European Journal of Sport Science

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tejs20

Plyometric exercise enhances twitch contractile properties but fails to improve voluntary rate of torque development in highly trained sprint athletes

Haiko Bruno Zimmermann, Filipe Estácio Costa, Raphael Sakugawa, Brian MacIntosh, Fernando Diefenthaeler & Juliano Dal Pupo

To cite this article: Haiko Bruno Zimmermann, Filipe Estácio Costa, Raphael Sakugawa, Brian MacIntosh, Fernando Diefenthaeler & Juliano Dal Pupo (2021): Plyometric exercise enhances twitch contractile properties but fails to improve voluntary rate of torque development in highly trained sprint athletes, European Journal of Sport Science, DOI: 10.1080/17461391.2021.1916083

To link to this article: https://doi.org/10.1080/17461391.2021.1916083

Published online: 16 May 2021.

EUROPEAN JOURNAL OF SPORT SCIENCE
https://doi.org/10.1080/17461391.2021.1916083

ORIGINAL RESEARCH

Plyometric exercise enhances twitch contractile properties but fails to improve voluntary rate of torque development in highly trained sprint athletes

Haiko Bruno Zimmermann [a,*], Filipe Estácio Costa[a], Raphael Sakugawa[a], Brian MacIntosh [b], Fernando Diefenthaeler [a] and Juliano Dal Pupo[a]

[a]Biomechanics Laboratory, Center of Sports, Federal University of Santa Catarina, Florianopolis, Brazil; [b]Human Performance Laboratory, Faculty of Kinesiology, University of Calgary, Calgary, Canada

ABSTRACT

Purpose: The objective of this study was to evaluate a plyometric conditioning activity (3 sets of 5 countermovement jumps, [CA]) for twitch properties and voluntary knee extension. *Methods*: After a familiarization session, fourteen highly trained sprint athletes, 12 men (23.25 ± 7.17 years) and 2 women (23.0 ± 2.8 years) performed 2 experiments, each in a randomized order (crossover design). In one experiment, the time-course of twitch contractile properties was evaluated with and without the previous CA at 2, min intervals to 10 min of recovery. In the second session, maximal voluntary knee extension was evaluated at the same recovery intervals, for control and experimental condition in random order. *Results*: Mixed-model ANOVA with Bonferroni post-hoc revealed significant differences between pre-test and 2 min ($p < 0.01$, ES = 0.42) and 4 min ($p < 0.01$, ES = 0.20) for peak twitch torque of quadriceps femoris muscles confirming postactivation potentiation [PAP] at these times. Twitch rate of torque development (RTD) was significantly greater than pre-test value only at 2 min ($p < 0.01$, ES = 0.58) after the CA. Twitch contraction time and ½ relaxation time were not significantly difference from pre-test values after the CA ($p > 0.05$). No significant difference was observed for voluntary RTD following CA. *Conclusion*: The plyometric CA increased twitch peak torque and RTD consistent with PAP; however, there was no effect of CA on voluntary RTD of knee extension at any time after the plyometric CA. Even with PAP confirmed, we observed that the CA fails to improve isometric RTD of quadriceps femoris muscles.

Highlights

- A plyometric CA significantly increased twitch peak torque (at 2 and 4 min) and twitch rate of torque development (at 2 min) of quadriceps femoris muscles, indicating postactivation potentiation (PAP).
- No effect was observed for twitch contraction time and ½ relaxation time after the CA.
- No improvement was observed on voluntary rate of torque development evaluated at the same time intervals.

KEYWORDS
Voluntary performance; sprints; postactivation performance enhancement; conditioning contraction; twitch properties

Abbreviations

PAP	Postactivation potentiation
PAPE	Postactivation performance enhancement
CA	Conditioning activity
MVC	Maximal voluntary contraction
PT	Peak torque
CT	Contraction time
½	time Half-relaxation time
ICC	Intraclass correlation coefficient
TEM	Typical Error of Measurement
CV	Coefficient of variation
SD	Standard deviation
RTD	Rate of torque development

Introduction

Postactivation potentiation (PAP) is a phenomenon traditionally characterized as an increased contractile response for a known activation observed after a voluntary conditioning contraction (i.e. conditioning activity [CA]) (MacIntosh, 2010; MacIntosh, Robillard, & Tomaras, 2012). The primary mechanism responsible for PAP relies on myosin light chain kinase (MLCK), which is activated by increased intracellular free [Ca^{2+}],

CONTACT Haiko Bruno Zimmermann hbzim@hotmail.com Biomechanics Laboratory, Center of Sports, Federal University of Santa Catarina, Campus Reitor João David Ferreira Lima, Trindade, Florianopolis, Santa Catarina, Brazil 88040–900
*Present address: Regional University of Blumenau (FURB), Blumenau, Brazil.

and results in phosphorylation of the regulatory light chains of myosin (Grange, Vandenboom, & Houston, 1993). This phosphorylation promotes mobility of the myosin heads and increases the probability of cross-bridge interaction (MacIntosh, 2010). To confirm the presence of PAP, contractile response (twitch) after supramaximal single-pulse electrical stimulation needs to be monitored before and after the CA. These stimuli allow assessment of any improvement in the muscle's intrinsic contractile response and help to determine the time-course over which the muscle demonstrates PAP after the CA. PAP confirmation through electrical stimulation has been extensively used in previous studies and, in general, increased twitch peak torque (PT) and/or rate of torque development (RTD) ranging from 10.7% to 60% has been reported (Bergmann, Kramer, & Gruber, 2013; Folland, Wakamatsu, & Fimland, 2008; Fukutani, Miyamoto, Kanehisa, Yanai, & Kawakami, 2012, 2013, 2014; Hodgson, Docherty, & Zehr, 2008; Mitchell & Sale, 2011).

PAP has been suggested to be associated with athletic performance improvements in voluntary activities (Sale, 2002; Wilson et al., 2013), referred as postactivation performance enhancement (PAPE) (Blazevich & Babault, 2019; Cuenca-Fernández et al., 2017; Prieske, Behrens, Chaabene, Granacher, & Maffiuletti, 2020; Zimmermann, MacIntosh, & Dal Pupo, 2020). It is anticipated that peak rate of force development will be increased in association with PAP and this will result in enhanced brief maximal effort contraction (Sale, 2002). However, recent systematic reviews (Blazevich & Babault, 2019; Prieske et al., 2020; Zimmermann et al., 2020) showed that the occurrence of PAP (confirmed by increased twitch PT) does not necessarily mean that voluntary performance will also be improved. According to Zimmermann et al. (2020), a potentialized state (PAP) seems to be able to improve voluntary performance when high PAP values are observed. It is known that the efficacy by which a CA can induce PAP and enhance muscular performance depends on the balance between fatigue and potentiation (Wilson et al., 2013). This balance is strongly influenced the intensity and duration of the CA and the rest interval before the performance test. The strength of individuals is also important (Seitz & Haff, 2016).

Several studies have been conducted to assess if CAs could elicit PAP and PAPE for brief maximal voluntary muscle contractions (Gossen and Sale 2000; Baudry & Duchateau, 2007; Gago et al., 2020). It is possible to find in the literature a wide range of CA protocols, but plyometric contraction stimulus is relatively novel and is easy to apply in practice (i.e. shortly before a competition), since the use of sophisticated equipment (squat cage, leg press, and dynamometer chair) usually will not be available, limiting the application of the activities with high loads as warm-up CA (Johnson, Baudin, Ley, & Collins, 2019). The study of Till and Cooke (2009) was one of the first to investigate the use of plyometric exercise as a CA and the results showed that 1 set of 5 vertical jumps was not capable of improving subsequent sprint performance in soccer players. It can be speculated that the low volume of the protocol was not enough to induce high levels of PAP and consequently affect voluntary performance, since a recent meta-analysis showed that multiple sets seem to be more positive (Seitz & Haff, 2016), with high PAP values required to affect voluntary performance (Zimmermann et al., 2020). Twitch measures were not taken by Till and Cook (2009), so it cannot be determined whether PAP was present or not.

Several studies (Bergmann et al., 2013; Bogdanis, Tsoukos, & Veligekas, 2017; Bridgeman, McGuigan, Gill, & Dulson, 2017; Chen, Wang, Peng, Yu, & Wang, 2013; Kümmel et al., 2016, 2017b; Zimmermann, Knihs, Diefenthaler, MacIntosh, & Dal Pupo, 2021) have used plyometric-based CA, and found positive results on athletic movements performance (e.g. sprints, long jump, drop jumps, vertical jumps). Among these studies, only some of them (Bergmann et al., 2013; Kümmel, Kramer, Cronin, & Gruber, 2017b; Zimmermann et al., 2021) verified the presence of PAP following plyometric CAs, relating this with the presence of PAPE. If PAP has contributed to PAPE, then it would be expected that peak rate of torque development of the voluntary contraction would be increased. This would be difficult to evaluate in a whole-body movement. Analysing contractile responses in a single muscle group like the quadriceps femoris (or the plantar flexors, as did Bergmann et al. 2013 and Kümmel et al. 2016), is important because they are considered a primary agonist muscle group in the main movements involving the lower limb. From a practical perspective, the confirmation of PAP (elevated intrinsic force generating capacity) and the best recovery interval after the plyometric CA could help coaches better delineate warm-up strategies incorporating these ease-of-use CAs, since possible positive effects using plyometric CA may be decisive for any sport in which rapid force development is needed (e.g. track and field, rugby, soccer). In addition, the twitch measures can assist in understanding the physiological mechanisms that acutely affect human performance (positively or negatively) after CAs.

In consideration of the background information presented above, the aim of this study was to evaluate the twitch contractile properties of the quadriceps femoris muscles in highly trained sprint athletes and its time-course after plyometric CA consisting of 3 sets of 5 CMJs. This will help to elucidate possible physiological mechanisms that may contribute or not to enhance performance. In addition, we aim to determine if plyometric-based CA can affect the voluntary RTD in the quadriceps femoris. The main hypothesis of this study is that plyometric CA can improve twitch response and this will correspond to increased RTD in maximal voluntary effort of highly trained sprinters.

Methods

Subjects

Fourteen sprint athletes, including twelve men (age: 23.25 ± 7.17 years; height: 179.0 ± 9.5 cm; body mass: 72.5 ± 12.2 kg) and two women (age: 23 ± 2.82 years; height: 169.0 ± 0.7 cm; body mass: 55.5 ± 0.7 kg) participated in this study. The sample size was calculated a priori based on a statistical power of 0.8, an effect size of 0.5 and an alpha level of $p < 0.05$ (Cohen, 1988). A minimum sample size of 11 individuals was obtained (G*Power – software package 3.1.9.2). We recruited 14 athletes to account for possible sample loss. The athletes were sprinters with 100 m personal best time ranging from 10.38 to 11.45 s for men and from 11.77 to 11.92 s for women. The participants were actively engaged in sprint training 5 days/week, weight training 2 d/week, and had a minimum of 3 years of experience in sprint training, competing at a national level. Moreover, no subject had any type of injury that could limit their physical performance during the tests. The recruited participants were instructed to avoid training during the evaluations, to eat and hydrate similarly at the same time before the tests, and to avoid caffeine-containing drinks for the 24 h prior to testing. All study participants were informed about the research objectives and the proposed methodology, and signed the Informed Consent Form. Parental consent was obtained for the 2 athletes who were under 18 years of age. The study was approved by the local ethics committee and was conducted according to the Declaration of Helsinki.

Experimental design

The present study was conducted with two objectives: (1) to verify the effects of a plyometric CA (3 sets of 5 countermovement jumps) on muscle twitch contractile properties of the quadriceps femoris muscles through the application of supramaximal electrical stimulation; (2) to verify the influence of a plyometric CA on voluntary RTD during a maximal isometric contraction of knee extensors. This study used a cross-over design, with a control and experimental condition, in which the same participants performed both experiments (PAP and PAPE measurements) in a randomized order, following the recommendation of previous reviews (Blazevich & Babault, 2019; MacIntosh et al., 2012).

The study was conducted over 3 sessions. In the first session, athletes were familiarized with the continuous countermovement jumps (CA), isometric contraction of knee extensors, and application of the electrical stimulus (twitch). On the second session, the time-course of twitch contractile properties was evaluated with and

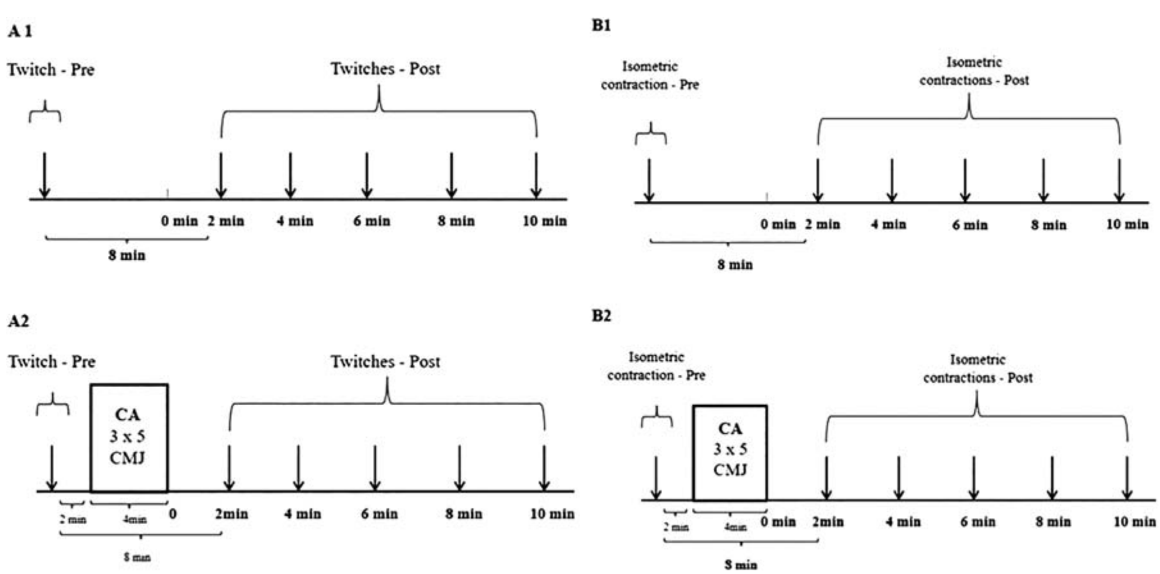

Figure 1. Experimental design for determination of twitch contractile properties for control (A1) and experimental (A2) condition and experimental design for determination voluntary performance of the quadriceps femoris muscles for control (B1) and experimental (B2) condition.

without the plyometric CA (experimental and control condition, respectively – Figure 1, panels A1 and A2) in a randomized order. During the third session, at least 24 h after the second session, a maximal isometric contraction of knee extensor muscles was used to calculate the voluntary RTD for control (without previous plyometric CA in a random order) and experimental conditions (with previous plyometric CA) over the same time intervals as the previous session for the twitches (Figure 1, panels B1 and B2). This would allow determination if the modifications associated with PAP and PAPE occur with the same recovery pattern.

Determination of twitch contractile properties

Before the evaluations, the athletes remained sitting quietly for at least 10 min to remove any warm-up or residual PAP that walking to the laboratory might have caused. This allows true interpretation of the real effect of only the CA (MacIntosh et al., 2012). Then, participants were positioned on the isokinetic dynamometer (Biodex Medical Systems 4, Shirley, NY, USA) with the lateral epicondyle of the knee aligned with its axis. The knee was positioned at 70° of flexion, considering 0° with the knee fully extended. Two self-adhesive electrodes (ValuTrode, Axelgaard, Fallbrook, CA, USA) were used for surface stimulation. The anode (97.5 cm^2 area) was positioned below the gluteal fold and the cathode (circular, 5 cm^2) in the femoral triangle over the femoral nerve. Initial twitch contractions served as the control condition. Rectangular pulses of 0.2 ms duration were applied using an electrical stimulator (Digitimer, Hertfordshire, UK – model DS7A/DS7AH) initially with submaximal current and high voltage (400 V). Electrode placement was adjusted to yield the highest twitch torque. After detecting the best electrode position, the current of the electrical stimulation was progressively increased until the highest twitch torque was observed. For this, the intensity of the stimulus was increased by approximately 15 mA at 5 s intervals until three successive increases of current no longer resulted in torque increases (Johnson et al., 2019). The lowest current to maximally activate the muscles was called the maximal current. To guarantee the activation of all motor units, a current 50% above the maximal current was then selected for subsequent twitch stimulation (Bergmann et al., 2013).

Two conditions were performed to determine the effects of the CA on the contractile properties: twitches at control (without previous plyometric CA) and experimental condition (with previous plyometric CA) separated by 20 min rest in between. The plyometric CA used in this study was 3 sets of 5 countermovement jumps with 1 min interval between sets. During the jump set, the athletes were instructed to keep their hands on the hips and keep the maximum intensity throughout all 5 jumps in all 3 sets. In the experimental condition, participants were rapidly position in the dynamometer chair with electrodes remaining in the same position, immediately after the last jump. The entire experimental session lasted approximately 18 min. Supramaximal stimulations (150% of maximum current) were applied at the same time intervals (2, 4, 6, 8, and 10 min after the CA) to determine quadriceps femoris contractile properties at each of these intervals. These time intervals were selected based on the metanalyses by Wilson et al. (2013) and.Seitz and Haff (2016) which showed that intervals of up to 10 min are adequate to increase performance; on the other hand, PAP effects decline very fast after the CA, reaching only small effects after 5 min (Blazevich and Babault, 2019).

During the control measurements, the participants remained seated on the dynamometer without actively contracting the muscles during the entire session. The following twitch properties were evaluated: (a) twitch peak torque (PT); calculated as the highest value of the torque–time curve, (b) twitch contraction time (CT), calculated as the duration of the twitch contraction from the onset of force development to the peak torque; (c) half relaxation time (½time), measured as the time from peak torque to 50% of active force; (d) the twitch maximal rate of torque development, obtained from the peak of the first derivative of the torque signal. All measures were made in accordance with what was done in the study of Baudry and Duchateau (2007) and the calculations were made using custom-made scripts in MATLAB® (Mathworks Inc., Natick, MA, USA). Also, the magnitude of PAP (i.e. augmented PT) was calculated using the following formula: PAP = (peak torque at post twitch / peak torque at Pre-CA Twitch × 100).

Determination of the effect of the CA on voluntary performance

In the experimental condition, participants performed the CA and after the last jump they were carefully positioned on the isokinetic dynamometer where they performed maximum isometric knee extensor muscle contractions each lasting 1–2 s, at same time intervals adopted for twitch contractile properties evaluations. The evaluator emphasized the "as fast as possible" command during all the isometric contractions. The same procedures were performed in the control condition, but without inclusion of CA. Figure 1 (B1 and B2 panels) illustrates the protocol for the evaluation of voluntary performance of the isometric contractions performed with maximal effort.

From the torque measurement, two RTD were calculated: at 100 ms after the onset of contraction ($RTD_{0\text{-}100}$) and the maximum slope of the torque–time curve (RTD_{PEAK}). The onset of torque for $RTD_{0\text{-}100}$ was defined as the point where the torque curve first exceeded the highest noise in the 500 ms prior to contraction, as previously used by Folland et al. (2008).

Statistical analyses

The within-session reliability was calculated in the pre-condition using the Intraclass Correlation Coefficient (ICC2:1), with the following classification: <0.50 poor; 0.50–0.75 moderate; 0.75–0.90 good; and >0.90 excellent (Fleiss, 1986). In addition, the typical error of measurement (TEM) (standard deviation of the differences of pre-test measures in experimental and control condition / square root of two) expressed in absolute values and as coefficient of variation were calculated. Mixed-model ANOVA (time x condition) with Bonferroni post-hoc was used for analysis. Data sphericity was tested by Mauchly tests and the Greenhouse-Geisser correction was used when necessary. Effect sizes (ES) were calculated (post–pre / pooled SD) for all variables, considering pre vs. 2 min, pre vs. 4 min, pre vs. 6 min, pre vs. 8 min and pre vs. 10 min, for control and experimental conditions. ES was classified as <0.2 trivial; 0.2–0.6 small; 0.6–1.2 moderate; 1.2–2.0 large; 2.0–4 very large; and >4.0 near perfect (Hopkins, Marshall, Batterham, & Hanin, 2009). The significance level adopted was $p < 0.05$. Statistical procedures were performed using SPSS® (Statistical Package for Social Sciences) v.17.0 (SPSS Inc., Chicago, IL, USA) software.

Results

Excellent within-session reliability was observed for voluntary RTD and for twitch variables (ICC values >0.90). In addition, the values of TEM (%) were relatively low, between 1.78-7.49% for all variables presented.

There was significant interaction of condition (control or experimental) vs. time ($p < 0.01$; F = 27.0; df = 5), for twitch PT (Figure 2). According to post-hoc analysis, there was an increase from pre (43.0 ± 15.0 N·m) to 2 min (50.0 ± 17.0; 17.19 ± 11.84%; $p < 0.01$, ES = 0.42) and to 4 min (46.2 ± 15.6; 17.19 ± 11.84%; $p < 0.01$, ES = 0.20) in the experimental condition. For control condition no significant differences were found ($p > 0.05$ across the time intervals).

For twitch RTD a significant condition X time interaction was observed ($p < 0.01$; F = 19.9; df = 5), and post-hoc analysis revealed an increase from pre (525.7 ± 168.8 N·m/s) to 2 min (638.5 ± 204.7 N·m/s; $p < 0.01$, ES = 0.58) in the experimental condition (Figure 3).

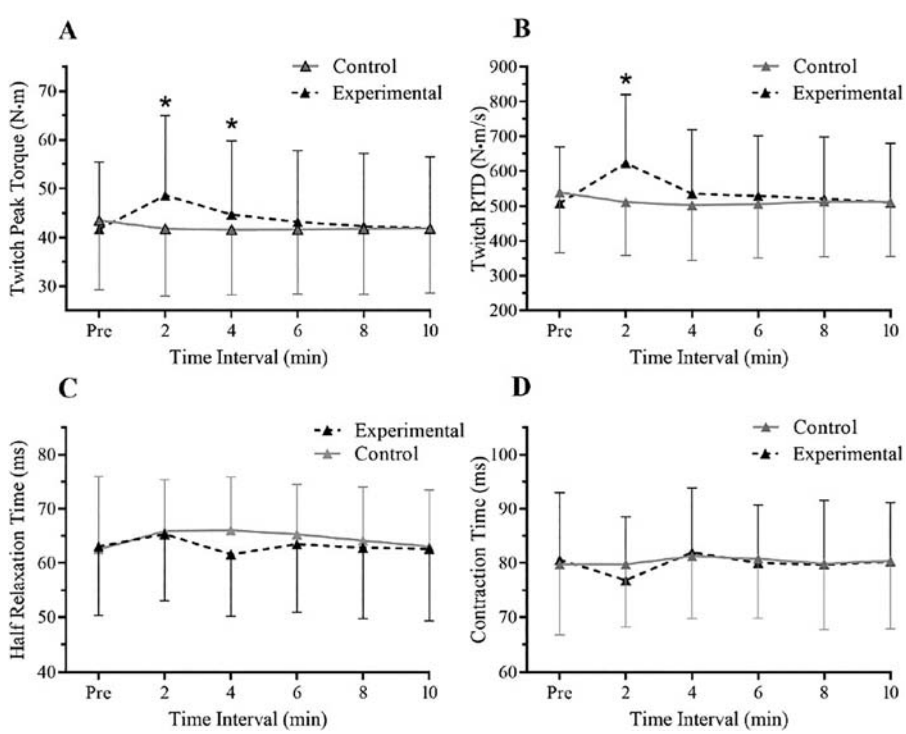

Figure 2. Values of twitch parameters for control and experimental condition at each time interval. Panel A: Twitch PT; Panel B: Twitch RTD; Panel C: Half-relaxation time; Panel D: Contraction time. * Indicates significant difference ($p < 0.05$).

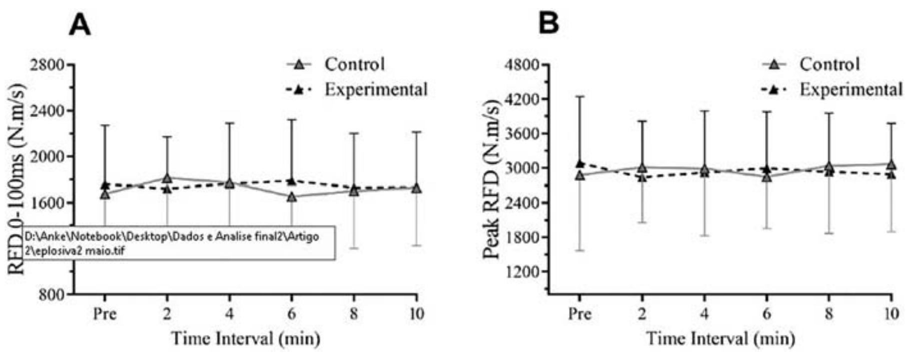

Figure 3. Comparison of voluntary rate of torque development in first 100 ms (RTD_{0-100} – Panel A) and peak (RTD_{peak} – Panel B) between conditions and time intervals. Triangles represent the mean value at each time interval, joined by horizontal lines and the vertical bars (error bars) represent the SD of each mean value at each time interval.

Table 1. Percent changes and effect sizes for voluntary RTD and twitch contractile properties when compared to pre-measure in each condition.

	Pre vs. 2 min Δ% (ES)	Pre vs. 4 min Δ% (ES)	Pre vs. 6 min Δ% (ES)	Pre vs. 8 min Δ% (ES)	Pre vs. 10 min Δ% (ES)
Twitch PT					
Control	−4.12% (0.11)	−4.39% (0.12)	−4.27% (0.12)	−4.01% (0.11)	−3.85% (0.10)
Experimental	+13.94%(0.42)	+6.90% (0.20)	+3.88% (0.11)	+2.6% (0.07)	+1.46%(0.04)
Twitch $_{RTD}$					
Control	−1.73%(0.05)	−1.89%(0.05)	−1.29%(0.04)	−0.67%(0.02)	−2.77%(0.08)
Experimental	+16.15%(0.49)	+1.69%(0.05)	−4.18%(0.11)	−3.10%(0.08)	−6.84%(0.17)
Twitch CT					
Control	+0.31+(0.02)	+1.87%(0.14)	+2.48%(0.19)	+0.31%(0.02)	+1.56%(0.11)
Experimental	−2.90%(0.23)	+3.03%(0.25)	+2.14%(0.18)	+1.54%(0.13)	+3.33%(0.28)
Twitch ½time					
Control	0%(0.00)	+0.75%(0.05)	−0.76%(0.05)	−1.55%(0.09)	+2.74%(0.16)
Experimental	+3.77%(0.25)	+3.77%(0.24)	+5.90%(0.39)	+2.29%(0.15)	+0.79%(0.05)
RTD_{0-100}					
Control	+5.16% (0.19)	+4.13% (0.14)	−3.81% (0.13)	−0.29% (0.01)	+0.88% (0.03)
Experimental	−3.42% (0.12)	−0.42% (0.01)	−0.24% (0.00)	−3.17% (0.11)	−1.69% (0.06)
RTD_{peak}					
Control	+4.86% (0.13)	+4.14% (0.10)	+−0.69% (0.01)	+6.04% (0.15)	+5.18% (0.13)
Experimental	−10.84% (0.28)	−6.26% (0.16)	−6.37% (0.17)	−8.35% (0.22)	−7.66% (0.22)

ES: *effect size;* Δ%: percent changes from pre-test.

Twitch RTD at other time intervals were not significantly different from pre-test values ($p > 0.05$).

For twitch CT and ½time no interaction was observed for condition vs. time ($p = 0.18$; F = 1.5; df = 5 and $p =$ 0.58, F = 0.7; df = 5 respectively), as well as no significant main effect was observed for the condition ($p = 0.84$, F = 0.4; df = 5 and $p = 0.58$, F = 0.7, df = 5, respectively) or time ($p = 0.18$; F = 1.8; df = 5 and $p = 0.10$; F = 2; df = 5, respectively).

Figure 3 shows the results of voluntary RTD of quadriceps femoris muscles before and after the plyometric CA. Voluntary isometric RTD_{PEAK} of knee extension showed no significant condition X time interaction (p = 0.06; F = 2.1; df = 5). Similarly, there was no significant difference between conditions ($p = 0.86$, F = 0.3) or over time ($p = 0.79$; F = 0.7; df = 5). Similar results were found for the voluntary isometric RTD_{0-100}, with no condition X time interaction ($p = 0.08$; F = 1.9; df = 5) as well as no effect of condition ($p = 0.96$, F = 0.0; df = 5) or time (p = 0.63; F = 0.2; df = 5).

Table 1 shows the percent change and the effect sizes (ES) comparing contractile measures at pre-test with each subsequent measure over time. Only trivial or small ES were observed for these measures at all-time points.

Discussion

The aim of this study was to evaluate the effects of a plyometric CA on contractile properties (using twitches) and on isometric RTD of knee extensor muscles of sprint athletes at different recovery intervals (2, 4, 6, 8, and 10 min). The main hypothesis of this study is that plyometric CA can improve twitch response and this will correspond to increased RTD in maximal voluntary effort of highly trained sprinters. The main findings showed that the plyometric CA significantly increased twitch PT (at 2 and 4 min) and twitch RTD (at 2 min) of quadriceps femoris muscles, indicating postactivation potentiation (PAP), thus, confirming our first hypothesis. However, no improvement was observed on voluntary RTD evaluated at the same time intervals, thus, rejecting our second hypothesis.

The occurrence of PAP in the present study was demonstrated by improvements in twitch PT at 2 and 4 min time intervals after the CA and twitch RTD only at 2 min. The most acceptable physiological mechanism explaining the increase in these twitch parameters after a CA is the phosphorylation of RLC due to the transfer of a phosphate group from adenosine triphosphate to a specific site on myosin (Vandenboom, 2017). This phosphorylation is thought to increase sensitivity of the contractile apparatus to the calcium released from the sarcoplasmic reticulum (Sweeney, Bowman, & Stull, 1993) because the phosphorylation increases the rate of engagement of cross-bridges (MacIntosh, 2010). When the number of cross-bridges increases, the force produced by the muscle also increases (Fukutani & Herzog, 2019). Alternative mechanisms have also been proposed (MacIntosh, 2010) and recent work suggests that increased concentration of Ca^{2+} in the myoplasm probably contributes to activity dependent potentiation (Glass, Cheng, & MacIntosh, 2020).

Among the twitch parameters evaluated, no effect was observed for contraction time and ½ relaxation time. For an individual to generate rapid movements in activities where consecutive agonist and antagonist muscle contractions are required, it is assumed that quick force relaxation and quick force generation could be a limiting factor (Mathern, Anhorn, & Uygur, 2019). The rate of muscle relaxation is mainly controlled by sarcoendoplasmic reticulum calcium transport ATPase (SERCA) and occurs when the available calcium is pumped back into the sarcoplasmic reticulum (Rossi & Dirksen, 2006). These results indirectly suggest that highly trained sprint athletes, who probably contain a high proportion of fast-twitch fibres in the leg muscles, do not modify the activity of this ion pump in an acute manner after a plyometric CA. So, it can be speculated that SERCA found in fast-twitch fibres was not affected by plyometric CA, consequently not affecting the voluntary performance. This also shows that, although phosphorylation of RLC is the main mechanism for an increase in PT and twitch RTD, a plyometric CA seems to not affect contraction time and ½ relaxation time. More studies using endurance athletes and other athletic populations need to be performed to test if different results may be found.

No effect was obtained for the voluntary performance evaluated here as RTD_{PEAK} and RTD_{0-100} in a maximal isometric contraction of the knee extensors. As showed recently, the occurrence of PAP does not necessarily mean that PAPE will also be observed (Blazevich & Babault, 2019; Prieske et al., 2020; Zimmermann et al., 2020), however PAPE can occur in the absence of PAP (Thomas, Toward, West, Howatson, & Goodall, 2017), presumably by a different mechanism. In a recent systematic review, it was verified that very high PAP levels need to be generated to affect voluntary performance (Zimmermann et al., 2020). Baudry and Duchateau (2007) observed PAP at 200% relative to the preconditioning contraction with concomitant enhanced voluntary performance at the corresponding time. Based on that, we can speculate that the enhanced twitch contractile response could have been of insufficient magnitude in our study to cause any modification in the voluntary performance. In addition, according to meta-analyses data, PAPE is more likely to occur at intervals of 5–12 min after the CA (Seitz & Haff, 2016; Wilson et al., 2013), at a time when PAP has already decreased or is absent. Considering this, it can also be speculated that other mechanisms (reviewed in detail by Blazevich & Babault, 2019) may be more important in manifesting positive effects on voluntary performance.

On the other hand, in a recent study (Zimmermann et al., 2021) using the same CA protocol (3 sets of 5 countermovement jumps), PAPE was evident as an increased 30 m sprint performance at 2 and 4 min of recovery time. This can lead us to think that some specific mechanism associated with stretch-shortening cycle was optimized after the jump-based CA and was capable of benefiting sprint performance that is also a stretch-shortening cycle-based exercise. The improvement in sprint performance cannot be attributed to PAP associated RTD assessed in an isometric manner. Evidence of a specific effect of plyometric conditioning activities came from the studies of Bergmann et al. (2013) and Kümmel et al. (2017b). They observed that 10 maximal repetitive reactive jumps (2 leg hops) used as CA enhanced DJ performance ranging between 5% and 12% in recreationally active men. This reinforces the idea of a specific adaptation to movements that incorporate stretch-shortening cycle. However, in contrast with Zimmermann et al. (2021), Kümmel et al. (2016) failed to show changes in 30 m sprint times in elite sprint athletes. We can speculate that the CA (10 hops) did not provide a stimulus with necessary intensity or volume for muscles involved in the sprints. It is important to highlight that different CA used with distinct muscles activated could explain the different results (Wilson et al., 2013).

It is possible that improved drop-jump performance (Kümmel, Cronin, Kramer, Avela, & Gruber, 2017a) can be explained by a mechanism independent of PAP. Kümmel et al. (2017a) observed a reduced fascicle lengthening in the transition from muscle-tendon unit lengthening to shortening after 10 repetitive reactive hops. The authors assume that this would result in an increased elongation of the passive elastic structures of the muscle-tendon unit, such as the calcaneal tendon or the connective tissue within the muscle. These results suggest improved stretch-shortening cycle function of storing and reusing elastic energy in the musculotendinous structures enabling more stored energy to be converted into mechanical work. Based on that, plyometric CA seems to produce specific adaptations that are able to improve the stretch-shortening cycle function, but not isometric RTD. From the molecular level, Brown and Loeb (1998) found an increase in force generated during a rapid muscle stretch after tetanic stimulus possibly explained through calcium mediated alterations in titin stiffness. This increased stiffness could also influence the transmission of force to Z disks in the sarcomere and consequently along the muscle fibres (Herzog, Schappacher, DuVall, Leonard, & Herzog, 2016) and in theory positively affect performance, since some level of stiffness is required for optimal stretch-shortening cycle utilization (Dal Pupo, Dias, Gheller, Detanico, & Santos, 2013). These speculations should be further explored after plyometric exercises to evaluate if specific stretch-shortening cycle mechanisms and elastic energy reuse can be optimized after plyometric-based CA that could only benefit related activities.

Another possible explanation for the lack of voluntary performance increases even with PAP has been confirmed comes from the fact that when RTD is calculated from the first milliseconds the neural discharge rate appears to be the main determinant (Andersen & Aagaard, 2006; Maffiuletti et al., 2016). A rapid/ballistic contraction, like the voluntary knee isometric contraction used in our study, is characterized by a highly synchronized burst of activity at the onset of the action (Van Cutsem, Duchateau, & Hainaut, 1998). As stated before, the force production by the muscle depends on the number of motor units recruited, and the rates at which motor neurons discharge action potentials (rate coding) (Maffiuletti et al., 2016). Consistent with this, the lack of improvements in RTD could be explained from the neural point of view, since changes in muscle properties do not seem to be determinant for RTD in sprint athletes.

Some limitations can be highlighted in this study. The first one is the lack of neuromuscular measures (H-reflex, M-wave) that could help explain the lack of improvement in voluntary RTD, thus future studies should include these measures after plyometric CA. In addition, voluntary performance depends on fatigue, muscle temperature, water content, activation/motivation, motor pattern interference (Blazevich & Babault, 2019) and these need to be strictly tested in future studies using plyometric CAs. As strengths of the present study we can highlight the type of CA (plyometric) chosen because it has ease of application in a variety of sports including track and field. This CA can be used as a warm-up procedure without special equipment and can be performed in small spaces. However, our results with highly trained sprint athletes who are highly familiarized with strength training, showed no improvement in voluntary RTD. Future studies should test the stretch-shortening cycle specificity using single and multi-joint exercises after plyometric CA to confirm or not a specific optimized mechanism related to stretch-shortening cycle.

Conclusion

In summary, our plyometric protocol consisting of 3 sets of 5 countermovement jumps was able to improve the intrinsic muscle properties (twitch PT and RTD) determined through involuntary electrical stimulation at 2 and 4 min after conditioning activity; however our results suggest that this enhanced muscle state did not translate to improvements in voluntary RTD. Therefore, the assumed mechanism of PAP was not likely the mechanism by which this CA enhanced sprint performance in our previous study (Zimmermann et al., 2021).

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Haiko Bruno Zimmermann http://orcid.org/0000-0003-3703-5808
Brian MacIntosh http://orcid.org/0000-0002-7475-9939
Fernando Diefenthaeler http://orcid.org/0000-0001-5632-8994

References

Andersen, L. L., & Aagaard, P. (2006). Influence of maximal muscle strength and intrinsic muscle contractile properties on contractile rate of force development. *European Journal of Applied Physiology*, *96*(1), 46–52. doi:10.1007/s00421-005-0070-z

Baudry, S., & Duchateau, J. (2007). Postactivation potentiation in a human muscle: Effect on the rate of torque development of tetanic and voluntary isometric contractions. *Journal of Applied Physiology*, *102*(4), 1394–1401. doi:10.1152/japplphysiol.01254.2006

Bergmann, J., Kramer, A., & Gruber, M. (2013). Repetitive hops induce postactivation potentiation in triceps surae as well as an increase in the jump height of subsequent maximal drop jumps. *PLoS One*, *8*(10), e77705. doi:10.1371/journal.pone.0077705

Blazevich, A. J., & Babault, N. (2019). Post-activation potentiation versus post-activation performance enhancement in humans: Historical perspective, underlying mechanisms, and current issues. *Frontiers in Physiology*, *10*(November), doi:10.3389/fphys.2019.01359

Bogdanis, G. C., Tsoukos, A., & Veligekas, P. (2017). Improvement of long-jump performance during competition using a plyometric exercise. *International Journal of Sports Physiology and Performance*, *12*(2), 235–240. doi:10.1123/ijspp.2016-0116

Bridgeman, L. A., McGuigan, M. R., Gill, N. D., & Dulson, D. K. (2017). The effects of accentuated eccentric loading on the drop jump exercise and the subsequent postactivation potentiation response. *Journal of Strength and Conditioning Research*, *31*(6), 1620–1626. doi:10.1519/JSC.0000000000001630

Brown, I. E., & Loeb, G. E. (1998). Post-activation potentiation-a clue for simplifying models of muscle dynamics1. *American Zoologist*, *38*(4), 743–754. doi:10.1093/icb/38.4.743

Chen, Z. R., Wang, Y. H., Peng, H. T., Yu, C. F., & Wang, M. H. (2013). The acute effect of drop jump protocols with different volumes and recovery time on countermovement jump performance. *Journal of Strength and Conditioning Research*, *27*(1), 154–158. doi:10.1519/JSC.0b013e3182518407

Cohen, J. (1988). *Statistical power analysis for the Behavioral Sciences*. New York: Routledge Academic.

Cuenca-Fernández, F., Smith, I. C., Jordan, M. J., MacIntosh, B. R., López-Contreras, G., Arellano, R., & Herzog, W. (2017). Nonlocalized postactivation performance enhancement (PAPE) effects in trained athletes: A pilot study. *Applied Physiology, Nutrition, and Metabolism*, *42*(10), 1122–1125. doi:10.1139/apnm-2017-0217

Dal Pupo, J., Dias, J. A., Gheller, R. G., Detanico, D., & Santos, S. G. D. (2013). Stiffness, intralimb coordination, and joint modulation during a continuous vertical jump test. *Sports Biomechanics*, *12*(3), 259–271. doi:10.1080/14763141.2013.769619

Fleiss, J. L. (1986). *Design and analysis of clinical experiments.* New York: Willey.

Folland, J. P., Wakamatsu, T., & Fimland, M. S. (2008). The influence of maximal isometric activity on twitch and H-reflex potentiation, and quadriceps femoris performance. *European Journal of Applied Physiology*, *104*(4), 739–748. doi:10.1007/s00421-008-0823-6

Fukutani, A., & Herzog, W. (2019). Current understanding of residual force enhancement: Cross-bridge component and non-cross-bridge component. *International Journal of Molecular Sciences*, *20*, 5479. doi:10.3390/ijms20215479

Fukutani, A., Hirata, K., Miyamoto, N., Kanehisa, H., Yanai, T., & Kawakami, Y. (2014). Effect of conditioning contraction intensity on postactivation potentiation is muscle dependent. *Journal of Electromyography and Kinesiology*, *24*(2), 240–245. doi:10.1016/j.jelekin.2014.01.002

Fukutani, A., Miyamoto, N., Kanehisa, H., Yanai, T., & Kawakami, Y. (2012). Influence of the intensity of a conditioning contraction on the subsequent twitch torque and maximal voluntary concentric torque. *Journal of Electromyography and Kinesiology*, *22*(4), 560–565. doi:10.1016/j.jelekin.2012.03.007

Fukutani, A., Miyamoto, N., Kanehisa, H., Yanai, T., & Kawakami, Y. (2013). Potentiation of isokinetic torque is velocity-dependent following an isometric conditioning contraction. *Springerplus*, *2*(1), 1–10. doi:10.1186/2193-1801-2-554

Gago, P., Zoellner, A., Cézar Lima da Silva, J., & Ekblom, M. M. (2020). Post activation potentiation and concentric contraction performance. *Journal of Strength and Conditioning Research*, *34*, 1600–1608. doi:10.1519/JSC.0000000000002427

Glass, L. D., Cheng, A. J., & MacIntosh, B. R. (2020). Calcium sensitivity during staircase with sequential incompletely fused contractions. *Journal of Muscle Research and Cell Motility*, *0123456789*, doi:10.1007/s10974-019-09572-4

Gossen, E. R., Sale, D. G. (2000). Effect of postactivation potentiation on dynamic knee extension performance. *European Journal Of Applied Physiology*, *83*(6), 524–530. doi:10.1007/s004210000304

Grange, R. W., Vandenboom, R., & Houston, M. E. (1993). Physiological significance of myosin phosphorylation in skeletal muscle. *Canadian Journal of Applied Physiology*, *18*(3), 229–242. doi:10.1139/h93-020

Herzog, W., Schappacher, G., DuVall, M., Leonard, T. R., & Herzog, J. A. (2016). Residual force enhancement following eccentric contractions: A new mechanism involving titin. *Physiology*, *31*(4), 300–312. doi:10.1152/physiol.00049.2014

Hodgson, M. J., Docherty, D., & Zehr, E. P. (2008). Postactivation potentiation of force is independent of H-reflex excitability. *International Journal of Sports Physiology and Performance*, *3*(2), 219–231. doi:10.1123/ijspp.3.2.219

Hopkins, W. G., Marshall, S. W., Batterham, A. M., & Hanin, J. (2009). Progressive statistics for studies in sports medicine and exercise science. *Medicine & Science in Sports &Exercise*, *41*(1), 3–12. doi:10.1249/MSS.0b013e31818cb278

Johnson, M., Baudin, P., Ley, A. L., & Collins, D. F. (2019). A warm-up routine that incorporates a plyometric protocol potentiates the force-generating capacity of the quadriceps muscles. *Journal of Strength and Conditioning Research*, *33*(2), 380–389. doi:10.1519/JSC.0000000000002054

Kümmel, J., Bergmann, J., Prieske, O., Kramer, A., Granacher, U., & Gruber, M. (2016). Effects of conditioning hops on drop jump and sprint performance: A randomized crossover pilot study in elite athletes. *BMC Sports Science, Medicine and Rehabilitation*, *8*(1), 1. doi:10.1186/s13102-016-0027-z

Kümmel, J., Cronin, N. J., Kramer, A., Avela, J., & Gruber, M. (2017a). Conditioning hops increase triceps surae muscle force and achilles tendon strain energy in the stretch-shortening cycle. *Scandinavian Journal of Medicine & Science in Sports*, *28*(1), 126–137. doi:10.1111/sms.12870

Kümmel, J., Kramer, A., Cronin, N. J., & Gruber, M. (2017b). Postactivation potentiation can counteract declines in force and power that occur after stretching. *Scandinavian Journal of Medicine & Science in Sports*, *27*(12), 1750–1760. doi:10.1111/sms.12817

MacIntosh, B. R. (2010). Cellular and whole muscle studies of activity dependent potentiation. *In Biotecnologia Aplicada*, 315–342. doi:10.1007/978-1-4419-6366-6_18

MacIntosh, B. R., Robillard, M.-E., & Tomaras, E. K. (2012). Should postactivation potentiation be the goal of your warm-up? *Applied Physiology, Nutrition, and Metabolism*, *37*(3), 546–550. doi:10.1139/h2012-016

Maffiuletti, N. A., Aagaard, P., Blazevich, A. J., Folland, J., Tillin, N., & Duchateau, J. (2016). Rate of force development: Physiological and methodological considerations. *European Journal of Applied Physiology*, *116*(6), 1091–1116. doi:10.1007/s00421-016-3346-6

Mathern, R. M., Anhorn, M., & Uygur, M. (2019). A novel method to assess rate of force relaxation: Reliability and comparisons with rate of force development across various muscles. *European Journal of Applied Physiology*, *119*(1), 291–300. doi:10.1007/s00421-018-4024-7

Mitchell, C. J., & Sale, D. G. (2011). Enhancement of jump performance after a 5-RM squat is associated with postactivation potentiation. *European Journal of Applied Physiology*, *111*(8), 1957–1963. doi:10.1007/s00421-010-1823-x

Prieske, O., Behrens, M., Chaabene, H., Granacher, U., & Maffiuletti, N. A. (2020). Time to differentiate postactivation "potentiation" from "performance enhancement" in the strength and conditioning community. *Sports Medicine*, *0123456789*, doi:10.1007/s40279-020-01300-0

Rossi, A. E., & Dirksen, R. T. (2006). Sarcoplasmic reticulum: The dynamic calcium governor of muscle. *Muscle and Nerve*, *33*(6), 715–731. doi:10.1002/mus.20512

Sale, D. G. (2002). Postactivation potentiation: Role in human performance. *Exercise and Sport Sciences Reviews*, *30*(3), 138–143. doi:10.1136/bjsm.2002.003392

Seitz, L. B., & Haff, G. G. (2016). Factors modulating post-activation potentiation of jump, sprint, throw, and upper-body ballistic performances: A systematic review with meta-analysis. *Sports Medicine*, *46*(2), 231–240. doi:10.1007/s40279-015-0415-7

Sweeney, H. L., Bowman, B. F., & Stull, J. T. (1993). Myosin light chain phosphorylation in vertebrate striated muscle: Regulation and function. *American Journal of Physiology*, *264*(5 Pt 1), C1085-95. doi:10.1152/ajpcell.1993.264.5.C1085

Till, K. A., & Cooke, C. (2009). The effects of postactivation potentiation on sprint and jump performance of male academy soccer players. *Journal of Strength and Conditioning Research*, *23*, 1960–1967. doi:10.1519/JSC.0b013e3181b8666e

Thomas, K., Toward, A., West, D. J., Howatson, G., & Goodall, S. (2017). Heavy-resistance exercise-induced increases in jump performance are not explained by changes in neuromuscular function. *Scandinavian Journal of Medicine & Science in Sports*, *27*(1), 35–44. doi:10.1111/sms.12626

Van Cutsem, M., Duchateau, J., & Hainaut, K. (1998). Changes in single motor unit behaviour contribute to the increase in contraction speed after dynamic training in humans. *The Journal of Physiology*, *513*(Pt 1(1)), 295–305. doi:10.1111/j.1469-7793.1998.295by.x

Vandenboom, R. (2017). Modulation of skeletal muscle contraction by myosin phosphorylation. *Comprehensive Physiology*, *7*(1), 171–212. doi:10.1002/cphy.c150044

Wilson, J. M. C., Duncan, N. M., Marin, P. J., Brown, L. E., Loenneke, J. P., Wilson, S. M. C., … Ugrinowitsch, C. (2013). Meta-analysis of postactivation potentiation and power: Effects of conditioning activity, volume, gender, rest periods, and training status. *Journal of Strength and Conditioning Research*, *27*(3), 854–859. doi:10.1519/JSC.0b013e31825c2bdb

Zimmermann, H. B., Knihs, D., Diefenthaler, F., MacIntosh, B., & Dal Pupo, J. (2021). Continuous jumps enhance twitch peak torque and sprint performance in highly trained sprint athletes. *International Journal of Sports Physiology and Performance*, 1–8. doi:10.1123/ijspp.2020-0240

Zimmermann, H. B., MacIntosh, B. R., & Dal Pupo, J. (2020). Does postactivation potentiation (PAP) increase voluntary performance? *Applied Physiology, Nutrition, and Metabolism*, *45*(4), 349–356. doi:10.1139/apnm-2019-0406