

Does postactivation potentiation (PAP) increase voluntary performance?



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Abstract: The transient increase in torque of an electrically evoked twitch following a voluntary contraction is called postactivation potentiation (PAP). Phosphorylation of myosin regulatory light chains is the most accepted mechanism explaining the enhanced electrically evoked twitch torque. While many authors attribute voluntary postactivation performance enhancement (PAPE) to the positive effects of PAP, few actually confirmed that contraction was indeed potentiated using electrical stimulation (twitch response) at the time that PAPE was measured. Thus, this review aims to investigate if increases in voluntary performance after a conditioning contraction (CC) are related to the PAP phenomenon. For this, studies that confirmed the presence of PAP through an evoked response after a voluntary CC and concurrently evaluated PAPE were reviewed. Some studies reported increases in PAPE when PAP reaches extremely high values. However, PAPE has also been reported when PAP was not present, and unchanged/diminished performance has been identified when PAP was present. This range of observations demonstrates that mechanisms of PAPE are different from mechanisms of PAP. These mechanisms of PAPE still need to be understood and those studying PAPE should not assume that regulatory light chain phosphorylation is the mechanism for such enhanced voluntary performance.

Novelty

- The occurrence of PAP does not necessarily mean that the voluntary performance will be improved.
- Improvement in voluntary performance is sometimes observed when the PAP level reaches extremely high values.
- Other mechanisms may be more relevant than that for PAP in the manifestation of acute increases in performance following a conditioning contraction.

Key words: skeletal muscle function, sports performance, athlete training, conditioning contraction, twitch, sprint running.

Résumé : L'augmentation transitoire du moment de force d'une secousse évoquée électriquement à la suite d'une contraction volontaire est appelée potentialisation postactivation (« PAP »). La phosphorylation des chaînes légères régulatrices de myosine est le mécanisme le plus accepté pour expliquer l'amélioration du moment de force de la secousse évoquée électriquement. Alors que de nombreux auteurs attribuent l'amélioration postactivation de la performance volontaire (« PAPE ») aux effets positifs de la PAP, peu confirme, documentation à l'appui, que la contraction est effectivement potentialisée par la stimulation électrique (déclenchant la secousse) au moment de la mesure de la PAPE. La présente analyse vise donc à déterminer si les augmentations de la performance volontaire après une contraction de conditionnement (« CC ») sont liées au phénomène de PAP. À cette fin, les études confirmant la présence d'une PAP par une réponse évoquée après une CC volontaire et par une PAPE évaluée simultanément sont incluses dans l'analyse. Certaines études révèlent une augmentation de la PAPE lorsque la PAP atteint des valeurs extrêmement élevées. Cependant, la PAPE est également observée en l'absence de PAP et des performances inchangées / diminuées sont observées en présence d'une PAP. Cette gamme d'observations révèle que les mécanismes de la PAPE sont différents des mécanismes d'une PAP. Ces mécanismes de la PAPE doivent encore être étudiés et ceux qui analysent la PAPE ne doivent pas supposer que la phosphorylation de la chaîne légère de régulation est le mécanisme permettant l'amélioration de telles performances volontaires. [Traduit par la Rédaction]

Les nouveautés

- La présence de la PAP ne signifie pas nécessairement que la performance volontaire sera améliorée.
- Une amélioration de la performance volontaire est parfois observée lorsque le niveau de PAP atteint des valeurs extrêmement élevées.
- D'autres mécanismes peuvent être plus pertinents que ceux de la PAP dans la manifestation d'augmentations ponctuelles de la performance après une contraction de conditionnement.

Mots-clés : fonction des muscles squelettiques, performance sportive, entraînement des athlètes, contraction de conditionnement, contraction, sprint à la course.

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1. Introduction

The contraction history partially determines skeletal muscle contractile responses (Sale 2002, 2004; Hodgson et al. 2005). One of the consequences of contraction history is fatigue, leading to reduction in strength, speed, work, and muscle power (Sargeant 2007), which negatively affects performance (Sale 2002; MacIntosh and Shahi 2011). Another consequence of contraction history, i.e., previous muscle activation, is an increased subsequent contractile response for a known activation, commonly evaluated with electrical stimulation (MacIntosh and Willis 2000; MacIntosh et al. 2012). When previous contraction originates from a voluntary activation, the subsequent increase of a contractile response for a known activation is referred to as postactivation potentiation (PAP). Alternatively, when previous contraction originates from an electrically evoked contraction the subsequent increase of contractile response has been called post-tetanic potentiation (MacIntosh 2010). The previous muscle activation is referred to as conditioning contraction (CC) (Tillin and Bishop 2009; MacIntosh et al. 2012). The effect of previous muscle contraction on subsequent torque increase of evoked responses has already been documented, mainly with studies involving animals (Brown and Tuttle 1926; Brown and von Euler 1938). The main accepted mechanism associated with increased torque due to prior activation is phosphorylation of the myosin regulatory light chains (RLC) (Manning and Stull 1979; Grange et al. 1993; Vandenboom et al. 1993), which increases calcium sensitivity of the contractile apparatus (Persechini et al. 1985; Vandenboom 2017), enhancing the interaction between actin and myosin in the active muscle (Sweeney and Stull 1990).

Although PAP does not increase maximal force, it does increase the rate of force development (RFD), even with maximal effort. Sale (2002) suggests that theoretically, PAP could be used as part of a warm-up routine in preparation for a high-intensity performance because it could increase peak force when contraction duration is short. This speculation set off a series of research studies to see if the CCs that would be expected to elicit PAP could enhance subsequent performance of brief maximal effort movements. It should be pointed out, however, that enhanced voluntary performance after a high-intensity CC can occur by several mechanisms, not just the mechanism known to be associated with PAP.

This notion that PAP could be part of a warm-up has created confusion in the literature. The term PAP has been used in several studies where the presence of PAP has not been confirmed with evoked responses and probably was not present (MacIntosh et al. 2012). This confusion was pointed out by Cuenca-Fernandez et al. (2017). Several studies have been completed putatively evaluating the apparent role of PAP in enhancing voluntary performance, without confirming that potentiation of the contractile properties was present by using supramaximal stimulation. The design of these studies has typically involved the following sequence: performance test, conditioning contraction, wait, and performance test. The second performance test is often a better performance than the first and the authors assume that PAP caused the improvement, even when the wait was sufficient to allow full dephosphorylation of the RLC of myosin. Cuenca-Fernandez et al. (2017) demonstrated that a second performance test is improved relative to a first performance test, even when no CC was permitted. This observation indicates that mechanisms other than PAP contribute to this improved performance. Several factors unrelated to the phosphorylation of the myosin RLC, but considered part of warm-up, could contribute to improved voluntary performance. These alternative mechanisms include temperature increases (Bishop 2003; McGowan et al. 2015; Silva et al. 2018), increased excitability of motoneurons (Folland et al. 2008), increased recruitment of motor units (Tillin and Bishop 2009), acute elevations in plasma catecholamines levels (Cairns and Borrani

2015), increases in the circulating concentration of testosterone after exercise (Crewther et al. 2011), learning effect and familiarization with the main task (MacIntosh et al. 2012), and placebo effect and subject motivation (Beedie and Foad 2009). In these cases, it is practically impossible to determine the contribution of each of these potential factors to the performance of the second performance test.

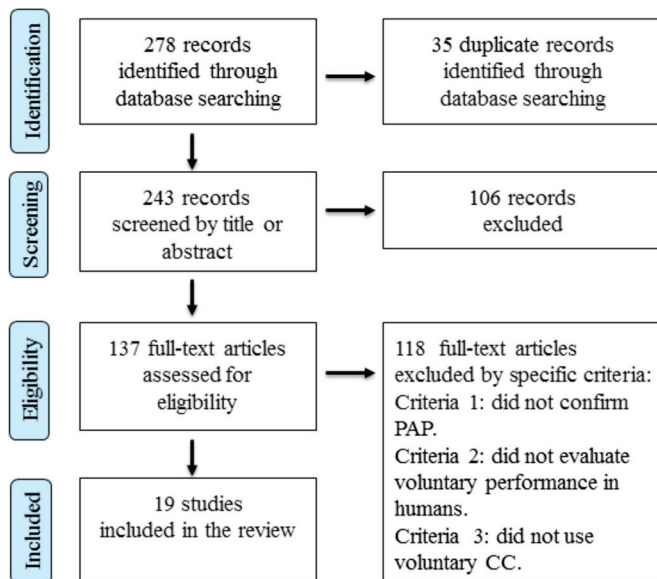
Based on these observations, Cuenca-Fernández et al. (2017) have suggested the term postactivation performance enhancement (PAPE) be used to reflect an increase in performance of a task following a voluntary contraction. This enhanced performance may be influenced in part by PAP as well as by any other mechanisms mentioned above. Thus, it is important to emphasize that care should be taken when interpreting studies inferring participation of the PAP phenomenon when the voluntary performance is assessed without information about the contractile properties through an electrically evoked response. When contractile properties are not assessed, one can only speculate that PAP was present and was a contributing factor in the results when performance was accomplished at a time when light chain phosphorylation should be present, as suggested by many authors (Rassier et al. 1999; MacIntosh 2010; Tomaras and MacIntosh 2011; MacIntosh et al. 2012; Fukutani et al. 2014b; Gago et al. 2014). Moreover, even when PAP has been confirmed to exist at the time of the improved performance, the above list of alternative mechanisms cannot be simply discarded; the actual role of this “artificially observed” torque increase in voluntary performance has not yet been fully clarified (Vandenboom 2017).

Thus, this review aims to investigate if increases in voluntary performance after a CC are related to the PAP phenomenon. For this, studies that confirmed the presence of PAP through an evoked (brief supramaximal stimulation) response after a voluntary CC and occurred at the same time as a subsequent voluntary performance will be evaluated. These 2 independent measures would ensure that the muscle was indeed potentiated at the specific time when the performance was tested. In addition, the possible physiological mechanisms involved will also be discussed. Most of the recent studies in the literature, that mention PAP, did not confirm PAP, leaving doubt if an enhanced contractile response was present when the second performance test was measured. In this case, other mechanism may have caused the improvements. This review will better clarify the role of PAP and the related possible acute changes on voluntary performance associated with it.

2. Methodological procedures

An electronic search was conducted to identify relevant scientific articles for the purpose of this review, using PubMed and Scopus databases with the following descriptors: postactivation potentiation, PAP, twitch, and performance. Two-hundred and seventy-eight articles were initially found. After deletion of the duplicate articles, there were 243 articles remaining. The individual analysis of the title and the abstracts of the articles allowed the application of the inclusion and exclusion criteria (Fig. 1). After F1 reading the titles and abstracts, 137 articles were selected. These were the articles that involved measurement of PAP and voluntary performance in humans. Then, after a detailed reading of the complete articles, 19 articles were included in the results table. As criteria to be included they had to be original human subject investigations and use a voluntary CC with confirmation of PAP through an evoked response with supramaximal stimulation at the same recovery interval that the second voluntary performance was measured. Articles that did not confirm PAP through supramaximal electrical stimulation or were performed in animals were excluded. The flow diagram (Fig. 1) shows the screening processes.

Fig. 1. PRISMA flow diagram: studies that underwent the review process. CC, conditioning contraction; PAP, postactivation potentiation.



3. Results

Table 1 presents details of methods and main results of the 19 studies included in this review that analyzed voluntary performance with confirmation of PAP.

4. Discussion

4.1. The role of PAP in voluntary performance

There are many studies that attribute a possible voluntary performance improvement to the positive effects of PAP, but few of them measured whether contractile properties were indeed potentiated using supramaximal electrical stimulation (twitch response) at the same recovery intervals that voluntary performance was measured. Performance enhancement associated with prior voluntary conditioning contraction should be referred to as PAPE and the mechanism can be considered unknown, unless PAP is confirmed to coexist with PAPE. In this review, we analyzed only studies that confirmed PAP, avoiding those articles where PAP was simply assumed. We verified that all studies reported contractile response improvements immediately after a CC; however, only in some specific cases were these improvements observed in the contractile properties associated with a concurrent improved voluntary performance. It was also observed in some studies that improvements of performance (PAPE) occurred at times for which PAP was not present, suggesting that factors other than PAP contribute to acutely enhance voluntary performance after a CC.

There is a large difference in the magnitude of increase of a twitch (which represents the most sensitive contractile response) and the increase in voluntary performance after a CC (Cuenca-Fernández et al. 2017). The torque increase in the twitch observed with electrical stimulation is maximal immediately after a CC, with values approaching 200% (depending on the muscle evaluated) and torque falls exponentially over time, approaching the pre-CC value within a few minutes (Baudry and Duchateau 2004). Increases in voluntary performance usually occur at longer and distinct intervals, generally from 5 to 12 min (Wilson et al. 2013; Seitz and Haff 2016) at a time when PAP has already decreased dramatically or is absent. Thus, it is possible that most of the studies in the literature that did not evaluate the contractile properties for confirmation of PAP have incorrectly attributed the improved voluntary performance to PAP. Furthermore, even in

studies in which PAP was confirmed, it is still not possible to guarantee that in fact the increased performance was due to PAP or some other mechanism not yet known.

Baudry and Duchateau (2007a) were the first authors to report improvements in voluntary performance of thumb adductors (9%–24%) after a CC with confirmation of PAP through supramaximal electrical stimulation at the specific time points where performance was evaluated. However, the time-course and magnitude of the responses differed considerably. The increase in RFD in the twitch (200%) was maximal immediately after the CC and dissipated over the next 10 min, whereas high-frequency evoked contractions (17%) and isometric voluntary ballistic performance (9%–24%) had their peaks at 1 min after CC and enhancement lasted 5 and 2 min, respectively. The difference in the improvement of the high-frequency train (250 Hz) compared with the twitch (both evoked electrically), shows that a saturation process limits the magnitude of PAP in successive responses within a train of stimuli. This saturation process had already been demonstrated by Baudry et al. (2005), who observed that PAP saturation increases when stimulation frequency is increased (Baudry et al. 2005). This may be an indication that the impact of PAP on voluntary contractions is limited, since frequencies greater than 100 Hz are comparable to the observed frequencies during voluntary ballistic contractions (Van Cutsem et al. 1998). In a similar study, Baudry and Duchateau (2007b) found that an MVC of 6 s was able to increase peak angular velocity during voluntary ballistic contractions (14%), but, in the same way, the magnitude during the voluntary contractions was extremely limited compared with the improvements observed in the peak angular velocity for a single stimulus (twitch: ~182%). In these 2 studies, the levels of PAP were extremely high and just small increases were observed in voluntary ballistic performance of the thumb adductors at specific intervals in the recovery period. Furthermore, voluntary performance improvements lasted only 2 min, even when PAP measured with twitch contractions was significant for 10 min. This is an important result and demonstrates the nonlinearity between PAP magnitude and acute changes in performance.

Distinct time-course and magnitude differences between PAP (twitch properties) and voluntary performance have been consistently reported in the literature. Consistent with the studies cited above for the thumb adductor, Miyamoto et al. (2011) observed that following an MVC of 6 s, the concentric voluntary isokinetic torque of the plantar flexors was increased only at 1–3 min after the CC. In contrast, the PAP measured by twitch was maximum (178.6%) immediately after the CC, falling exponentially until disappearing at 10 min. It is noted that even at intervals where PAP was still significant (4–5 min in the recovery period), voluntary performance was not modified, suggesting that high levels of PAP are necessary to impact voluntary performance, else PAP does not play a decisive role in the acute modulation of performance. It is also possible that fatigue is expressed differently between twitch contractions and high frequency or voluntary contractions. Another interesting aspect was seen by Fukutani et al. (2012), in which 6-s MVCs of the plantar flexors were performed with different intensities (40%, 60%, 80%, and 100%). The authors observed that all intensities were followed by significant PAP, which was proportional to the intensity of CC. Concentric voluntary torque (180°/s) was only improved after the 80% and 100% MVC conditions. This observation also suggests that contractions of higher intensities and elevated levels of PAP are necessary to contribute to positive changes in performance.

The angular velocity of the main activity tested may also play some role in the manifestation of positive effects associated with PAP. Fukutani et al. (2013) observed that concentric voluntary torque increased 7% immediately after CC only at angular velocity of 180°/s, but not at 30°/s. Similar to the other studies cited above, PAP lasted longer (5 min), while concentric torque increased only immediately after. Interestingly, at both angular velocities the

Table 1. Overview of studies that analyzed voluntary performance with confirmation of PAP.

Study	N	Conditioning contraction	Volume	Rest interval	Measurements/design	Main results
Baudry and Duchateau 2007a	10	MVC of thumb adductor	6 s	5 s, 1, 2, 3, 4, 5, and 10 min	Twitch, high-frequency stimulation (or voluntary isometric ballistic contractions), CC	<ul style="list-style-type: none"> ↑ Twitch RFD for 10 min ↑ High-frequency stimulation RFD for 5 min ↑ Voluntary isometric ballistic contractions RFD for 2 min
Baudry and Duchateau 2007b	10	MVC of thumb adductor	6 s	5 s, 1, 2, 3, 4, 5, and 10 min	Twitch, high-frequency stimulation (or voluntary dynamic ballistic contractions), CC	<ul style="list-style-type: none"> ↑ Twitch angular velocity for 10 min ↑ High-frequency stimulation angular velocity for 4–5 min ↑ Voluntary dynamic ballistic contractions angular velocity for 4–5 min
Bergmann et al. 2013	12	Maximal 2-legged hops	10	30 s to 5 min	Twitch, CC, twitch; DJ, CC, DJ	<ul style="list-style-type: none"> ↑ Twitch for 5 min ↑ DJ
Fukutani et al. 2012	12	MVC of plantar flexors	6 s at 40%, 60%, 80%, and 100% of MVC	Immediately after	Twitch; voluntary isokinetic torque, CC, twitch, voluntary isokinetic torque	<ul style="list-style-type: none"> ↑ Twitch ↑ Dynamic voluntary concentric torque only in condition 80% and 100% MVC
Fukutani et al. 2013	12	MVC of plantar flexors	6 s	3 s, 1, and 5 min	Twitch, dynamic torque at 30°/s and 180°/s, CC, twitch, dynamic concentric torque at 30°/s and 180°/s	<ul style="list-style-type: none"> ↑ Dynamic concentric torque at 180°/s
Fukutani et al. 2014b	8	Squat	5 reps at 45%, 5 reps at 60%, 3 reps at 75%, and 3 reps at 90% 5 reps at 45%, 5 reps at 60%, and 3 reps at 75%	30 s and 1 min	Twitch, CMJ, CC, twitch, CMJ	<ul style="list-style-type: none"> ↑ Twitch ↑ CMJ
Folland et al. 2008	8	MVC of knee extensors	10 s	0.10, 0.25, 0.40, 2, 2.30, 4, 4.30, 6, 8, 10, 14, and 18 min	Twitch, CC, twitch, H-reflex; voluntary performances, CC, voluntary performances	<ul style="list-style-type: none"> ↑ H-reflex for 5–11 min ↑ Twitch for 18 min ↔ Voluntary performance unchanged
Gago et al. 2018	9	MVC of plantar flexor	6 s	0.5, 1.5, 3, 6, and 15 min	Voluntary concentric contraction, CC, voluntary concentric contraction; twitch, CC, twitch	<ul style="list-style-type: none"> ↑ Twitch for 8 min ↑ Dynamic peak concentric torque between 1.5–5 min ↑ Dynamic concentric RFD between 1.5–5 min
Gossen and Sale 2000	10	MVC of knee extensors	10 s	15 s	Twitch, CC, twitch, dynamic knee extension	<ul style="list-style-type: none"> ↑ Twitch ↔ Peak velocity and power
Hodgson et al. 2008	13	MVC of plantar flexors	3x5 s	Immediately after. Every 30 s for 11 min	Twitch, H-reflex, isometric plantar flexion, CC, twitch, H-reflex, isometric plantar flexion	<ul style="list-style-type: none"> ↑ Twitch for 1 min ↔ H-reflex ↔ Isometric voluntary peak torque ↔ Isometric RFD
Mitchell and Sale 2011	11	Squat	5 RM	4 min	Twitch, CMJ, CC, twitch, CMJ	<ul style="list-style-type: none"> ↑ Twitch ↑ CMJ
Miyamoto et al. 2011	9	MVC of plantar flexors	6 s	5 s, 1, 2, 3, 4, 5, and 10 min	Twitch, voluntary isokinetic torque, CC, twitch, voluntary isokinetic	<ul style="list-style-type: none"> ↑ Twitch for 10 min ↑ Dynamic voluntary isokinetic torque between 1–3 min
Miyamoto et al. 2012	13	MVC of knee extensors	3, 5, and 10 s voluntary 5 s tetanic (20 hz)	1, 3, and 5 min	Twitch, voluntary isokinetic torque, CC, twitch, voluntary isokinetic torque	<ul style="list-style-type: none"> ↑ Twitch ↑ Dynamic voluntary isokinetic torque between 1–3 min
Nibali et al. 2013	8	Squat	5 RM	4, 8, and 12 min	Twitch, SJ, CC, twitch, SJ	<ul style="list-style-type: none"> ↑ Twitch ↔ Performance did not follow PAP variation
Pearson and Hussain 2014	8	Isometric squat	3, 5, and 7 s	4 min	CMJ, twitch, CC, CMJ, twitch	<ul style="list-style-type: none"> ↔ Twitch ↔ CMJ

Table 1 (continued).

Study	N	Conditioning contraction	Volume	Rest interval	Measurements/design	Main results
Prieske et al. 2018	12	Leg press/double-leg stances on a balance board	3× 8–10 reps	7 min	Twitch, MVC, twitch, CMJ, DJ, CC, MVC, twitch, CMJ, DJ	↑ Twitch ↔ Performance
Seitz et al. 2015	17	Isokinetic knee extensions	4 knee extensions at 60°/s, 4 and 12 at 180°/s, and 4 and 20 at 300°/s	1, 4, 7, 10, and 13 min	Twitch, dynamic knee extensions, CC, twitch, dynamic knee extensions	↑ Twitch ↑ Voluntary torque at 4 min and 7 min
Smith et al. 2014	11	MVC and tetanic (50 Hz) of tibialis anterior tibial	10 s	Immediately after	Twitch, CC, twitch, isometric voluntary ballistic contractions	↑ Twitch ↓ Isometric voluntary ballistic RFD
Thomas et al. 2017	11	Squat	3×3 at 80%, 90%, and 100% RM	8 min	Twitch, CMJ, CC, CMJ twitch	↑ CMJ ↓ Twitch

Note: CMJ, countermovement jump; DJ, drop jump; MVC, maximal voluntary contraction; PAP, postactivation potentiation; reps, repetitions; RFD, rate of force development; RM, repetition maximum; SJ, squat jump.

magnitude of the PAP was similar; however, an increase in voluntary torque was observed only in the high-speed condition. It has been suggested that the positive effect of a CC and corresponding phosphorylation of myosin RLC has more effect when the magnitude of interaction between actin and myosin filaments has been reduced (Sweeney et al. 1993). For example, potentiation due to prior contraction is greater at a short length where the filaments are further apart than at a long length where Ca^{2+} sensitivity is already enhanced by closer filaments (Rassier and MacIntosh 2002b). It is known that the number of attached cross-bridges decreases as the velocity of fiber shortening is increased (Piazzesi et al. 2007); thus, it can be speculated that at high angular velocities the effects of PAP (increased sensitivity to calcium due to phosphorylation of myosin RLC) would be able to diminish these effects on voluntary performance. This idea is also supported by the fact that higher PAP (twitch properties) was found during rapid shortening than slow shortening (Babault et al. 2008) and that PAP depends on direction and velocity of ongoing muscle length changes (Gago et al. 2014).

4.2. Potential factors disrupting the link between PAP and voluntary performance

In contrast to the studies cited above, other investigations have failed to observe improvements in voluntary performance even with confirmation of PAP (Gossen and Sale 2000; Folland et al. 2008; Hodgson et al. 2008). Gossen and Sale (2000), for example, did not find improvements in peak velocity or power in ballistic dynamic knee extensions (intermediate loads between 15%–60% MVC) at 15 s after a 10-s MVC at a time when PAP was significant ($53\% \pm 4\%$). Hodgson et al. (2008) also did not observe a significant increase in the peak voluntary torque or in the mean RFD (only at some specific time intervals) of plantar flexors after 3×5 -s MVC, even when significant PAP was observed (20.7%). Similarly, Folland et al. (2008) reported no significant increase in RFD or isokinetic torque of knee extensors after 10-s MVC at a time when both neural measurements (enhanced H-reflex) and PAP (16%) were clearly evident. It is speculated that when the calcium concentration is high enough to cause activation of all possible cross-bridges, the effects of the phosphorylation of the RLC are minimal (Smith et al. 2014), as seen in a voluntary activity, in which the concentration of calcium is much higher than in a twitch (Fukutani et al. 2012). Maximum voluntary efforts are of relatively high frequency, limiting the possibility that PAP can improve maximum effort performance (MacIntosh et al. 2012). This may explain the large torque increase in the twitch and the absence of improvements in voluntary performance in these studies. Also, it is possible that the assessment of distinct muscle groups (knee extensors, plantar flexors, and thumb adductors) with different fiber-type distributions (Johnson et al. 1973) has resulted in different responses since phosphorylation appears to be more prevalent in type II fibers (Hamada et al. 2000, 2003; Vandenboom 2017). In addition, an extremely high PAP level, approximately 150%–200% (Baudry and Duchateau 2007a, 2007b), was observed in the studies that reported positive responses for subsequent voluntary performance. This is in contrast to the studies where the voluntary performance did not change at times where PAP values were 16%–53% (Gossen and Sale 2000; Folland et al. 2008; Hodgson et al. 2008).

When the evaluated voluntary performance involves a more complex task such as vertical jumps, the results are even more contradictory. Nibali et al. (2013) conducted an interesting study and observed that 6 of the 8 subjects evaluated demonstrated PAP at different intervals, but this did not result in increased power or RFD in squat jump. Similarly, 3 of the 8 subjects increased the power, while 5 of the 8 increased the RFD at several intervals, even without PAP in some of the evaluated intervals. Changes in jump-associated variables that did not follow the PAP magnitude suggest that other factors are more involved in voluntary perfor-

mance enhancement than PAP is. [Thomas et al. \(2017\)](#) observed a significant increase in jump performance 8 min after the CC, which involved a squat protocol (3 × 3 repetitions with 80%, 90%, and 100% repetition maximums (RM)). Not only was PAP no longer present at that time, but the twitch was depressed. In this study, an acute neural modulation was also tested, but no changes were observed in measures of voluntary activation or corticospinal excitability. These data suggest that improvement in voluntary performance is mediated by other mechanisms and the neuromuscular basis of this improvement still needs to be elucidated.

Similarly, [Prieske et al. \(2018\)](#) verified that jump performance (countermovement jump (CMJ) and drop jump (DJ)) was significantly improved even without the coexistence of PAP at the intervals tested. Surprisingly, in the condition in which PAP was present, the jump performances did not change, whereas when the performance improved, PAP was not observed. Thus, the authors also concluded that PAP does not directly translate into voluntary performance enhancements. [Pearson and Hussain \(2014\)](#) did not observe significant PAP at 4 min after 3-, 5-, and 7-s MVCs, nor did jump height increase. Surprisingly, jump performance was decreased even with small twitch torque increase (PAP not significant) observed. [Mitchell and Sale \(2011\)](#) found that 5RM in the back squat generated PAP of 10.7% at 4 min of recovery. A 2.9% increase was observed in CMJ height in another session at the same recovery interval using the same squat protocol as CC. The correlation between PAP magnitude and increase in CMJ was not significant ($r = 0.24$). [Bergmann et al. \(2013\)](#) observed that 30 s after performing 10 maximal 2-legged hops, there was an increase of $32 \pm 8\%$ in twitch peak torque of the triceps surae muscles. DJ performance was improved by 12% at the same recovery interval. The correlation between PAP and change in DJ rebound height was not significant ($r^2 = 0.26$).

Based on these studies, we can conclude that for PAP to contribute to an increase in voluntary performance, PAP must be extremely high. However, voluntary performance improvement has also been reported when PAP was not present and unchanged/diminished performance has been identified when PAP was present. These observations demonstrate that other mechanisms may be more decisive in the acute increases in voluntary performance after a high-intensity warm-up and these alternative mechanisms contribute to improved performance that should be referred to as PAPE. These alternative mechanisms still need to be better clarified.

4.3. Phosphorylation of myosin RLC as the main mechanism related to PAP

The main physiological mechanism explaining the increase in twitch torque after a previous contraction is the phosphorylation of the myosin RLC due to the transfer of a phosphate group from a high-energy adenosine triphosphate to a specific site on myosin ([Szczena-Cordary 2003](#); [Vandenboom 2017](#)). This is a way to provide a kind of short-term memory for the system, allowing myosin to remember that it was recently activated ([MacIntosh 2010](#)). Phosphorylation is mediated by the enzyme myosin light chain kinase ([Sweeney et al. 1993](#); [Vandenboom 2017](#)) and increases the sensitivity of the contractile apparatus to the calcium released from the sarcoplasmic reticulum ([Sweeney et al. 1993](#)). The modulatory influence of this phosphorylation is exerted via structural changes in the contractile apparatus that influence the formation and kinetics of cross-bridges ([Vandenboom 2017](#)). More specifically, phosphorylation increases the mobility of the myosin head by placing it closer to the binding sites on actin. This increases the rate of engagement of cross-bridges ([MacIntosh 2010](#)), inducing an increase in the transition from a state of “nongeneration of force” to a state of “force generation” ([Baudry et al. 2008](#)) and explains the enhanced torque and RFD of an elicited twitch following a CC ([MacIntosh 2010](#)).

The relative increase in force for a given increase in calcium sensitivity is greater when the concentrations Ca^{2+} are low, as seen in a twitch ([Sale 2002](#); [Hodgson et al. 2005](#)). At high calcium concentrations this increased sensitivity has little effect, as observed in maximal tetanic contractions ([Vandenboom et al. 1993](#); [Abbate et al. 2000](#); [MacIntosh and Willis 2000](#); [Sale 2002](#)). The concentration of calcium in a tetanic contraction is proportional to the frequency of activation used ([Chin et al. 1997](#); [Glass et al. 2018](#)), so the enhancement of force decreases as frequency of activation increases ([MacIntosh and Willis 2000](#)).

A conditioning contraction can have both positive and negative impacts on contractile response. In addition to potentiation, the conditioning contraction can also result in fatigue, resulting in coexistence of fatigue and potentiation ([Rassier and MacIntosh 2000](#)). When PAP and fatigue are present, it is possible that fatigue will dominate as the activation frequency increases ([MacIntosh 2010](#)), simply because the impact of light chain phosphorylation is less.

Increased sensitivity to calcium is also observed at long muscle lengths, independent of RLC phosphorylation, since stretching a fiber also causes the actin filaments to be closer to the myosin heads ([MacIntosh 2010](#)). This independent mechanism of altered calcium sensitivity is interactive, reducing the impact of RLC phosphorylation at long lengths, since calcium sensitivity is already high ([MacIntosh 2010](#)). This is supported by studies that found higher PAP levels at short muscle lengths ([Vandervoort and McComas 1983](#); [O’Leary et al. 1997](#); [Rassier and MacIntosh 2002](#); [Place et al. 2005](#); [Kuzyk et al. 2018](#)). Skinned fiber experiments have confirmed that when the lattice spacing is expanded, the sensitivity to calcium is lower ([Yang et al. 1998](#)) and the effects of increased calcium sensitivity due to phosphorylation of the RLC is greater.

Recruiting all fibers during the CC is important to achieve maximum potentiation of the RLC since only RLC of the fibers recruited during contraction can be phosphorylated ([Fukutani et al. 2014a](#)). It also appears that type II fibers demonstrate higher phosphorylation and PAP magnitudes after a CC ([Gordon et al. 1990](#); [Hamada et al. 2000](#)), which is indirectly corroborated by higher PAP seen in dorsiflexors than in plantar flexors after 10-s MVC ([Vandervoort et al. 1983](#)), higher PAP in gastrocnemius compared with soleus muscles ([Vandervoort and McComas 1983](#)), and higher PAP in power athletes compared with endurance athletes ([Pääsuke et al. 2007](#)). Furthermore, the activity of the enzyme myosin light chain kinase that regulates phosphorylation seems to be proportional to the composition of fast fibers of the vastus lateralis ([Houston et al. 1985](#)); this would result in greater phosphorylation of myosin RLC in fast-twitch fibers in response to a CC ([Sweeney et al. 1993](#)).

In summary, each myosin RLC has a specific site for incorporation of a phosphate molecule ([Tillin and Bishop 2009](#)) and this site is phosphorylated when a muscle contraction is initiated. The more intense the contraction, the more fibers are recruited and the greater the level of phosphorylation observed. Obviously, the CC should recruit the same muscle groups as the main performance test, such that the fibers used in the task could be phosphorylated and demonstrate PAP. During the time that the RLCs are phosphorylated, the torque of a twitch is increased ([Manning and Stull 1979](#)) due to increased calcium sensitivity and concomitant improvements of interaction between the actin and myosin filaments. The fact that calcium sensitivity is already increased at long lengths makes the phosphorylation less effective and PAP is suppressed in this condition. The effect of this phosphorylation on a subsequent high-intensity task is still unclear.

5. Conclusions

Based on the studies analyzed in this review, it can be observed that PAP is a highly reproducible phenomenon and the most ac-

cepted mechanism associated with the improvement of the contractile properties is the phosphorylation of the myosin RLC. However, the occurrence of PAP, confirmed by supramaximal electrical stimulation, does not necessarily mean that a voluntary performance will be improved. Studies included in this review that monitored the contractile properties also demonstrated that improvements in voluntary performance were only observed when the PAP level after the CC reached extremely high values (~150%). Conversely, some studies have also observed improvements in voluntary performance at times when PAP was not present. This demonstrates that other mechanisms are more relevant than PAP in the manifestation of acute increases in performance (PAPE). However, this does not eliminate the importance of PAP, but leads us to think that the manipulation of the myosin RLC phosphorylation and the observed increase in the torque of a twitch, after a CC, only translates into optimization of voluntary performance in some specific cases, such as when PAP magnitude is extremely high. Therefore, care should be taken when interpreting results when PAP is not measured. It is inappropriate to assume that a muscle that demonstrates PAP will have superior voluntary performance, because that is not always observed.

Conflict of interest statement

The authors have no conflicts of interest to report.

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