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Original Article

On the mechanisms of post-activation potentiation: the contribution of neural factors

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Abstract:
The responsible mechanisms for post-activation potentiation have been a popular research issue during the past years. One commonly mentioned mechanism is the force enhancement via phosphorylation of myosin regulatory light chains, which affects the sensitivity of the actin – myosin to Ca^{2+}. An alternative factor that could contribute or affect post-activation potentiation could be of neural nature. The increase in motor neuron excitability and the recruitment of more motor units could lead to higher rate of force development. H-reflex has been used to investigate possible neural adaptations during post activation potentiation. Methodological considerations and conflicting results have appeared due to different applied methods, which are discussed. Clearly, there is a need for further studies to support or reject the hypothesis of neural contribution to the occurrence of post-activation potentiation phenomenon.
Key Words: muscle, potentiation, neural adaptation, H-reflex, twitch torque

Introduction

Definition of post-activation potentiation

It has been consistently shown that a conditioning contraction may affect twitch torque by enhancing peak twitch torque and the rate of torque development, as well as by decreasing the time-to-peak torque. This phenomenon has been described as Post-Activation Potentiation (PAP). The conditioning contraction (also referred as conditioning stimulus) can be a series of evoked twitches (Sale, 2002; Verkhoshansky & Tetyan, 1973), an evoked tetanic contraction (Desmedt & Hainaut, 1968) or a sustained maximal voluntary contraction (Hamada, Sale, MacDougall, & Tarnopolsky, 2000). Furthermore, such conditioning stimuli enhance not only the muscle twitch properties but may also potentially enhance muscle performance, when explosive tasks such as jumping or sprinting are tested (Mitchell & Sale, 2011; Xenofondos et al., 2010). This gives PAP a broader meaning when used in the literature.

Contribution of peripheral mechanisms on PAP

The phenomenon of PAP may be explained by changes that occur on muscular level and more particularly by the phosphorylation of myosin regulatory light-chains. The myosin molecule consists of six subunits, two heavy and four light chains (Szczesna, 2003). Each heavy chain contains the head and a tail and each pair of light chain consists of an essential light chain and a regulatory light chain. The exact function of essential light chain is not ascertained yet, but it is believed to contribute to the structural stability of myosin. The regulatory light chain has the ability to phosphorylate and thus participates actively during muscle contraction (Aguilar & Mitchell, 2010). Etymologically, the word phosphorylation is characterized as the process in which one or more phosphate groups (P_i) is added to a molecule. Practically, the light chain phosphorylation of myosin refers to the ability of the regulatory light chains to bind to a molecule of phosphorus. For this to occur, an enzyme is necessary, namely the light chain kinase. Kinases are enzymes that catalyze the phosphate compound using the P_i of ATP. Kinases are activated as Ca^{2+} is released from the sarcoplasmic reticulum during muscle contraction (Manning & Stull, 1982). Ca^{2+} release in the muscle milieu, increases of the concentration of calmodulin, which activates the light chain kinase and in turn phosphorylates the regulatory light chains (Levine, Chantler, Kensler, & Woodhead, 1991).

The phosphorylation of the regulatory light chains is believed to enhance subsequent contractions by modifying the orientation of the myosin head, and moving it away from its thick filament backbone. This increases the probability of the cross bridges to interact, and thus enhances the speed with which the cross bridges bind (Hodgson, Docherty, & Robbins, 2005). This is expressed as an increase in the sensitivity of the

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actin - myosin complex on Ca^{2+} (Szczesna et al., 2002), which results in the production of work with less Ca^{2+} required. Fast skeletal fibers have less myosin phosphatase and more myosin light chain kinases, and therefore extended phosphorylation of myosin regulatory light chains occurs (Kamm & Stull, 2011; Moore & Stull, 1984). For this reason it is argued that the phenomenon of PAP is greater in muscles with higher percentage of type two fibers (Hamada et al., 2000; Manning & Stull, 1982).

Contribution of neural mechanisms on PAP

Neural enhancement is another possibility that has been proposed as an alternative contributor to PAP. The nervous system can increase or decrease the intensity of a muscle contraction by changing the number of recruited motor units and by modifying their firing rate (Milner-Brown, Stein, & Yemm, 1973). Henneman and colleagues (1965), described the motor unit recruitment order as the "size principle", where the intensity of a contraction is related to the size of the cell bodies of the recruited motor units. More particularly, by increasing the intensity of the contraction increases the number of the recruited motor units starting from smaller to larger, i.e. from slower to faster ones. This implies that in order to recruit fast motor units voluntarily, the intensity of the contraction should be high to maximum.

One way for evaluating the function of the central nervous system, and particularly the excitability of α-motor neurons through the reflex pathway, is the method of H-reflex. The H-reflex technique has been broadly used to estimate alterations in the α-motoneurone excitability, via the Ia afferents, at pre- and/or post-synaptic level. It was the first method to study spinal pathways in animals and humans and can be used to examine reflexes in various neurological conditions (Fisher, 1992), in pain (Leroux, Belanger, & Boucher, 1995), in musculoskeletal injuries (Hopkins, Ingersoll, Edwards, & Cordova, 2000), as well as for studying exercise-induced neuromuscular adaptations in humans (Zehr, 2002). Changes to the H-reflex amplitude can be caused either by technical factors, such as the subject's properties, like age (Tsuruike, Koceja, Kyonosuke, & Shima, 2003), or endogenous causes, like presynaptic or post-synaptic mechanisms. Furthermore, there are many methodological issues that the researcher has to take into account (Zehr, 2002). Nevertheless, when all factors are considered, H-reflex can be a very useful tool to evaluate the influence of contractile history on neuromuscular response (Hodgson et al., 2005).

In the case of force enhancement after a conditioning contraction due to PAP, it could be expected that α-motoneuron excitability increases and/or presynaptic inhibition on the Ia afferents decreases. Both of these mechanisms would lead to an increase in the H-reflex amplitude after a conditioning contraction. This indicates that additional motor units have been recruited through the reflex pathway. According to the size principle, these motor units have higher thresholds and therefore are larger and faster. The increasing activation of motor units could lead to increased mechanical output (Hodgson et al., 2005), and that could explain the augmentation in torque and rate of torque development after a conditioning contraction.

H-reflex studies examining PAP

The effect of PAP on the H-reflex amplitude has received considerable attention in the past few years. However, our knowledge and understanding of its behavior is still limited. Only a few studies have examined the twitch torque and the H-reflex before and after PAP in soleus and gastrocnemius of adults (Güillich & Schmidtbleicher, 1996; Hodgson, Docherty, & Zehr, 2008; Iglesias-Soler, Paredes, Carballeira, Márquez, & Fernández-Del-Olmo, 2011; Trimble & Harp, 1998). A summary of the findings of these studies is shown in table 1.

Table 1. Summary of studies examining the neural enhancement on PAP

Authors	Subjects (sex and training status)	Conditioning contraction [type of contraction sets / repetitions duration / rest]	Muscle	Outcome						
				Reflex Properties					Torque Properties	
				Variable	Potentiation		Depression		Electrical Twitch	Voluntary
					Time (min)	Percentage of increase	Time	Percentage of decrease		
Güillich and Schmidtbleicher (1996)	M & F ATH: n=10 UT: n=7	isometric 1 / 5 5" / 60"	Soleus	H-reflex	4 -11	20%				ATH EFD 4-13 min 19%
			LGas		4-11	32%; ATH: 42%; UT: 11%	0-60"	NA		
Trimble and Harp (1998)	M & F UT n=10	concentric – eccentric 8 / 10 NA / 20"	Soleus	H/M ratio	NA	NS 17% (n=5)	0-60"	36%		
			LGas		3-10	20 % (n=5)	0-60"	28%		
Hodgson et al. (2008)	M ATH n=13	isometric 1/3 5" / 55"	Soleus	H/M ratio	NS	NS	0-60"	NS	20.7%	RFD: NS
			LGas		NS	NS (n=5)	0-60"	NS (n=5)		
Iglesias – Soler et al. (2011)	M UT n=14	isometric 1/1 10" / -	Soleus	H/M ratio	NS	NS	NS	NS		MEC P. at 4 min
Folland et al. (2008)	M UT n=8	isometric 1/1 10" / -	Quad F	H/M ratio	5-11	42%	NS	NS	66.6%	IRFD: NS IT: NS

ATH = athletes; UT = untrained; M = males; F = females; n = number of subjects; LGas = lateral gastrocnemius; Quad F = quadriceps femoris; EFD = explosive force development; RFD = rate of force development; IRFD = isometric rate of force development; IT = isokinetic torque; MEC P = mechanical power; NS = non-significant difference; NA = not available information.

The first study examining the PAP phenomenon evaluating the H-reflex was assessed by Güillich and Schmidtbleicher (1996). The conditioning stimulus involved the plantar flexor muscles, and the participants executed 5 5-sec isometric maximum voluntary contractions (MVC), with 1 min rest interval in between. The results revealed a significant depression of the lateral gastrocnemius H-reflex during the first minute after the isometric MVC. Moreover, the H-reflex amplitude was potentiated significantly within a time window of 4 to 11 minutes post-conditioning. In the lateral gastrocnemius the potentiation was higher (32%) than the soleus (20%). The potentiation was more evident in athletes (42% potentiation), who were trained for speed and strength, compared to untrained students (11% potentiation). Furthermore, the group of athletes presented a significant potentiation of plantar flexion explosive force 4 to 13 min after the conditioning stimulus. The authors concluded that the force output gain is highly related to neuronal factors. However, the researchers did not normalize the measured H-reflex to the maximum M-wave amplitude. Hence, in case changes in the maximum M-wave occurred, it is not clear how these findings should be interpreted.

Two years later, Trimble & Harp (1998), observed a depression of soleus (36%) and lateral gastrocnemius (28%) H-reflex, immediately after an intense session of volitional resistance exercises. More specifically, 8 sets of 10 concentric – eccentric plantar flexions were applied to ten subjects. Examining the results of this study more thoroughly, only five out of ten subjects demonstrated a significant potentiation for the lateral gastrocnemius (20%), but not for the soleus muscle (17%), in which there was an increase, but not a statistically significant one. Finally, the authors suggest a possible neural enhancement as a mechanism of PAP.

In a more recent study, Hodgson et al. (2008) examined the PAP during plantar flexion in thirteen trained subjects. The conditioning stimulus was 3 MVCs of 5 seconds duration. They showed no changes in H-reflex amplitude within 10 minutes after the MVCs. More specifically, after the conditioning contraction, the H/M ratio of the soleus and gastrocnemius muscles was decreased during the first minute and recovered thereafter with no statistically significant difference from the values before the conditioning stimulus. We have to note that, for the gastrocnemius muscle, the collection of data referred to only 5 subjects, and this might be a limitation to generalize the results. Moreover, a significant increase of twitch peak torque in 2 and 15 sec after the conditioning contraction, as well as, a minor increase in the rate of force development, was obtained. The authors concluded that the mechanism of PAP is not related to any neural factors, and they suggested that, the phosphorylation of myosin regulation light chains is the main mechanism of twitch potentiation.

The latest study regarding the H-reflex on the issue of PAP (Iglesias-Soler et al., 2011), examined the effect of different in duration (7-10 sec) and intensity (10–100% MVC) conditioning stimuli during isometric contractions. The results did not show a significant change in H-reflex or any other related parameters after the isometric conditioning stimulus. Nevertheless, a significant enhancement occurred in mechanical power 4 min after the MVC. The researchers concluded that the enhancement in the mechanical power is not related to spinal excitability. Beyond the methodological aspects and the conflicting results in the aforementioned studies, the researchers focused mainly on the soleus muscle. The soleus is well known that has a low proportion of type II muscle fibers and has a decreased potential to be influenced from PAP (Hamada et al., 2000). However, only Folland et al. (2008), attempted to link PAP with neural enhancement in a mixed muscle. After using as a conditioning contraction a 10 sec isometric MVC, Folland and his colleagues measured twitch torque, H-reflex and the performance of the examined muscle (quadriceps femoris) of eight recreationally active males. The results showed that twitch torque increased by 66.6% right after the conditioning contraction, the H/M ratio increased by 42% between the 5th and 11th min post-conditioning stimulus, and the muscle performance demonstrated no significant alteration. The researchers underlined the different time course of mechanical and reflex potentiation and the existence of PAP in a mixed skeletal muscle. Considering the above, the studies measuring H-reflex during PAP are heterogeneous and have several methodological limitations and their findings are conflicting. Future studies should be oriented to examine three different major issues: 1) the determination of the optimal conditioning stimulus to attain PAP, 2) the exact time course of potentiation of twitch torque and H-reflex, and 3) the effect of PAP on human performance on the field.

Conclusions

Summarizing all previous studies many questions arise. Due to different methodological approaches, i.e. varying conditioning contractions (type, duration, repetition, sets), diverse subject's training background (trained, untrained) or even different muscles examined, it would be arbitrary to reach a solid conclusion about a neural contribution on PAP. Although the current literature provides evidence on the impact of a neural enhancement on PAP, further studies are required to clarify this issue. Furthermore, due to the fact that PAP and fatigue can co-exist and counterbalance each other (Rassier & Macintosh, 2000), there is an open field for research on the optimal duration, rest interval and number of conditioning contractions that should be applied in training programs in order to maximize athletic performance.

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