

POST-ACTIVATION POTENTIATION OF SKELETAL MUSCLES AND ITS EFFECT ON ENHANCEMENT OF HUMAN MOTOR PERFORMANCE: A REVIEW

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Abstract:

The force enhancement of isometric twitch contraction after a conditioning maximal voluntary contraction (MVC) has been referred to as post-activation potentiation (PAP). This review describes the possible physiological mechanisms underlying PAP and the studies that have investigated the PAP in differently trained athletes, and outlines how PAP might be used for enhancement of human motor performance. There are two proposed mechanisms of PAP: (1) the phosphorylation of myosin regulatory light chains, which renders actin-myosin more sensitive to Ca²⁺ released from the sarcoplasmic reticulum during subsequent muscle contractions, and (2) an increased synaptic excitation within the spinal cord, resulting in increased force-generating capacity of the involved muscle groups. PAP is the greatest immediately after a brief isometric MVC and then decreases rapidly but is still evident for 5-10 min. PAP score in plantarflexor and knee extensor muscles in elite power-trained athletes is significantly higher than in age- and gender-matched endurance-trained athletes and untrained subjects. PAP induced by short isometric MVCs has been found to increase knee extension isokinetic peak torque, vertical jumping and bench press performance. Researchers have observed a significant enhancement of jumping performance after a conditioning five-repetition maximum barbell back squat and different warm-up exercises. However, it is not possible to ascertain if the observed enhancements in motor performance are due to the mechanisms responsible for PAP, or are simply a manifestation of the training stimulus or variability in the performance measure. Thus, the role of PAP in enhancement of human motor/athletic performance should be the basis for future research.

Key words: neuromuscular physiology, post-activation potentiation, motor performance, sports training.

ПОСТАКТИВАЦИОННОЕ ПОТЕНЦИРОВАНИЕ СКЕЛЕТНЫХ МЫШЦ ЧЕЛОВЕКА И ВЛИЯНИЕ ЭТОГО НА ДВИГАТЕЛЬНЫЕ КАЧЕСТВА: ОБЗОР ЛИТЕРАТУРЫ

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Аннотация:

Термин «постактивационное потенцирование» (ПАП) приводится для описания феномена увеличения силы изометрического сокращения скелетных мышц после предыдущего максимального произвольного сокращения (МПС). В обзоре литературы описываются возможные физиологические механизмы ПАП, исследования, которые изучали ПАП мышц спортсменов различных видов тренировки, а также основы того, как феномен ПАП может быть применён для улучшения двигательных качеств человека. Существует два возможных механизма ПАП: (1) фосфорилирование регуляторных легких цепей миозина, что увеличивает чувствительность комплекса актин-миозин к Ca²⁺, освобождающемуся из саркоплазматического ретикулума во время последовательных мышечных сокращений; (2) повышение синаптического возбуждения спинальных мотонейронов, что приводит к увеличению способности генерации силы вовлеченных мышечных групп. ПАП имеет наибольшую величину незамедлительно после короткого изометрического МПС и затем быстро уменьшается, оставаясь существенной в течение 5-10 минут. Величина ПАП мышц подошвенных сгибателей стопы и разгибателей коленного сустава значительно выше у высоко-квалифицированных спортсменов силовых и скоростно-силовых видов спорта, чем у спортсменов видов спорта с преимущественной тренировкой на выносливость и нетренированных лиц такого же возраста и пола. ПАП, индуцируемое коротким изометрическим МПС, приводит к увеличению изокинетического момента силы при разгибании коленного сустава, удлинению высоты вертикального прыжка и улучшению результата жима лёжа. Исследователями было найдено значительное

увеличение высоты вертикального прыжка после пятикратного приседания со штангой и различных упражнений для разминки. Однако на данном этапе невозможно уточнить, наступает ли наблюдаемое улучшение двигательных качеств вследствие включения механизмов, ответственных за ПАП, или это является простой манифестацией тренировочных стимулов или различием в измерениях. Таким образом, изучение роли ПАП в улучшении двигательных качеств человека могло бы представлять интерес для последующих исследований.

Ключевые слова: нервно-мышечная физиология; постактивационное потенцирование; двигательные качества; спортивная тренировка.

INTRODUCTION

The response of skeletal muscles to volitional or electrical stimuli is affected by its contractile history (Westerblad et al., 1991; Sale, 2002). The two most prevalent measures of neuromuscular output used to quantify the effect of previous activation history of subsequent muscle force production (conditioning contraction) have been: (1) electrically evoked isometric twitch force (see Sale, 2002); and (2) Hoffmann reflex (H-reflex) amplitude (Gollhofer et al., 1998; Trimble and Harp, 1998). Examples of conditioning contractions are a series of electrically evoked isometric twitches (staircase or *treppe*), electrically evoked isometric tetanic contractions, a sustained isometric maximal voluntary contraction (MVC), and a series of dynamic contractions (Sale, 2004). The force enhancement of isometric twitch contraction after a conditioning tetanic contraction or maximal voluntary contraction (MVC) has been referred to as a post-tetanic potentiation and post-activation potentiation (PAP), respectively (Gossen and Sale, 2000; Hamada et al., 2000; Binder-MacLeod et al., 2002). A twitch is a brief muscle contraction in response to a single presynaptic action potential or a single, synchronized volley of action potentials (Latash, 1998; Hodgson et al., 2005). The force of a twitch contraction is increased after the following conditioning contractions: (1) a sustained isometric MVC (Gossen and Sale, 2000; Hamada et al., 2000; Pääsuke et al., 2007); an electrically evoked isometric tetanic contraction (O'Leary et al., 1997; Requena et al., 2005) or (3) repeated sub-fusion stimuli (MacIntosh and Willis, 2000). In addition to enhancing isometric twitch peak force, the preceding forms of conditioning contractions have also been shown to increase the rates of force development (RFD) and relaxation (RR) of isometric twitch contraction (Pääsuke et al., 2007; Froyd et al.,

2013) and decrease its time to twitch peak force (Grange et al., 1993). This effect is physiologically well established and known commonly as twitch potentiation. However, its functional relevance to human motor performance is less clear (Hodgson et al., 2005).

Although the physiological mechanisms of post-tetanic potentiation and PAP have not been extensively investigated (Iglesias-Soler et al., 2011), two processes have been proposed to explain these phenomena (Hodgson et al., 2005): (1) an increase in Ca²⁺ sensitivity of the myofilaments (Metzger et al., 1989) that could lead to twitch potentiation; and (2) a reflex potentiation that leads to an enhancement in the muscle response to an afferent neural volley. The reflex potentiation after different sets of conditioning contractions has been investigated using H-reflex technique (Güllich and Schmidtbleicher, 1996; Folland et al., 2008; Iglesias-Soler et al., 2011). However, Hodgson et al. (2008) have reported post-activation potentiation during isometric explosive plantarflexion without reflex potentiation. Thus, the exact role of spinal excitability in post-activation potentiation is unclear.

In addition to examining the mechanisms that may account for PAP, applied movement science studies have investigated the effect of contractile history induced by means of a maximal or near-maximal preloading exercise on subsequent dependent measures of mechanical power performance, such as vertical jump height and rate of force development in an explosive movement (Young et al., 1998; Duthie et al., 2002; Baker, 2003; Jensen and Ebben, 2003).

The aims of this article are: (1) to describe the possible physiological mechanisms underlying PAP and the effect of duration and intensity of the conditioning isometric contractions on PAP; (2) to review the physiological studies that have investigated PAP in differently (strength-, power-

and endurance-) trained athletes; (3) to review the applied movement science studies that have investigated the role of PAP in enhancement of human motor performance.

THE PHYSIOLOGICAL MECHANISMS AND TIME-COURSE OF PAP

There are two proposed mechanisms of PAP. The first is the phosphorylation of myosin regulatory light chains, which renders actin-myosin more sensitive to Ca^{2+} released from the sarcoplasmic reticulum during subsequent muscle contractions (Grange et al., 1993; Sweeney et al., 1993; Vanderboom et al., 1995). As a result, the force of each successive twitch contraction is increased. The second mechanism is that brief heavy-resistance exercise prior to plyometric exercise causes increased synaptic excitation within the spinal cord, which in turn results in increased post-synaptic potential and subsequent increased force-generating capacity of the involved muscle groups. The most important muscle characteristic affecting PAP is fibre type. Muscles with the shortest twitch contraction and half-relaxation time and highest proportion of fast-twitch (Type II) muscle fibres have the greatest PAP response (O'Leary et al., 1997; Grange et al., 1993). The higher PAP score in fast-twitch muscle fibres is probably related to their greater capacity of myosin regulatory light chains phosphorylation in response to high-frequency activation (Grange et al., 1993). A notable feature of PAP is that it has no effect on the force of high frequency tetanic isometric contractions, because in such contractions a saturating concentration of Ca^{2+} is attained, making any increase in Ca^{2+} sensitivity inconsequential (Sale, 2004).

Contractile activity produces both fatigue and PAP, and it is the balance between the two that determines whether the subsequent contractile response is enhanced, diminished, or unchanged (MacIntosh and Rassier, 2002). The poststimulus state depends on timelines of PAP and fatigue. Both PAP and fatigue may increase immediately following contractile activity and then gradually return to the prestimulus levels (Sale, 2002; Robbins, 2005). The coexistence of fatigue and PAP may result in a net potentiated state, a net attenuated state, or a constant state as compared

to the prestimulus state (Robbins, 2005).

It has been suggested that PAP may have a special role in compensating for the impaired excitation-contraction coupling that occurs with fatigue. Impaired excitation-contraction coupling is responsible for low frequency neuromuscular fatigue – in other words, the disproportionate loss of low frequency tetanic force. This is the exact opposite of PAP, which is a disproportionate increase in low frequency tetanic force. Thus, PAP may compensate for low frequency fatigue (Rassier and MacIntosh, 2000; Sale, 2004). Many endurance activities, such as running, cycling and swimming consist of repeated brief concentric or eccentric-concentric contractions in which motor units discharge briefly at fairly high rates, whereas in concentric compared with isometric contractions, PAP and low frequency can act at higher frequencies. (Sale, 2004).

Strength and power performance typically requires that in case of brief maximal effort, all relevant motor units are recruited and firing at maximal possible rates. PAP would appear to offer little benefit when motor units are discharging at very high rates, because it cannot increase high frequency force. However, it can increase isometric rate of force development, even at relatively high stimulation frequencies at which isometric force is not increased by PAP (Sale, 2002). Furthermore, in fast shortening contractions, the effect of PAP is present at still higher frequencies (Abbate et al., 2000; Sale, 2004).

The literature indicates that the duration and intensity of conditioning isometric contractions is an important factor that determines PAP. Several studies have demonstrated the greatest PAP at 5 to 10 s isometric MVC (Vandervoort et al., 1983; O'Leary et al., 1997; Hamada, 2000; Baudry and Duchateau, 2007; Iglesias-Soler et al., 2011). It has been shown that isometric contractions less than 25% of MVC do not lead to any conditioning effect (Requena et al., 2008). A significant PAP has been noted after conditioning isometric contractions more than 75% MVC (Vandervoort et al., 1983). It has been shown that to obtain a PAP during explosive ballistic movements, the intensity and duration of the isometric conditioning must be controlled,

whereas the improvement in power output is not related to spinal H-reflex excitability (Iglesias-Soler et al., 2011). PAP is the greatest immediately after a brief (5-10 s) isometric MVC and then decreases rapidly but is still evident for approximately 5 min (see Pääsuke et al., 2007, Fig. 1) to 10 min (O'Leary et al., 1997). PAP is associated with a shortened twitch contraction time (Green and Jones 1989; Petrella et al., 1989; Pääsuke et al., 2000) and increased twitch maximal RFD and RR (Green and Jones, 1989; Grange et al., 1993; Pääsuke et al., 2000, 2007, Froyd et al., 2013), and with shortened (O'Leary et al., 1997) or unchanged (Baudry and Duchateau, 2004; Pääsuke et al., 2002, 2007) twitch half-relaxation time.

PAP IN SKELETAL MUSCLES OF DIFFERENTLY TRAINED ATHLETES

The electrically evoked twitch contractile properties of skeletal muscles and capacity for PAP, respectively, can be used for the evaluation of specific adaptation of the human neuromuscular system to different types of training. Several longitudinal strength training studies have assessed changes in PAP but the results of these studies have not been consistent. Hicks et al. (1991) suggested that 12-week strength training of dorsiflexor muscles in elderly subjects increased PAP. However, Rice et al. (1993) indicated that PAP in elbow extensor muscles was unaffected by 24-week dynamic strength training in elderly men. Similarly, Sleivert et al. (1999) reported that 10-week isometric strength training of the KE muscles in young men did not change PAP. It has been suggested that PAP effect on sprint performance in junior basketball players, who did not previously follow systematic resistance training, emerges after a 10-week resistance/sprint combined training programme (Tsimachidis et al., 2013).

PAP of electrically evoked twitch in skeletal muscles in differently trained athletes has been assessed by cross-sectional studies. A greater PAP in plantarflexor and elbow extensor muscles has been reported in elite male endurance-trained and moderate strength-trained athletes compared with the untrained men (Hamada et al., 2000). One of our studies indicated that PAP in plantarflexor

muscles in elite male power-trained athletes was significantly greater than in age- and gender-matched endurance-trained athletes (Pääsuke et al., 1998). The majority of previously conducted studies have assessed PAP in skeletal muscles in differently trained athletes only immediately (at 2–5 s) after the brief conditioning isometric MVC without the assessment of time course of PAP decline. Only Hamada et al. (2000) compared the PAP score and its time course of decline in the upper limb (elbow extensor) and lower limb (plantarflexor) muscles in elite male endurance-trained athletes (triathletes and long distance runners), moderately trained male recreational strength athletes and untrained men before and following 5 min period of recovery after a 10 s conditioning isometric MVC. The results suggested that in triathletes, who train both upper and lower limb muscles, PAP was enhanced in elbow extensor and plantarflexor muscles, whereas in long distance runners, who train only the lower limbs, enhanced PAP was observed in plantarflexor muscles. Strength-trained recreational athletes, who performed upper and lower limb weight training, also had enhanced PAP in both measured muscle groups. Thus, the greater PAP was specific to the muscles trained. The above mentioned study indicated the presence of a significant PAP in plantarflexor muscles for all measured groups during 5 min post-MVC, whereas a significant PAP in elbow extensor muscles was observed only immediately post-MVC. The authors hypothesized that the mechanisms by which training increases PAP may differ in case of endurance and strength training, whereas the results supported evidence of increased fatigue resistance in endurance-trained athletes but did not provide direct evidence of adaptation within slow-twitch (Type I) muscle fibres that might increase PAP.

The results of one of our studies indicate that PAP in knee extensor muscles is enhanced in power-trained but not in endurance-trained female athletes (Pääsuke et al., 2007). The magnitude of PAP immediately after the conditioning MVC was greater and its decline was slower in power-trained compared with endurance-trained athletes. Immediately post-MVC, twitch speed-related characteristics (maximal rates of force

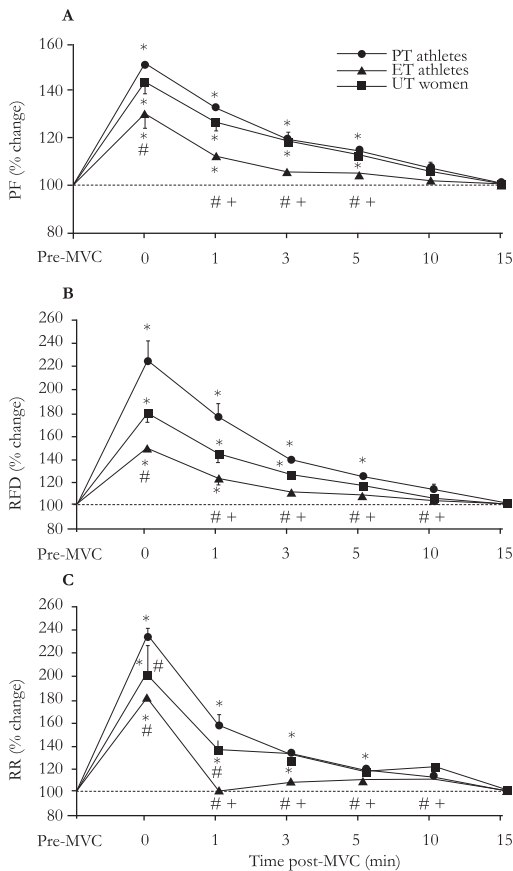


Fig. 1 Changes in isometric twitch peak force (PF) (A), twitch maximal rates of force development (B) and relaxation (C) of the knee extensor muscles in female power (PT) and endurance-trained (ET) athletes and untrained (UT) women after a 10-s conditioning MVC. Values, expressed as percent of pre-MVC value (dashed line), are means \pm SE.
 * Significantly different from pre-MVC values ($P < 0.05$); # Significantly different compared with the PT athletes ($P < 0.05$); + Significantly different compared with the UT women ($P < 0.05$) (Pääsuke et al., 2007).

development and relaxation) were potentiated to a greater extent than twitch peak torque. The time course characteristics of isometric twitch contraction (contraction and half-relaxation times) were not significantly altered by conditioning MVC.

Our another study (Ereline et al., 2011) compared twitch contractile properties, including PAP, of plantarflexor muscles in male athletes who train for power and endurance simultaneously (Nordic combined athletes) with athletes who train for endurance (cross-country skiers) and sedentary individuals. Nordic combined athletes

had a significantly greater twitch post-activation potentiation than the other two groups. No significant differences in the measured twitch contraction characteristics were found in cross-country skiers and sedentary males. We concluded that the twitch PAP of the plantarflexor muscles differed markedly in athletes who train for power and endurance simultaneously compared with athletes who predominantly train for endurance. As an indicator of long-term adaptation to simultaneous power and endurance training, increased twitch force-generation and potentiation capacity in the plantarflexor muscles were observed in Nordic combined athletes.

THE ROLE OF PAP IN ENHANCEMENT IN MOTOR PERFORMANCE

A number of applied movement science studies examined the effect of PAP on enhancement of motor performance. PAP induced by short isometric MVCs has been found to increase knee extension isokinetic peak torque (French et al., 2003), vertical jumping height (Güllich and Schmidtbleicher, 1996; French et al., 2003) and bench press performance (Güllich and Schmidtbleicher, 1996). However, Gossen and Sale (2000) conducted a study in which a 10-s isometric MVC was followed 15 s later by dynamic contractions. Performance, as measured by dynamic knee extension, was not enhanced after conditioning isometric MVC but rather was attenuated. The investigators concluded that at 15 s after a conditioning contraction the effects of fatigue elicited via the 10-s isometric MVC were greater than the benefits of any elicited PAP.

Mitchell and Sale (2011) tested whether a five-repetition maximum (5-RM) back squat both induced PAP and increased height of subsequently performed counter-movement jumps (CMJ). Researchers observed a significant enhancement of jumping performance 4 min after a conditioning 5-RM barbell back squat. It was concluded that PAP may have contributed to the increase in CMJ height, but the correlation between the magnitude of PAP and the percentage increase in CMJ height was not significant. Young et al. (1998) also found a significant improvement in vertical jump height 4

min after a 5-RM heavy-load half squat. Radcliffe and Radcliffe (1996) conducted a study in which 5 warm-up protocols were performed: a standard warm-up, a warm-up plus 4 sets of back squats at 75–85% 4 repetition maximum (4-RM), a warm-up plus 4 sets of 4 power snatches at 75–85% 4-RM, a warm-up plus 4 sets of 4 loaded jumps with 15–20% body weight added, and a warm-up plus 4 sets of 4 unloaded jumps. Following the warm-up protocols, 3 maximal effort horizontal CMJs were performed. The results indicated that the jump distance was significantly greater for men after the warm-up plus snatch protocol than after the standard warm-up alone. The investigators concluded that using the power snatch in a warm-up protocol significantly improved horizontal CMJ performance. However, a study conducted by Duthie et al. (2002) failed to demonstrate enhancement in jump squat performance over 3 consecutive trials using 3 different protocols (included the combination of 3 sets of three-repetition maximum half squats with 3 sets of 4 jump squats performed at 30% of one-repetition maximum). In this study, performance enhancement was not observed in any of the 3 sets of 4 jump squats in any of the training protocols.

Baker (2003) investigated PAP in the upper body and found a significant increase in power output following a six-repetition maximum bench press executed at 65% 1-RM. However, Hrysomallis and Kidgell (2001) who also assessed PAP in the upper body, did not find significant enhancement in a 5-RM bench press performance after explosive push-ups. They suggested that the absence of PAP could be due to a number of reasons, including the supposition that the requirements to elicit PAP in the upper body may differ from those required to elicit PAP in the lower body.

Nibali et al. (2013) suggested that obtaining mechanistic measures of PAP in the daily training environment of highly trained athletes is impractical. They assessed electrically evoked twitch properties of the knee extensor muscles and jump squat kinetics of highly trained men

in response to a 5-RM back squat conditioning stimulus. Linear regression was used to determine the relationship between post-pre changes in kinetic variables of jumping and muscle twitch peak force and rate of force development. The researchers concluded that jump squat concentric mean power and rate of force development are valid measures of muscle PAP, capable of detecting changes in athletic performance in response to the PAP phenomenon. One of our studies (Requena et al., 2011) examined the relationship between twitch PAP in knee extensor muscles, and sprinting and vertical jumping performance in professional Spanish soccer players. A significant negative correlation was found between 15-m sprint time and jump height in CMJ and squat jump. PAP of twitch peak torque correlated significantly positively with jump height in CMJ and squat jump, and negatively with 15-m sprint time. We concluded that twitch PAP in KE muscles was significantly correlated with performance in vertical jumping and sprinting in male professional soccer players, whereas the magnitude of PAP in soccer players was similar to that observed previously in power-trained athletes.

CONCLUSION

The phenomenon of PAP in human skeletal muscles has been used for evaluating the acute or short-term neuromuscular adaptation to exercise (the coexistence of potentiation and fatigue has been suggested) and chronic or long-term neuromuscular adaptation to strength, power, endurance or combined training. A number of studies have been successful in eliciting PAP in the form of enhancements in motor/athletic performance. However, it is not possible to ascertain whether the observed enhancement in motor performance is due to the mechanisms responsible for PAP, or is a manifestation of the training stimulus (e.g. warm-up) or indicates the variability in the performance measure. Thus, more research is required in order to clarify the functional significance of PAP, and in particular, how the enhancement in motor performance is caused by the mechanisms responsible for PAP.

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