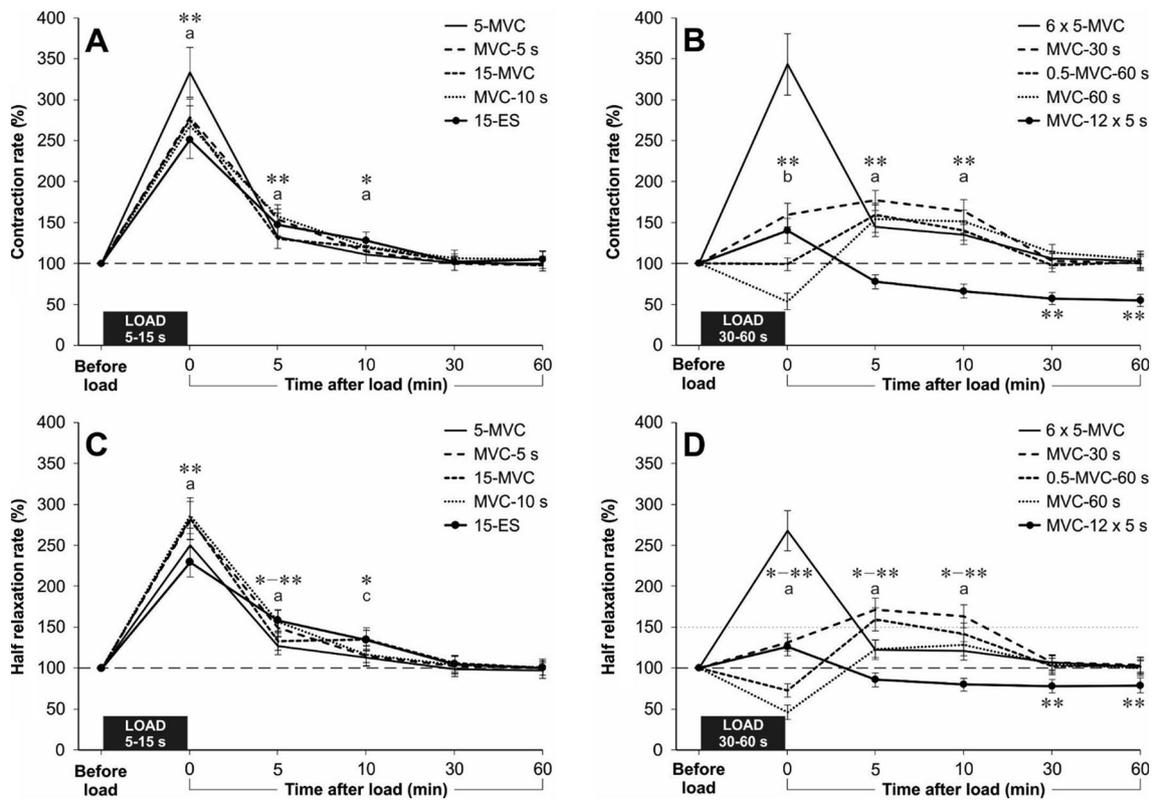
Our research results showed that 5 min after the 15-MVC, 15-ES, and 6×5-MVC MC protocols, 100 Hz-induced torque increased significantly (potentiated) ( $P < 0.05$ ) (Table 4). After all of the 60 s MC protocols and after MVC-30 s, as well as after 15-ES, the 100 Hz-induced torque

decreased significantly; however, after the 12×5-MVC protocol, it did not recover to its initial value, even after 60 min.

MVC increased significantly ( $P < 0.05$ ) only 10 min after 6×5-MVC and 15-MVC (Table 5). The MVC values recorded 5 min after all MC protocols did not differ from their initial (before MC) values, with the exception of the case in which the MVC value recovered only after 60 min after MVC-12×5 s.

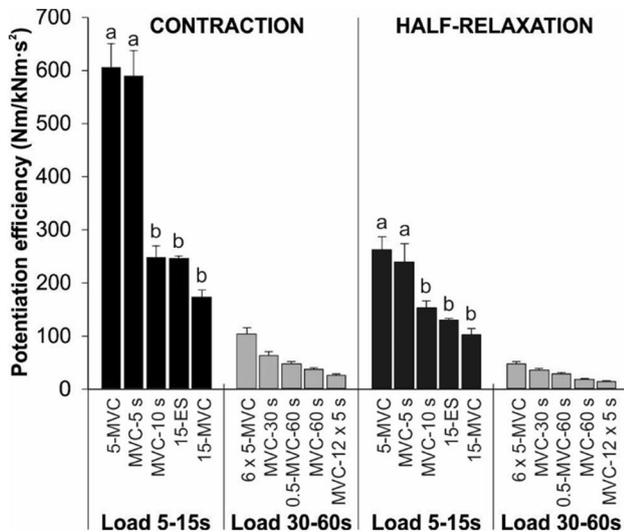
## Discussion

The main observation of the present study is that PAP was most effective after a 5-s MVC regardless of muscle activation pattern. Hence, the magnitude and timing of PAP were a function of preceding exercise duration with extended (30–60 s) protocols producing more pronounced fatigue and reduced potentiation. Interestingly, PAP was evident not



**Fig. 1** Changes in the percentage of muscle contraction (Pt/CT) and half-relaxation (Pt/RT $\frac{1}{2}$ ) rate after the muscle conditioning protocols. Values are the mean  $\pm$  SD. Asterisks and lowercase letters indicate significant differences between before the load and at the appropriate

measuring time after the load: \* $P < 0.05$ ; \*\* $P < 0.001$ ; a, for all indicators; b, for all indicators with the exception of 0.5-MVC-60 s; c, for all indicators with the exception of 5-MVC



**Fig. 2** Quadriceps muscle twitch contraction (Pt/CT) and half-relaxation (Pt/RT $\frac{1}{2}$ ) rate potentiation effectiveness (potentiation rate/torque-time integral) after the muscle conditioning protocols. Values are the mean  $\pm$  SD. Significant differences: a,  $P < 0.001$  compared with other contraction and half-relaxation indications; b,  $P < 0.001$  compared with indications after a load of 30–60 s

only for twitch but also for tetanic and voluntary contraction torque at several conditions.

### Quadriceps muscle twitch and 20 Hz torque potentiation

PAP represents an increase in muscle isometric twitch and low-frequency tetanic force following conditioning activity (Sale 2002). In line with this, we also found that Pt increased significantly after eight of the research protocols, and that the 20-Hz torque significantly increased after five of the protocols compared with the initial value. The degree of potentiation in intact muscles is associated with the degree of phosphorylation of the regulatory light chains of myosin, which causes an increase in Ca $^{2+}$  sensitivity (Vandenboom 2016; Cheng et al. 2017; Gittings et al. 2017). PAP has a small effect on the force of high-frequency tetanic contractions because in such contractions the “saturating” concentration of Ca $^{2+}$  is attained, rendering any increase in Ca $^{2+}$  sensitivity inconsequential (Sale 2002).

Recently other mechanisms for PAP have been suggested that involve stimulation-induced increases in resting myoplasmic [Ca $^{2+}$ ] that possibly mediate a more advantageous

**Table 4** Potentiation and fatigue of electrically induced skeletal muscle contraction torque at 20 Hz and 100 Hz after different muscle conditioning protocols

Protocols	Before	After 0 min	5 min	10 min	30 min	60 min
Electrically induced contraction torque at 20 Hz (P20)						
LOAD 5–15 s						
5-MVC	100	109.2* (9.8)	107.4 (10.2)	103.2 (11.1)	102.4 (8.1)	100.1 (7.9)
MVC-5 s	100	107.8* (7.2)	102.9 (10.5)	100.1 (8.8)	100.1 (8.1)	103.4 (7.9)
15-MVC	100	108.4* (10.1)	106.9 (11.8)	107.8 (12.9)	100.5 (11.2)	98.9 (11.4)
MVC-10 s	100	106.3* (7.1)	104.7 (11.2)	101.8 (8.8)	97.1 (7.8)	98.4 (7.9)
15-ES	100	99.9 (7.5)	106.8 (10.8)	105.8 (10.2)	94.5 (8.8)	96.3 (7.2)
LOAD 30–60 s						
6×5-MVC	100	115.8* (12.6)	106.7 (13.6)	98.4 (16.4)	97.8 (14.1)	99.2 (11.5)
MVC-30 s	100	80.2** (11.4)	99.4 (12.4)	96.4 (11.5)	91.1* (7.9)	90.4* (8.2)
0.5-MVC-60 s	100	83.8** (9.9)	106.8 (14.2)	101.9 (8.8)	90.2* (10.2)	92.2* (9.9)
MVC-60 s	100	54.5** (7.9)	97.9 (9.9)	90.2* (7.8)	81.2** (8.8)	80.8** (9.5)
MVC-12×5 s	100	63.9** (11.5)	57.5** (14.5)	54.5** (10.2)	50.1** (8.8)	52.9** (7.9)
Electrically induced contraction torque at 100 Hz (P100)						
LOAD 5–15 s						
5-MVC	100	104.2 (7.8)	105.4 (8.4)	103.2 (10.2)	100.8 (7.8)	102.4 (7.4)
MVC-5 s	100	104.5 (8.8)	105.2 (8.1)	103.2 (8.2)	100.5 (7.9)	100.4 (10.5)
15-MVC	100	98.6 (9.5)	109.9* (8.1)	103.7 (5.9)	101.8 (7.5)	98.9 (7.7)
MVC-10 s	100	93.9 (8.1)	97.9 (7.7)	101.2 (7.7)	99.5 (6.8)	97.9 (7.1)
15-ES	100	92.1* (7.1)	108.5* (8.1)	102.9 (7.1)	99.8 (9.1)	100.2 (8.2)
LOAD 30–60 s						
6×5-MVC	100	101.8 (8.1)	108.3* (9.3)	102.4 (8.1)	101.2 (9.2)	100.9 (8.2)
MVC-30 s	100	72.5** (7.2)	99.8 (9.1)	97.8 (10.2)	100.2 (8.2)	101.5 (7.9)
0.5-MVC-60 s	100	78.9** (10.2)	98.8 (8.8)	101.5 (7.9)	103.5 (7.8)	103.9 (8.2)
MVC-60 s	100	57.8** (8.8)	97.2 (11.2)	100.8 (12.4)	97.5 (11.1)	98.8 (10.5)
MVC-12×5 s	100	71.5** (8.1)	76.8** (8.9)	82.8** (9.9)	83.7** (8.6)	83.8* (11.2)

Values are given as means in per cent compared to before conditioning protocol. Standard deviations are given in parentheses

MVC maximal voluntary isometric quadriceps muscle contraction, ES electrical stimulation

\* $P < 0.05$ , \*\* $P < 0.001$  compared with before muscle conditioning protocols

**Table 5** Changes in maximal voluntary contraction (MVC) after different muscle conditioning protocols

Protocols	Before	After 0 min	5 min	10 min	30 min	60 min
LOAD 5–15 s						
5-MVC	100	102.9 (4.8)	100.9 (5.2)	99.2 (4.2)	101.1 (5.7)	100.2 (5.7)
MVC-5 s	100	97.9 (6.1)	100.9 (7.4)	103.4 (8.5)	100.5 (7.1)	97.8 (8.9)
15-MVC	100	89.7* (9.7)	104.8 (8.1)	108.3* (7.3)	97.8 (12.3)	99.8 (7.1)
MVC-10 s	100	96.4* (4.5)	102.1 (5.5)	101.9 (6.5)	98.9 (8.5)	102.5 (7.1)
15-ES	100	93.2* (7.1)	104.2 (9.1)	103.5 (10.1)	97.5 (8.9)	98.2 (8.2)
LOAD 30–60 s						
6×5-MVC	100	100.2 (7.4)	105.4 (8.1)	109.8* (7.1)	98.8 (11.2)	99.2 (7.9)
MVC-30 s	100	82.1** (9.3)	96.2 (10.5)	97.5 (7.5)	99.9 (10.4)	101.2 (7.9)
0.5-MVC-60 s	100	86.4** (8.1)	97.5 (8.4)	99.5 (7.2)	102.5 (8.9)	103.1 (8.7)
MVC-60 s	100	50.2** (7.9)	95.1 (12.8)	95.8 (9.9)	96.5 (11.8)	97.9 (10.1)
MVC-12×5 s	100	90.1* (9.7)	87.3* (13.3)	91.8* (9.2)	91.5* (10.2)	93.5 (8.4)

Values are given as means in per cent compared to before conditioning protocol. Standard deviations are given in parentheses

MVC maximal voluntary isometric quadriceps muscle contraction, ES electrical stimulation

\* $P < 0.05$ , \*\* $P < 0.001$  compared with before muscle conditioning protocols

condition for torque development during activation, where the thick filament could be considered as primed for activity (Vandenboom et al. 2013). Another mechanism that may enhance excitability might be a contraction-induced increase in the activity of the sodium–potassium pump, required to maintain  $\text{Na}^+$  and  $\text{K}^+$  gradients across the plasma membrane (Hicks and McComas 1989; Buchanan et al. 2002; Shushakov et al. 2007). In addition, twitch force may increase with increasing temperature (Vandenboom et al. 2013). However, the role of temperature is probably negligible as the protocols were motionless and rather short (longest for 60 s) to induce appreciable increases in temperature.

Although it is commonly accepted that during potentiation muscle contraction, rather than relaxation, is accelerated (Stull et al. 2011; Vandenboom 2016), we found that both the rate of twitch contraction and twitch half relaxation were accelerated during potentiation. It is established that repeated stimulation of unfatigued rodent fast-twitch skeletal muscle accelerates the kinetics of tension relaxation via an unknown mechanism (Smith et al. 2017). This effect varies according to muscle type and stimulation parameters, and has been observed at physiological temperatures for sub-maximal, but not maximal, contractions (Smith et al. 2017).

### **Evidence of potentiation of tetanic maximal torque induced with 100-Hz stimulation and MVC**

We found only one study that showed clearly that maximal tetanus force is potentiated when the mouse soleus muscle is electrically stimulated (Bruton et al. 1997). Bruton et al. (1997) showed that after a warm-up protocol (15 tetani at 2-s intervals), the tetanic force was increased significantly by 6% (4–6 min after the end of the muscle stimulation protocol), and inorganic phosphate level was almost halved in isolated mouse soleus muscles. Therefore, those authors concluded that a reduction in inorganic phosphate contributes to the force-potentiating effect of the warm-up protocol (Bruton et al. 1997). This coincides with the results of three of our protocols, i.e., 100 Hz force increased significantly (by about 8–10%) 5 min after 15-MVC, 15-ES, and 6×5-MVC. Moreover, in our case, 10 min after the 15-MVC and 6×5-MVC protocols, MVC increased significantly.

Other studies have shown that one bout of 5–6 s isometric MVC increased dynamic torque and power (Miyamoto et al. 2013). When the isometric MVC was used as a conditioning contraction, the maximal voluntary concentric torque was significantly enhanced at 1 and 3 min after MVC in the 5 s MVC trial only, but not in the 3- and 10-s MVC trials (Miyamoto et al. 2012). The meta-analysis reported by Gouvêa et al. (2013) showed that the potentiation of a standing jump is most effective 8–12 min after the MC stimulus. Another meta-analysis revealed that after a shallow squat with a large weight, there is a higher muscle potentiation for

the performance of ballistic exercises (jumping and running) than after a deep squat (Seitz and Haff 2016). Thomas et al. (2017) established that a large load increases the standing jump height by about 4%, but no changes were observed for maximum voluntary force, voluntary activation and corticospinal excitability. Dynamic stretching warm-up with the inclusion of resistance enhances jumping ability more at 3 min than immediately after, and this improvement is maintained at least 6 min after conditioning exercise (Needham et al. 2009). All these findings favor the PAP importance to performance, while it is vital to understand the relationships between factors that activate and inhibit the PAP mechanism.

### **Evidence of metabolic-related rapid initial recovery of tetanic torque and MVC**

Two likely mechanisms underlie the decreased force production observed after our ten protocols. First, prolonged (in our case, 5–60 s) contractions are accompanied by decreased central activation of motor units and possibly impaired action potential propagation within the muscle fibers (Kent-Braun 1999; Brazaitis et al. 2012). In line with a problem with central activation, we observed that while there were decreases in MVC, the electrically induced contraction torque remained unchanged after several MC protocols (15-MVC and MVC-10 s), signifying central fatigue. Second, myoplasmic accumulation of inorganic phosphate ions ( $\text{Pi}$ ) caused by the breakdown of phosphocreatine together with an increase in adenosine diphosphate (ADP) and hydrogen ion ( $\text{H}^+$ ) concentrations can lead to a decreased force production in fatigue (Allen et al. 2008). The phosphocreatine, inorganic phosphate ions, ADP and  $\text{H}^+$  recover to the control level within a few minutes after prolonged contractions (Allen et al. 2008) and this may explain the rapid recovery of 20 and 100 Hz tetanic torque and MVC observed after the MVC-30 s, MVC-60 s, and 0.5-MVC-60 s protocols. The fast recovery of tetanic force (especially at 100 Hz) within 5–10 min was more pronounced after metabolic-demanding protocols, especially after sustained contractions (MVC-30 s and MVC-60 s).

### **Slowly developing, prolonged torque depression at 20 and 100 Hz initiated by metabolically demanding exercise**

A prolonged torque depression that was more prominent at 20 Hz than at 100 Hz stimulation was observed only after the 30–60 s sustained protocols (MVC-30 s, MVC-60 s, MVC-12×5 s, and 0.5-MVC-60 s). This type of fatigue can theoretically be caused by decreased sarcoplasmic reticulum  $\text{Ca}^{2+}$  release and/or decreased myofibrillar  $\text{Ca}^{2+}$  sensitivity (Allen et al. 2008; Place et al. 2015). The results of recent studies show a coherent picture where the cellular ROS

handling determines whether the dominating cause of the force depression is decreased SR  $\text{Ca}^{2+}$  release or reduced myofibrillar  $\text{Ca}^{2+}$  sensitivity (Cheng et al. 2016). In the present study, reactive oxygen/nitrogen species (ROS) production likely has increased during lengthy protocols. Another phenomenon of muscle fatigue was observed in our studies, i.e., PCD. The PCD was defined as a delayed recovery of tetanic tension from fatigue in isolated amphibian muscle fibers (Westerblad and Lännergren 1986), and in mammalian (Lännergren et al. 1989) and human muscles (Skurvydas and Zachovajevs 1998). We found a delayed recovery of tetanic torque but only after the MVC-12×5 s protocol. The exact cause of this delayed recovery is unclear, but an important contribution from impaired excitation–contraction coupling is highly plausible (Allen et al. 2008).

### Evidence of the coexistence of potentiation and fatigue

Our results showed that all ten MC protocols caused twitch contraction rate potentiation. All 5–15 s protocols (6×5-MVC and MVC-12×5 s) triggered potentiation immediately after MC, and two protocols (MVC-60 s and 0.5-MVC-60 s) triggered potentiation 5–10 min after MC. It is interesting to note that the MVC-30 s protocol induced potentiation of the twitch contraction rate immediately after exercise and increased it slightly 5–10 min after exercise. A decrease in 100 Hz-induced torque was observed immediately after five of the research protocols, and LFF occurred after four of the research protocols. In summary, muscle potentiation dominated after all 5–15 s and 6×5-MVC protocols, fatigue was dominant after the MVC-12×5 s protocol, and fatigue did not exceed the delayed (5–10 min after MC) manifestation of potentiation after the continuous 30–60 s protocols. PAP compensates LFF well when the force is reduced at low stimulation frequencies (Skurvydas and Zachovajevs 1998; Rassier and Macintosh 2000). However, this depends on the size of LFF. In cases of high LFF fatigue, PAP is not observed (Skurvydas et al. 2016; Verbickas et al. 2017, 2018). As fatigue and potentiation mechanisms are rather complex, experimental studies often show the presence of a multifaceted interaction between potentiation and fatigue (Skurvydas and Zachovajevs 1998; Rassier and Macintosh 2000; Skurvydas et al. 2016; Rodriguez-Falces and Place 2017; Verbickas et al. 2017; Xenofondos et al. 2018). This renders it difficult to assess the relative importance of the different processes. Moreover, to understand better the fatigue/potentiation interaction, it is necessary to study not only the muscle but also the spinal and supraspinal mechanisms. This was one of our research limitations. For example, Rodriguez-Falces and Place (2017) showed that the investigation of the M-wave can help understand additional muscle activation mechanisms. Moreover,

we did not assess changes in muscle temperature, which can also affect the speed of muscle contraction and relaxation (Brazaitis et al. 2012).

### Conclusions

Post-activation muscle potentiation occurred after an array of muscle contraction protocols that differed in muscle activation pattern, mode and intensity. The post-activation was, however, most effective after brief (5 s) duration contractile activity. Intermediate duration (15–30 s) repetitive contractions induce not only twitch but also tetanic force potentiation regardless of activation mode. Our results show that the coexistence of muscle PAP, tetanic maximal force potentiation, rapid recovery of metabolic muscle, and central muscle activation processes, as well as prolonged LFF and prolonged PCD determine whether potentiation or reduction in force is ultimately seen after a series of contractions. These observations can be used to inform the design of protocols to efficiently enhance muscle power output and hence performance.

**Author contributions** AS and DM: conception and design of the study, AS, GJ, SK, DM, MB, DV, DK, MM and GM: data collection and analyses, AS: wrote the manuscript. All authors edited and approved the manuscript final version.

### Compliance with ethical standards

**Conflict of interest** The authors have no conflicts of interest.

### References

- Allen DG, Lamb GD, Westerblad H (2008) Skeletal muscle fatigue: cellular mechanisms. *Physiol Rev* 88:287–332. <https://doi.org/10.1152/physrev.00015.2007>
- Andrews SK, Horodyski JM, MacLeod DA, Whitten J, Behm DG (2016) The interaction of fatigue and potentiation following an acute bout of unilateral squats. *J Sports Sci Med* 15:625–632
- Bogdanis GC, Tsoukos A, Veligeas P, Tsolakis C, Terzis G (2014) Effects of muscle action type with equal impulse of conditioning activity on postactivation potentiation. *J Strength Cond Res* 28:2521–2528. <https://doi.org/10.1519/JSC.0000000000000444>
- Brazaitis M, Skurvydas A, Pukėnas K, Daniusevičiūtė L, Mickevicienė D, Solianik R (2012) The effect of temperature on amount and structure of motor variability during 2-minute maximum voluntary contraction. *Muscle Nerve* 46:799–809. <https://doi.org/10.1002/mus.23397>
- Bruton JD, Wretman C, Katz A, Westerblad H (1997) Increased tetanic force and reduced myoplasmic [Pi] following a brief series of tetani in mouse soleus muscle. *Am J Physiol* 272:870–874. <https://doi.org/10.1152/ajpcell.1997.272.3.C870>
- Buchanan R, Nielsen OB, Clausen T (2002) Excitation- and beta(2)-agonist induced activation of the Na(+)-K(+) pump in rat soleus muscle. *J Physiol* 545:229–240

- Cheng AJ, Yamada T, Rassier DE, Andersson DC, Westerblad H, Laner JT (2016) Reactive oxygen/nitrogen species and contractile function in skeletal muscle during fatigue and recovery. *J Physiol* 594:5149–5160. <https://doi.org/10.1113/JP270650>
- Cheng AJ, Neyroud D, Kayser B, Westerblad H, Place N (2017) Intramuscular contributions to low-frequency force potentiation induced by a high-frequency conditioning stimulation. *Front Physiol* 8:712. <https://doi.org/10.3389/fphys.2017.00712>
- Esformes JJ, Keenan M, Moody J, Bampouras TM (2011) Effect of different types of conditioning contraction on upper body post-activation potentiation. *J Strength Cond Res* 25:143–148. <https://doi.org/10.1519/JSC.0b013e31811fe7f3>
- Gittings W, Bunda J, Vandenboom R (2017) Myosin phosphorylation potentiated steady state work output without altering contractile economy of mouse fast skeletal muscles. *J Exp Biol* 221:jeb167742. <https://doi.org/10.1242/jeb.167742>
- Gouvêa AL, Fernandes IA, César EP, Silva WA, Gomes PS (2013) The effects of rest intervals on jumping performance: a meta-analysis on post-activation potentiation studies. *J Sports Sci* 31:459–467. <https://doi.org/10.1080/02640414.2012.738924>
- Hicks A, McComas AJ (1989) Increased sodium pump activity following repetitive stimulation of rat soleus muscles. *J Physiol* 414:337–349
- Jones DA (1996) High-and low-frequency fatigue revisited. *Acta Physiol Scand* 156:265–270. <https://doi.org/10.1046/j.1365-201X.1996.192000.x>
- Kamandulis S, Skurvydas A, Masiulis N, Mamkus G, Westerblad H (2010) The decrease in electrically evoked force production is delayed by a previous bout of stretch-shortening cycle exercise. *Acta Physiol (Oxf)* 198:91–98. <https://doi.org/10.1111/j.1748-1716.2009.02041.x>
- Kent-Braun JA (1999) Central and peripheral contributions to muscle fatigue in humans during sustained maximal effort. *Eur J Appl Physiol Occup Physiol* 80:57–63. <https://doi.org/10.1007/s004210050558>
- Kilduff LP, Cunningham DJ, Owen NJ, West DJ, Bracken RM, Cook CJ (2011) Effect of postactivation potentiation on swimming starts in international sprint swimmers. *J Strength Cond Res* 25:2418–2423. <https://doi.org/10.1519/JSC.0b013e318201bf7a>
- Lännergren J, Larsson L, Westerblad H (1989) A novel type of delayed tension reduction observed in rat motor units after intense activity. *J Physiol* 412:267–276
- Macintosh BR, Robillard ME, Tomaras EK (2012) Should postactivation potentiation be the goal of your warm-up? *Appl Physiol Nutr Metab* 37:546–550. <https://doi.org/10.1139/h2012-016>
- Miyamoto N, Kanehisa H, Kawakami Y (2012) Potentiation of maximal voluntary concentric torque in human quadriceps femoris. *Med Sci Sports Exerc* 44:1738–1746. <https://doi.org/10.1249/MSS.0b013e318256b813>
- Miyamoto N, Wakahara T, Ema R, Kawakami Y (2013) Further potentiation of dynamic muscle strength after resistance training. *Med Sci Sports Exerc* 45:1323–1330. <https://doi.org/10.1249/MSS.0b013e3182874c0e>
- Needham RA, Morse CI, Degens H (2009) The acute effect of different warm-up protocols on anaerobic performance in elite youth soccer players. *J Strength Cond Res* 23:2614–2620. <https://doi.org/10.1519/JSC.0b013e31811bf3ef>
- Nibali ML, Chapman DW, Robergs RA, Drinkwater EJ (2015) Considerations for determining the time course of post-activation potentiation. *Appl Physiol Nutr Metab* 40:1163–1170. <https://doi.org/10.1139/apnm-2015-0175>
- Place N, Ivarsson N, Venckunas T, Neyroud D, Brazaitis M, Cheng AJ et al (2015) Ryanodine receptor fragmentation and sarcoplasmic reticulum Ca<sup>2+</sup> leak after one session of high-intensity interval exercise. *Proc Natl Acad Sci USA* 112:15492–15497. <https://doi.org/10.1073/pnas.1507176112>
- Rassier DE, Macintosh BR (2000) Coexistence of potentiation and fatigue in skeletal muscle. *Braz J Med Biol Res* 33:499–508. <https://doi.org/10.1590/S0100-879X2000000500003>
- Requena B, Gapeyeva H, García I, Erelina J, Pääsuke M (2008) Twitch potentiation after voluntary versus electrically induced isometric contractions in human knee extensor muscles. *Eur J Appl Physiol* 104:463–472. <https://doi.org/10.1007/s00421-008-0793-8>
- Rodriguez-Falces J, Place N (2017) New insights into the potentiation of the first and second phases of the M-wave after voluntary contractions in the quadriceps muscle. *Muscle Nerve* 55:35–45. <https://doi.org/10.1002/mus.25186>
- Sale DG (2002) Postactivation potentiation: role in human performance. *Exerc Sport Sci Rev* 30:138–143
- Sasaki K, Tomioka Y, Ishii N (2012) Activation of fast-twitch fibers assessed with twitch potentiation. *Muscle Nerve* 46:218–227. <https://doi.org/10.1002/mus.23290>
- Seitz LB, Haff GG (2016) Factors modulating post-activation potentiation of jump, sprint, throw, and upper-body ballistic performances: a systematic review with meta-analysis. *Sports Med* 46:231–240. <https://doi.org/10.1007/s40279-015-0415-7>
- Shushakov V, Stubbe C, Peuckert A, Endeward V, Maassen N (2007) The relationships between plasma potassium, muscle excitability and fatigue during voluntary exercise in humans. *Exp Physiol* 92:705–715. <https://doi.org/10.1113/expphysiol.2006.036384>
- Skurvydas A, Zachovajevs P (1998) Is post-tetanic potentiation, low frequency fatigue (LFF) and pre-contraction depression (PCD) coexistent in intermittent isometric exercises of maximal intensity? *Acta Physiol Scand* 164:127–133. <https://doi.org/10.1046/j.1365-201X.1998.00415.x>
- Skurvydas A, Mamkus G, Kamandulis S, Dudoniene V, Valanciene D, Westerblad H (2016) Mechanisms of force depression caused by different types of physical exercise studied by direct electrical stimulation of human quadriceps muscle. *Eur J Appl Physiol* 116:2215–2224. <https://doi.org/10.1007/s00421-016-3473-0>
- Smith IC, Vandenboom R, Tupling AR (2017) Contraction-induced enhancement of relaxation during high force contractions of mouse lumbrical muscle at 37 °C. *J Exp Biol* 220:2870–2873. <https://doi.org/10.1242/jeb.158998>
- Stull JT, Kamm KE, Vandenboom R (2011) Myosin light chain kinase and the role of myosin light chain phosphorylation in skeletal muscle. *Arch Biochem Biophys* 510:120–128. <https://doi.org/10.1016/j.abb.2011.01.017>
- Thomas K, Toward A, West DJ, Howatson G, Goodall S (2017) Heavy-resistance exercise-induced increases in jump performance are not explained by changes in neuromuscular function. *Scand J Med Sci Sports* 27:35–44. <https://doi.org/10.1111/sms.12626>
- Tillin NA, Bishop D (2009) Factors modulating post-activation potentiation and its effect on performance of subsequent explosive activities. *Sports Med* 39:147–166. <https://doi.org/10.2165/00007256-200939020-00004>
- Vandenboom R (2016) Modulation of skeletal muscle contraction by myosin phosphorylation. *Compr Physiol* 7:171–212. <https://doi.org/10.1002/cphy.c150044>
- Vandenboom R, Gittings W, Smith IC, Grange RW, Stull JT (2013) Myosin phosphorylation and force potentiation in skeletal muscle: evidence from animal models. *J Muscle Res Cell Motil* 34:317–332. <https://doi.org/10.1007/s10974-013-9363-8>
- Verbickas V, Barauskiene N, Eimantas N, Kamandulis S, Rutkauskas S, Satkunskiene D et al (2017) Effect of sprint cycling and stretch-shortening cycle exercises on the neuromuscular, immune and stress indicators in young men. *J Physiol Pharmacol* 68:125–132
- Verbickas V, Kamandulis S, Snieckus A, Venckunas T, Barauskiene N, Brazaitis M et al (2018) Serum brain-derived neurotrophic factor and interleukin-6 response to high-volume mechanically demanding exercise. *Muscle Nerve* 57:E46–E51. <https://doi.org/10.1002/mus.25687>

- Westerblad H, Lännergren J (1986) Force and membrane potential during and after fatiguing, intermittent tetanic stimulation of single *Xenopus* muscle fibres. *Acta Physiol Scand* 128:369–378. <https://doi.org/10.1111/j.1748-1716.1986.tb07990.x>
- Wilson JM, Duncan NM, Marin PJ, Brown LE, Loenneke JP, Wilson SM et al (2013) Meta-analysis of postactivation potentiation and power: effects of conditioning activity, volume, gender, rest periods, and training status. *J Strength Cond Res* 27:854–859. <https://doi.org/10.1519/JSC.0b013e31825c2bdb>
- Xenofontos A, Bassa E, Vrabas IS, Kotzamanidis C, Patikas DA (2018) Muscle twitch torque during two different in volume isometric

exercise protocols: fatigue effects on post-activation potentiation. *J Strength Cond Res* 32:578–586. <https://doi.org/10.1519/JSC.0000000000002311>

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