

Vera-Ibáñez, A.; Romero-Arenas, S.; Marín-Pagán, C. y Márquez, G. (2018). Concurrencia de fatiga y potenciación tras una contracción voluntaria máxima sostenida / Concurrence of Fatigue and Potentiation After a Sustained Maximal Voluntary Contraction. Revista Internacional de Medicina y Ciencias de la Actividad Física y el Deporte vol. 18 (69) pp. 61-76
[Http://cdeporte.rediris.es/revista/revista69/artconcurrencia888.htm](http://cdeporte.rediris.es/revista/revista69/artconcurrencia888.htm)
DOI: <https://doi.org/10.15366/rimcafd2018.69.004>

ORIGINAL

CONCURRENCE OF FATIGUE AND POTENTIATION AFTER A SUSTAINED MAXIMAL VOLUNTARY CONTRACTION

CONCURRENCIA DE FATIGA Y POTENCIACIÓN TRAS UNA CONTRACCIÓN VOLUNTARIA MÁXIMA SOSTENIDA

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Código UNESCO / UNESCO code: 241010 Fisiología humana / Human Physiology.

Clasificación Consejo de Europa / Council of Europe Classification: 6. Fisiología del ejercicio / Exercise Physiology.

Recibido 25 de diciembre de 2015 **Received** December 25, 2015

Aceptado 7 de abril de 2016 **Accepted** April 7, 2016

ABSTRACT

The aim of the present study was to analyze the concurrence and interaction between different factors affecting the performance, such as central fatigue, peripheral fatigue and post-activation potentiation (PAP) after the performance of a maximal voluntary contraction (MVC) sustained until the loss of the 50% of the initial torque value. In order to assess the effects of central fatigue, peripheral fatigue and the PAP on the performance of the MVC, the twitch interpolation technique was used. Our findings revealed a loss of the force capability during at least 3'30" and that the recorded fatigue had central and peripheral contributions. Moreover, it has been observed an inhibition of the PAP after the completion of the sustained MVC during a brief interval (between 30'' and 1'30'). Furthermore, it has been observed the coexistence of the different studied phenomena, however, they showed different time course of the recovery.

KEY WORDS: Central fatigue, peripheral fatigue, post-activation potentiation, maximal twitch interpolation technique.

RESUMEN

El objetivo del presente estudio fue analizar la concurrencia e interacción existente entre diferentes factores que afectan al rendimiento, tales como son la fatiga central, la fatiga periférica y la potenciación post-activación (PPA) tras la realización de una contracción máxima voluntaria (CMV) sostenida hasta la pérdida del 50% en los valores de fuerza iniciales. Con el objetivo de valorar los efectos de la fatiga central, fatiga periférica y la PPA se utilizó la técnica de interpolación de descargas. Los resultados han revelado pérdidas en los valores de durante aproximadamente 3'30'' y que la fatiga dependió tanto de factores centrales como periféricos. También se produjo una inhibición de la PPA tras la realización de la CMV sostenida, durante un breve periodo de tiempo (entre 30'' y 1'30'). Además, se observó la coexistencia de los distintos fenómenos estudiados, que sin embargo, demostraron tener una curva de recuperación temporal diferente.

PALABRAS CLAVE: Fatiga central, fatiga periférica, potenciación post-activación, técnica de interpolación de descargas.

INTRODUCTION

Muscular fatigue is one of the most influential phenomena in athletic performance. It is defined as an increase in perception of effort accompanied by a decrease in the muscle ability to generate contractile force (Enoka & Stuart, 1992; Gandevia, 1992). It has been extensively studied using different approaches (cellular, neuromuscular, mechanical, etc...). It is also currently accepted that the cause of fatigue is mainly central and/or peripheral in origin (Taylor & Gandevia, 2008).

Central fatigue includes the most proximal processes to the neuromuscular junction and can be defined as a progressive failure in voluntary activation induced by any type of exercise (Taylor & Gandevia, 2001; 2008). This type of fatigue may be due to alterations in cortical excitability (Gandevia, Allen, Butler & Taylor, 1996), changes in motor-neuron firing rates (Bigland-Ritchie, Johansson, Lippold, Smith & Woods, 1983; Garland & McComas, 1990), and / or a decrease in spinal discharge (Macefield, Hagbarth, Gorman, Gandevia & Burke, 1991).

Peripheral fatigue includes the most distal processes to the neuromuscular junction, which induce a decrease in force production (Gandevia, 2001). This type of fatigue is due to alterations in muscle homeostasis, such as accumulation of metabolites (Baker, Kostov, Miller & Weiner, 1993; Cady, Jones, Lynn & Newham, 1989), increased intracellular pH (Kent-Braun, 1999) or variations in excitation-contraction coupling processes (Baker et al., 1993; Cady et al., 1989; DeGroot et al, 1993).

However, it is well known that fatigue coexist with the so called post-activation potentiation (PAP), phenomenon which positively affects the force capabilities (Robbins, 2005). PAP is defined as an increase in muscle performance after a conditioning contraction (Belanger, McComas & Elder, 1983; Vandervoort, Quinlan & McComas, 1983; Xenofondos et al., 2010). Two theories have been used to explain the PAP. The first theory involves an increased myosin light-chains phosphorylation just after the performance of a maximum voluntary contraction (MVC), which implies an increased sensitivity to the actin-myosin Ca^{2+} (Grange, Vandenboom & Houston, 1993; Palmer & Moore, 1989). The second theory hypothesized that PAP increases H reflex magnitude increasing the efficiency and transmission velocity of nerve impulses that reach the muscle (Hodgson, Docherty & Robbins, 2005).

Although it seems contradictory, it has been shown that both, fatigue and potentiation coexist temporarily and interfere within the sport performance depending on the intensity and duration of the conditioning stimulus (Chiu et al., 2003; Hamada, Sale, MacDougall & Tarnopolsky, 2000). This makes really complex the study of such phenomena (Garner, Hicks & McComas, 1989), since both fatigue and PAP start when the contractile activity begins and coexist later on (Krarup, 1981). Thus the prevalence of fatigue or PAP depends on the type, intensity and duration of exercise (Masiulis et al., 2007). Therefore, it can be concluded that the optimum performance occurs when potentiation predominates over fatigue (Hodgson et al., 2005).

Over the past century, different techniques have been developed to record the origin of fatigue and post-activation potentiation. Among the others, the "Twitch Interpolation Technique", introduced by Merton in 1954, is considered the "gold standard" (Gandevia, McNeil, Carroll & Taylor, 2013). This method consists in the interpolation of an electrical twitch to the motor nerve during a maximum voluntary contraction to obtain the voluntary activation (VA) (Allen, Gandevia & McKenzie, 1995), which give us information about the central drive (Gandevia, 2001). Different studies demonstrated the co-existence of both, central and peripheral fatigue after the performance of sustained maximal and sub-maximal voluntary contractions (Löscher, Cresswell & Thorstensson, 1996; McKenzie, Bigland-Ritchie, Gorman & Gandevia, 1992, Stackhouse, Dean, Lee & Binder-MacLeod, 2000), or after the completion of supramaximal high intensity whole body exercises (Fernandez del Olmo et al, 2013;. Girard, Bishop & Racinais, 2013).

In spite the multitude of studies performed in this field, there is a lack of knowledge on whether PAP, central and peripheral fatigue interacts just after the performance of a sustained MVC. Therefore, this study aimed to determine the time course of peripheral fatigue, central fatigue and PAP after the completion of a sustained maximal voluntary contraction performed by the knee extensors. We hypothesized that after the performance of a sustained MVC, central fatigue, peripheral fatigue and post-activation potentiation coexist within a different time curve of recovery.

MATERIAL AND METHODS

Subjects

Nine healthy males subjects were recruited for this study (age = 21 ± 4 years, height = 178 ± 5 cm in height, body mass = 70.2 ± 7.3 kg) all of them students of the Faculty of Sport of the Catholic University San Antonio. They were involved in vigorous physical activity (3.5 ± 0.8 hours per week). Any participant reported lower limb injuries as well as any health conditions precluding maximal strength activities. All subjects gave written consent about the experimental procedure. The experimental procedures were run in accordance with the Declaration of Helsinki and approved by the local ethics committee. *Procedure and instruments*

Firstly, the optimal site for the femoral nerve stimulation was located at the femoral triangle. This process is of great importance, since a small deviation could cause a contraction in unwanted muscles (Millet, Martin, Martin & Vergès, 2011). Then, we proceeded to fix the stimulation electrodes. The cathode was placed over the femoral triangle and the anode positioned between the great trochanter and the iliac crest (Fernandez del Olmo et al., 2013). Both electrodes (5x5 cm) were made of carbonized plastic and covered with an electro-conductive gel. A constant current stimulator (Digitimer DS7AH, Welwyn Garden City, UK) was used (rectangular pulse = 1 ms). Stimulation intensity was determined in accordance to Todd et al (2003). While subject remained at

rest, stimulation intensity was linearly increased until the resting twitch amplitude (Q_{tw}) plateaued. Then, the intensity of the electrical pulse was set to 120% of that required to elicit a maximum quadriceps twitch amplitude (Q_{tw}) and M-wave (M_{max}) and maintained constant throughout the experiment.

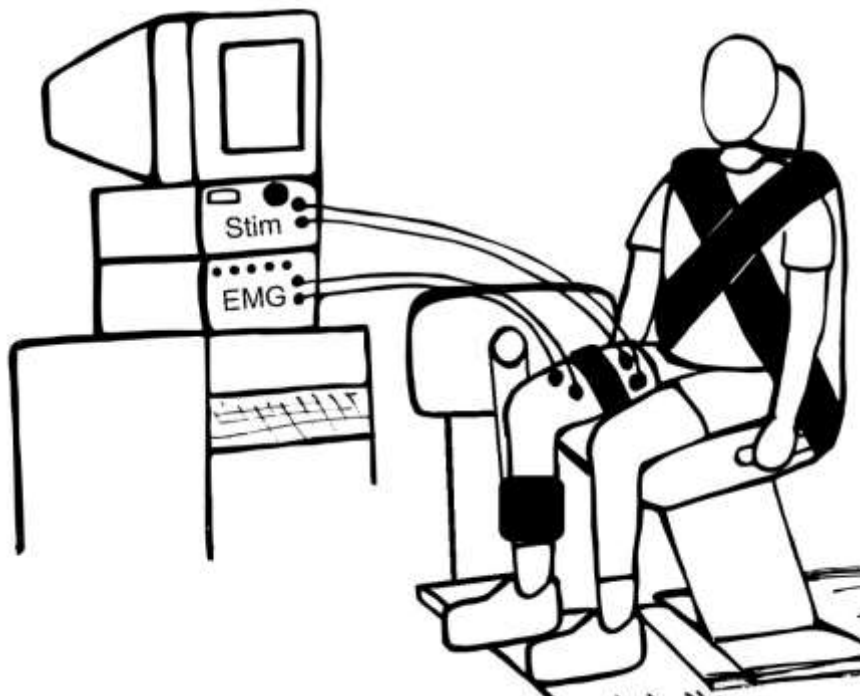


Figure 1. Experimental set up.

MVC were recorded with subjects placed in a seated position on a Biodex System 3® (Biodex Medical Systems, New York, USA) dynamometer and were securely strapped into the test chair. The chair had a long backrest, providing full back support. The hip and knee were fixed at 90° of flexion (see Figure 1).

For the electromyographic recordings, a KinePro system (Reykjavik, Iceland) was used. The sampling frequency was 1600 Hz, the band pass filter 16 -500 Hz and the common mode rejection ratio 110 dB. Surface electrodes were placed on the vastus lateralis (VL) with an inter-electrode distance of 20 mm. Skin were shaved, abraded and cleaned with alcohol following SENIAM recommendations (Hermens, Freriks, Dißelhorst-Klug & Rau, 2000).

Completed the preparation of the subject, we proceeded with a standardized warm-up. Then, we test the contractile properties of the knee extensor at rest, and the level of voluntary activation. For this purpose, three supramaximal stimuli were applied over the femoral nerve within the muscle relaxed with an inter-stimulus interval of 3 seconds (Q_{tw}). The subject was then asked to conduct a MVC of 5 seconds, in which supramaximal electric twithc was applied during the plateau phase Visual feedback was given to the subject in all trials. . Then, after the completion of the MVC, three more supramaximal stimuli were applied again to measure the potentiated twitch amplitude (Q_{tw_pot}).

After the initial block (baseline), the subject was asked to undertake a sustained MVC until the force was reduced approximately 50% with respect to the initial values recorded. Such a stimulus (called "fatigue block") is especially designed to induce high levels of fatigue (Bigland-Ritchie, Jones, Hosking & Edwards., 1978; Todd et al, 2003). After the cessation of that activity, an identical evaluation was performed as described above, at different time intervals: 0'30", 1'30", 2'30", 3'30" and 5'.

Study variables and data analysis

The different parameters analyzed are displayed in Figure 2. The maximal voluntary contraction (MVC) represents the maximal torque recorded just before the superimposed twitch. The resting twitch amplitude (Q_{tw}) represents the maximal torque elicited at rest when electrical stimulation is applied before the MVC. The potentiated twitch amplitude (Q_{tw_pot}) represents the maximal torque elicited at rest when electrical stimulation is applied just after the MVC. Changes in Q_{tw_pot} represents peripheral fatigue (Belanger & McComas, 1989). Voluntary activation (VA) was computed by the following equation: $VA (\%) = (1 - \text{Twitch superimposed} / Q_{tw_pot}) \times 100$. This equation establishes a relationship between the superimposed twitch (Q_{superp}) and the Q_{tw_pot} (Merton, 1954; Shield & Zhou, 2004). Post-activation potentiation was expressed as the increase (%) of the force evoked at rest after the performance of the MVC. It is computed using the next equation: $[Q_{tw_pot} / Q_{tw}] * 100$.

For the electromyographic variables, it was analyzed the peak to peak amplitude of the M_{max} from the VL which represents the maximal discharge of the motor neuron pool (Aagaad, Simonsen, Andersen, Magnusson & Dyhre-Poulsen, 2002).. It is presented as the average of the 3 supramaximal stimuli evoked at rest. The rmsEMG of VL was also analyzed and is expressed as the root mean square (rms) of the electromyographic signal (EMG) during an interval of one second duration just before the application of the superimposed twitch.

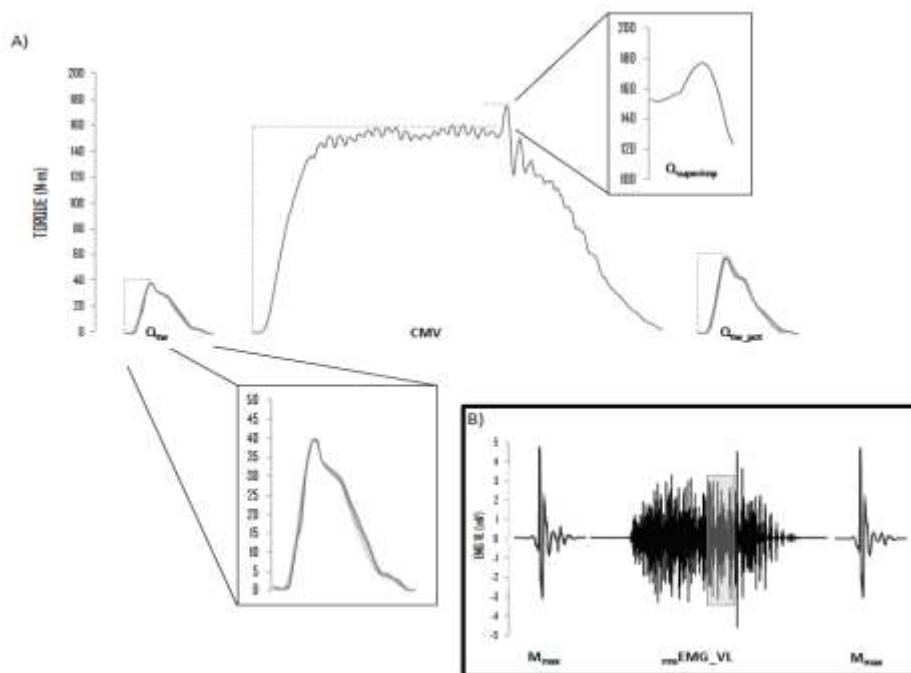


Figure 2. This figure shows an example of assessment block used throughout the experiment, where twitch interpolation technique was used, as well as the different analyzed variables. A) Torque trace recorded during the three resting twitches (Q_{tw}) before starting the MVC; then it could be observed the MVC torque and the superimposed twitch (Q_{superp}); finally, three potentiated twitches (Q_{tw_pot}) are displayed in the right panel. B) In the lower panel M_{max} (before and after the MVC) are displayed together with the EMG activity corresponding to the MVC.

Statistical analysis

It was firstly performed a descriptive analysis of each parameter (mean and standard deviation). Then normality was evaluated through the Shapiro-Wilk test. One way repeated measures ANOVA (RM- ANOVA) were performed using a within-subject factor (time) with six different levels (Pre and Post: 30"; 1'30"; 2'30"; 3' and 5'30"). When the main factor showed significant differences, pairwise comparisons with Bonferroni correction were used in order to test. The alpha level was set at $p \leq 0.05$. The statistical analysis was performed using the SPSS software (v. 18.00).

RESULTS

It should be firstly noted that the torque in the last two seconds of the sustained MVC was $55.4\% (\pm 9.8)$ of the initial peak torque. Moreover, the average duration of the sustained MVC was $44.9 (\pm 11.5)$ seconds. The sustained MVC produced different changes in the variables analyzed (MVC, %VA, Q_{tw} , Q_{tw_pot} , PAP (%), VL-Mmax, VL-rmsEMG), which are shown in Table 1.

Table 1. Mean (\pm SD) of the different parameters studied. The level of statistical significance is shown as follows: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	PRE	POST_30''	POST_1'30''	POST_2'30''	POST_3'30''	POST_5'
MVC (N•m)	235,77 ($\pm 69,55$)	190,24*** ($\pm 60,18$)	197,36*** ($\pm 66,39$)	207,43** ($\pm 60,83$)	211,2* ($\pm 54,28$)	220,46 ($\pm 61,23$)
VA (%)	86,82 ($\pm 7,72$)	80,11* ($\pm 10,39$)	76,28* ($\pm 14,43$)	70,76* ($\pm 18,23$)	75,1* ($\pm 17,31$)	84,36 ($\pm 10,55$)
Q_{tw} (N•m)	43,28 ($\pm 7,50$)	33,22** ($\pm 9,78$)	37,16* ($\pm 8,64$)	44,87 ($\pm 8,95$)	47,67 ($\pm 7,89$)	45,98 ($\pm 8,48$)
Q_{tw_pot} (N•m)	57,27 ($\pm 11,57$)	35,65*** ($\pm 8,37$)	46,06** ($\pm 9,34$)	54,60 ($\pm 9,97$)	57,14 ($\pm 10,97$)	58,62 ($\pm 10,68$)
PAP (%)	132,65 ($\pm 14,61$)	109,60** ($\pm 11,55$)	125,39 ($\pm 10,99$)	122,69 ($\pm 12,12$)	122,87 ($\pm 12,43$)	127,99 ($\pm 11,67$)
rmsEMGVL (mV)	1,23 ($\pm 0,37$)	1,14 ($\pm 0,42$)	1,03 ($\pm 0,43$)	1,10 ($\pm 0,41$)	1,13 ($\pm 0,31$)	1,15 ($\pm 0,52$)
M wave VL (mV)	6,16 ($\pm 2,33$)	5,90 ($\pm 2,20$)	6,00 ($\pm 2,28$)	6,10 ($\pm 2,0248$)	5,96 ($\pm 2,24$)	6,30 ($\pm 2,05$)

The RM-ANOVA of the MVC showed significant differences in the time factor ($F = 15.173$, $p \leq 0.001$). Paired comparisons revealed that MVC torque was significantly reduced until the last bout in comparison with the PRE test values ($p \leq 0.05$ for all comparisons). However, it should be mentioned that no differences were found between the MVC exerted before (pre) and after 5 minutes of recovery.

The RM-ANOVA revealed significant differences in the time factor ($F = 17.103$, $p \leq 0.001$) in the Q_{tw} . Paired comparisons showed that Q_{tw} levels were significantly reduced during 30" and 1'30" in comparison with the baseline values ($p \leq 0.05$ for both comparisons).

Regarding to the potentiated twitch RM-ANOVA revealed significant differences in the time factor ($F = 47.161$, $p \leq 0.001$). Paired comparisons showed a reduced Q_{tw_pot} during 30" and 1'30" blocks in relation to the pre-test values ($p \leq 0.05$ for both comparisons). No significant differences were found after 2'30", 3'30" and 5' recovery with respect to baseline. The analysis of voluntary activation analysis, the RM-ANOVA showed the existence of significant differences in the time factor ($F = 4.914$, $p \leq 0.005$). Paired comparisons revealed reduced VA during 30"; 1'30"; 2'30" and 3'30" blocks ($p \leq 0.05$ for all comparisons). It should be noted that no difference were found after 5' of recovery.

In the analysis of PAP, the RM-ANOVA showed a significant effect for the time factor ($F = 5.220$, $p \leq 0.005$). Paired comparisons showed an inhibition of the PAP just after the performance of the sustained MVC (during the post 0'30"). However, post hoc analysis revealed no significant differences in the subsequent time points (1'30", 2'30", 3'30" and 5') when compared to baseline values.

Neither the RMS nor the M_{max} were affected by the sustained MVC.

DISCUSSION

This study revealed the coexistence and interaction of different factors affecting peripheral fatigue, central fatigue and PAP after a maximum sustained effort. The most important result in the present study is the coexistence of different phenomena studied, which have shown an influence on recovery at different time points. While the PAP is inhibited only in the early stages of recovery, peripheral fatigue acts at least until 2'30" and central fatigue is the last factor to show a full recovery. Although it was widely studied in isolation (Kent-Braun, 1999; Nordlund, Thorstensson & Cresswell, 2004), few studies attempted to investigate its interaction after different types of effort (Masiulis et al, 2007; Rassier & Macintosh, 2000).

Peripheral fatigue

Present study revealed a 20% loss of MVC torque after the completion of the sustained MVC, being peripheral fatigue the main cause since the amplitude of Q_{tw_pot} (indicator of the existence of peripheral fatigue) decreased by 38%. Similar data were found in Kent-Braun (1999), where there was a 80% reduction of the torque evoked at rest after the performance of a sustained MVC for four minutes. Our results are also in accordance with those found by Todd et al. (2003) in the brachial biceps. In this study subjects experienced a 57% decrease in Q_{tw_pot} amplitude after the completion of a sustained MVC Schillings et al. (2003) also found a 38.2% loss after a 2 minutes MVC, being the 89% of this decrease attributed to peripheral factors. Furthermore, Gandevia et al. (1996) found a decrease of 25.9% in the force values and 29.5% in the magnitude of Q_{tw_pot} after the performance of 3 minutes MVCs. This overwhelming reduction in potentiated twitch reveals the predominance of peripheral factors as the main cause of loss of performance after these tasks. According to Hunter, Butler, Todd, Gandevia and Taylor (2006) in these high intensity efforts, the greatest contribution to the total fatigue is peripheral in origin. This statement is also supported by the results obtained by Schillings et al. (2003), which demonstrate that fatigue produced in the first minute (during a sustained MVC) is mainly triggered by a failure in the peripheral mechanisms.

Different mechanisms have been proposed to explain the abovementioned reductions, being the changes in muscle metabolism, such as the accumulation of lactate and H^+ , the depletion of the phosphocreatine (PCr), most common features. In the study by Kent-Braun (1999) was found a direct relationship between intramuscular pH and changes in strength, so that as the contraction passed, the pH decreased in parallel with the force values. On the other hand, It has been suggested that the increased inorganic phosphate (Pi), diprotonated inorganic phosphate (H_2PO_4) and hydrogen protons (H^+) can inhibit the contractile process due to changes produced in the calcium kinetics (Kent-Braun, 1999). Despite the prevalence of peripheral fatigue as the main cause of

the performance loss, it should be also considered the central factors as a potential cause.

Central fatigue

This study revealed a decrease of 8% in the VA (main indicator of central fatigue). This shows that central fatigue is also present and it should be considered as a limiting factor of performance. Schillings et al. (2003) and Todd et al. (2003) showed a reduction in voluntary activation by 12% and 10% respectively, after sustained MVCs. According to Löscher et al. (1996) and Sjøgaard, Gandevia, Todd, Petersen and Taylor (2006) the ability of the nervous system to maintain the proper muscle activation is directly related to the duration and type of the previous activity, ie, the length and type of contraction used during the fatigue protocol. Babault, Desbrosses, Fabre, Michaut and Pousson (2006) showed that isometric contractions produce higher levels of central fatigue than dynamic contractions. This may explain the rapid onset of central fatigue after our sustained "isometric" MVC. Another important fact that can be drawn from our study is the prolonged recovery of central mechanisms (between 3' and 5'30").

Central fatigue is triggered by changes in the electrical properties of the neurons and within the circuitry of the primary motor cortex, since different studies have found changes in cortical excitability after the performance of maximal (Gandevia et al., 1996) or supramaximal (Fernandez del Olmo et al., 2013) exercises. Another possible explanation is the decrease in motor units firing rate (Bigland-Ritchie et al., 1983; Garland & McComas, 1990), as well as the changes in spinal cord circuitry: i.e.: decrease in H-reflex excitability (Macefield et al., 1991). However, with this methodology (twitch interpolation), we cannot determine which of the above mechanisms is primarily responsible for the appearance of this type of fatigue. So that, new studies should be performed using single motor units recordings as well as the transcranial magnetic stimulation.

Post-activation potentiation

Our results also revealed that PAP is another factor that alters torque values. It is clear how PAP, is inhibited during a short period of time (0'-1'30"). However, this is the factor that needs less time to recover the initial values. Although the PAP persists during a time window of approximately five minutes (Baudry & Duchateau 2004; Gossen & Sale, 2000; Vandervoort & McComas, 1983), the influence of fatigue seems to be a fundamental factor (Tillin and Bishop, 2009). Therefore, one of the most important findings from this study is the rapid recovery of the PAP just after the sustained MVC and the coexistence with different types of fatigue.

Although PAP is commonly understood as an increase in performance after a conditioning activity, this study has shown that PAP was present despite it was masked by the fatigue effects. Tillin and Bishop (2009) consider that fatigue, rather than PAP, dictates during the earliest stages of recovery. Thus, these

authors conclude that after a conditioning contraction a recovery period is needed to decrease fatigue and so PAP could be preserved. In this sense, the concurrence of fatigue and PAP is directly related to the magnitude and characteristics of the conditioning stimulus. (Hamada, Sale, MacDougall and Tarnopolsky, 2003) showed how during repeated MVCs (5 sec) with knee extension (16 MVCs in total) PAP strongly influences the performance (127% of baseline) while after the third repetition the MVCs values were gradually declined (32% in the last contraction).

CONCLUSION

In conclusion, revealed a significant decrease in the force capabilities during at least 3'30". Moreover, the performance was affected by both peripheral and central fatigue.. Finally, peripheral fatigue, central fatigue and PAP temporarily coexist after the sustained MVC with different recovery curves. Therefore, depending on the time after the conditioning activity (e.g.: sustained MVC), the loss of strength depends more on PAP, peripheral or central fatigue. So that, present results should be taken into account when prescribing and planning exercise.

REFERENCES

- Aagaad, P., Simonsen, E. B., Andersen, J. L., Magnusson, P., & Dyhre-Poulsen, P. (2002). Neural adaptation to resistance training: changes in evoked V-wave and H-reflex responses. *Journal of Applied Physiology*, 92(6), 2309-2318. <https://doi.org/10.1152/jappphysiol.01185.2001>
- Allen, D. G., Lamb, G. D., & Westerblad, H. (2008). Skeletal muscle fatigue: cellular mechanisms. *Physiological reviews*, 88(1), 287-332. <https://doi.org/10.1152/physrev.00015.2007>
- Allen, G. M., Gandevia, S. C., & McKenzie, D. K. (1995). Reliability of measurements of muscle strength and voluntary activation using twitch interpolation. *Muscle & nerve*, 18(6), 593-600. <https://doi.org/10.1002/mus.880180605>
- Babault, N., Desbrosses, K., Fabre, M. S., Michaut, A., & Pousson, M. (2006). Neuromuscular fatigue development during maximal concentric and isometric knee extensions. *Journal of Applied Physiology*, 100(3), 780-785. <https://doi.org/10.1152/jappphysiol.00737.2005>
- Baker, A. J., Kostov, K. G., Miller, R. G., & Weiner, M. W. (1993). Slow force recovery after long-duration exercise: metabolic and activation factors in muscle fatigue. *Journal of Applied Physiology*, 74(5), 2294-2300. <https://doi.org/10.1152/jappl.1993.74.5.2294>
- Barcroft, H., & Millen, J. L. E. (1939). The blood flow through muscle during sustained contraction. *The Journal of physiology*, 97(1), 17-31. <https://doi.org/10.1113/jphysiol.1939.sp003789>
- Baudry, S., & Duchateau, J. (2004). Postactivation potentiation in human muscle is not related to the type of maximal conditioning contraction. *Muscle & nerve*, 30(3), 328-336. <https://doi.org/10.1002/mus.20101>
- Belanger, A. Y., McComas, A. J., & Elder, G. B. C. (1983). Physiological properties of two antagonistic human muscle groups. *European journal of applied*

- physiology and occupational physiology*, 51(3), 381-393.
<https://doi.org/10.1007/BF00429075>
- Belanger, A. Y., & McComas, A. J. (1989). Contractile properties of human skeletal muscle in childhood and adolescence. *European journal of applied physiology and occupational physiology*, 58(6), 563-567.
<https://doi.org/10.1007/BF00418500>
- Bigland-Ritchie, B., Johansson, R., Lippold, O. C., Smith, S., & Woods, J. J. (1983). Changes in motoneurone firing rates during sustained maximal voluntary contractions. *The Journal of Physiology*, 340(1), 335-346.
<https://doi.org/10.1113/jphysiol.1983.sp014765>
- Bigland-Ritchie, B., Jones, D. A., Hosking, G. P., & Edwards, R. H. T. (1978). Central and peripheral fatigue in sustained maximum voluntary contractions of human quadriceps muscle. *Clin Sci Mol Med*, 54(6), 609-614.
<https://doi.org/10.1042/cs0540609>
- Bigland-Ritchie, B., Jones, D. A., & Woods, J. J. (1979). Excitation frequency and muscle fatigue: electrical responses during human voluntary and stimulated contractions. *Experimental neurology*, 64(2), 414-427.
[https://doi.org/10.1016/0014-4886\(79\)90280-2](https://doi.org/10.1016/0014-4886(79)90280-2)
- Bigland-Ritchie, B., Kukulka, C. G., Lippold, O. C., & Woods, J. J. (1982). The absence of neuromuscular transmission failure in sustained maximal voluntary contractions. *The Journal of physiology*, 330(1), 265-278.
<https://doi.org/10.1113/jphysiol.1982.sp014340>
- Bigland-Ritchie, B., & Woods, J. J. (1984). Changes in muscle contractile properties and neural control during human muscular fatigue. *Muscle and Nerve* 7, 691-699. <https://doi.org/10.1002/mus.880070902>
- Cady, E. B., Jones, D. A., Lynn, J., & Newham, D. J. (1989). Changes in force and intracellular metabolites during fatigue of human skeletal muscle. *The Journal of Physiology*, 418(1), 311-325.
<https://doi.org/10.1113/jphysiol.1989.sp017842>
- Chiu, L. Z., Fry, A. C., Weiss, L. W., Schilling, B. K., Brown, L. E., & Smith, S. L. (2003). Postactivation potentiation response in athletic and recreationally trained individuals. *The Journal of Strength & Conditioning Research*, 17(4), 671-677.
- Degroot, M., Massie, B. M., Boska, M., Gober, J., Miller, R. G., & Weiner, M. W. (1993). Dissociation of [H⁺] from fatigue in human muscle detected by high time resolution ³¹P-NMR. *Muscle & nerve*, 16(1), 91-98.
<https://doi.org/10.1002/mus.880160115>
- Edwards, R. H., Hill, D. K., Jones, D. A., & Merton, P. A. (1977). Fatigue of long duration in human skeletal muscle after exercise. *The Journal of physiology*, 272(3), 769-778. <https://doi.org/10.1113/jphysiol.1977.sp012072>
- Enoka, R. M., & Stuart, D. G. (1992). Neurobiology of muscle fatigue. *J Appl Physiol*, 72(5), 1631-1648. <https://doi.org/10.1152/jappl.1992.72.5.1631>
- Fernández-del-Olmo, M., Rodríguez, F. A., Márquez, G., Iglesias, X., Marina, M., Benitez, A., ... & Acero, R. M. (2013). Isometric knee extensor fatigue following a Wingate test: peripheral and central mechanisms. *Scandinavian journal of medicine & science in sports*, 23(1), 57-65. <https://doi.org/10.1111/j.1600-0838.2011.01355.x>
- Gandevia, S. C. (1992). Some central and peripheral factors affecting human motoneuronal output in neuromuscular fatigue. *Sports Medicine*, 13(2), 93-98.
<https://doi.org/10.2165/00007256-199213020-00004>

- Gandevia, S. C. (2001). Spinal and supraspinal factors in human muscle fatigue. *Physiological reviews*, 81(4), 1725-1789. <https://doi.org/10.1152/physrev.2001.81.4.1725>
- Gandevia, S. C., Allen, G. M., Butler, J. E., & Taylor, J. L. (1996). Supraspinal factors in human muscle fatigue: evidence for suboptimal output from the motor cortex. *The Journal of physiology*, 490(Pt 2), 529-536. <https://doi.org/10.1113/jphysiol.1996.sp021164>
- Gandevia, S. C., McNeil, C. J., Carroll, T. J., & Taylor, J. L. (2013). Twitch interpolation: superimposed twitches decline progressively during a tetanic contraction of human adductor pollicis. *The Journal of physiology*, 591(5), 1373-1383. <https://doi.org/10.1113/jphysiol.2012.248989>
- Garland, S. J., & McComas, A. J. (1990). Reflex inhibition of human soleus muscle during fatigue. *The Journal of physiology*, 429(1), 17-27. <https://doi.org/10.1113/jphysiol.1990.sp018241>
- Garner, S. H., Hicks, A. L., & McComas, A. J. (1989). Prolongation of twitch potentiating mechanism throughout muscle fatigue and recovery. *Experimental neurology*, 103(3), 277-281. [https://doi.org/10.1016/0014-4886\(89\)90051-4](https://doi.org/10.1016/0014-4886(89)90051-4)
- Girard, O., Bishop, D. J., & Racinais, S. (2013). Neuromuscular adjustments of the quadriceps muscle after repeated cycling sprints. *PloS one*, 8(5), e61793. <https://doi.org/10.1371/journal.pone.0061793>
- 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. <https://doi.org/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. <https://doi.org/10.1139/h93-020>
- Hamada, T., Sale, D. G., MacDougall, J. D., & Tarnopolsky, M. A. (2000). Postactivation potentiation, fiber type, and twitch contraction time in human knee extensor muscles. *Journal of Applied Physiology*, 88(6), 2131-2137. <https://doi.org/10.1152/jappl.2000.88.6.2131>
- Hamada, T., Sale, D. G., MacDougall, J. D., & Tarnopolsky, M. A. (2003). Interaction of fibre type, potentiation and fatigue in human knee extensor muscles. *Acta physiologica scandinavica*, 178(2), 165-173. <https://doi.org/10.1046/j.1365-201X.2003.01121.x>
- Hermens, H. J., Freriks, B., Disselhorst-Klug, C., & Rau, G. (2000). Development of recommendations for SEMG sensors and sensor placement procedures. *Journal of electromyography and Kinesiology*, 10(5), 361-374. [https://doi.org/10.1016/S1050-6411\(00\)00027-4](https://doi.org/10.1016/S1050-6411(00)00027-4)
- Hodgson, M., Docherty, D., & Robbins, D. (2005). Post-activation potentiation. *Sports Medicine*, 35(7), 585-595. <https://doi.org/10.2165/00007256-200535070-00004>
- Humphreys, P. W., & Lind, A. R. (1963). The blood flow through active and inactive muscles of the forearm during sustained hand-grip contractions. *The Journal of physiology*, 166(1), 120-135. <https://doi.org/10.1113/jphysiol.1963.sp007094>
- Hunter, S. K., Butler, J. E., Todd, G., Gandevia, S. C., & Taylor, J. L. (2006). Supraspinal fatigue does not explain the sex difference in muscle fatigue of maximal contractions. *Journal of Applied Physiology*, 101(4), 1036-1044. <https://doi.org/10.1152/jappphysiol.00103.2006>

- Kay, D., St Clair Gibson, A., Mitchell, M. J., Lambert, M. I., & Noakes, T. D. (2000). Different neuromuscular recruitment patterns during eccentric, concentric and isometric contractions. *Journal of Electromyography and Kinesiology*, 10(6), 425-431 [https://doi.org/10.1016/S1050-6411\(00\)00031-6](https://doi.org/10.1016/S1050-6411(00)00031-6)
- Kent-Braun, J. A. (1999). Central and peripheral contributions to muscle fatigue in humans during sustained maximal effort. *European journal of applied physiology and occupational physiology*, 80(1), 57-63. <https://doi.org/10.1007/s004210050558>
- Krarup, C. (1981). Enhancement and diminution of mechanical tension evoked by staircase and by tetanus in rat muscle. *The Journal of physiology*, 311(1), 355-372. <https://doi.org/10.1113/jphysiol.1981.sp013589>
- Löscher, W. N., Cresswell, A. G., & Thorstensson, A. (1996). Central fatigue during a long-lasting submaximal contraction of the triceps surae. *Experimental Brain Research*, 108(2), 305-314. <https://doi.org/10.1007/BF00228103>
- Macefield, G., Hagbarth, K. E., Gorman, R., Gandevia, S. C., & Burke, D. (1991). Decline in spindle support to alpha-motoneurons during sustained voluntary contractions. *The Journal of physiology*, 440(1), 497-512. <https://doi.org/10.1113/jphysiol.1991.sp018721>
- Masiulis, N., Skurvydas, A., Kamandulis, S., Kudirkaitė, J., Sukockas, V., Valys, E., ... & Kamandulienė, L. (2007). Post-activation potentiation and fatigue of quadriceps muscle after continuous isometric contractions at maximal and submaximal intensities. *Education. Physical Training. Sport*, (67).
- McKenzie, D. K., Bigland-Ritchie, B., Gorman, R. B., & Gandevia, S. C. (1992). Central and peripheral fatigue of human diaphragm and limb muscles assessed by twitch interpolation. *The Journal of physiology*, 454(1), 643-656. <https://doi.org/10.1113/jphysiol.1992.sp019284>
- Merton, P. A. (1954). Voluntary strength and fatigue. *The Journal of physiology*, 123(3), 553-564. <https://doi.org/10.1113/jphysiol.1954.sp005070>
- Millet, G. Y., Martin, V., Martin, A., & Vergès, S. (2011). Electrical stimulation for testing neuromuscular function: from sport to pathology. *European journal of applied physiology*, 111(10), 2489-2500. <https://doi.org/10.1007/s00421-011-1996-y>
- Nordlund, M. M., Thorstensson, A., & Cresswell, A. G. (2004). Central and peripheral contributions to fatigue in relation to level of activation during repeated maximal voluntary isometric plantar flexions. *Journal of applied physiology*, 96(1), 218-225. <https://doi.org/10.1152/japplphysiol.00650.2003>
- Palmer, B. M., & Moore, R. L. (1989). Myosin light chain phosphorylation and tension potentiation in mouse skeletal muscle. *American Journal of Physiology-Cell Physiology*, 257(5), C1012-C1019. <https://doi.org/10.1152/ajpcell.1989.257.5.C1012>
- Rassier, D. E., & Macintosh, B. R. (2000). Coexistence of potentiation and fatigue in skeletal muscle. *Brazilian Journal of Medical and Biological Research*, 33(5), 499-508. <https://doi.org/10.1590/S0100-879X2000000500003>
- Robbins, D. W. (2005). Postactivation potentiation and its practical applicability. *The Journal of Strength & Conditioning Research*, 19(2), 453-458. <https://doi.org/10.1519/00124278-200505000-00035>
- Schillings, M. L., Hoefsloot, W., Stegeman, D. F., & Zwarts, M. J. (2003). Relative contributions of central and peripheral factors to fatigue during a

maximal sustained effort. *European journal of applied physiology*, 90(5-6), 562-568. <https://doi.org/10.1007/s00421-003-0913-4>

Schmitz, R. J., Arnold, B. L., Perrin, D. H., Granata, K. P., Gaesser, G. A., & Gansnedder, B. M. (2002). Effect of isotonic and isometric knee extension exercises on mechanical and electromyographical specificity of fatigue. *Isokinetics and exercise science*, 10(4), 167-175.

Shield, A., & Zhou, S. (2004). Assessing voluntary muscle activation with the twitch interpolation technique. *Sports Medicine*, 34(4), 253-267. <https://doi.org/10.2165/00007256-200434040-00005>

Søgaard, K., Gandevia, S. C., Todd, G., Petersen, N. T., & Taylor, J. L. (2006). The effect of sustained low-intensity contractions on supraspinal fatigue in human elbow flexor muscles. *The Journal of physiology*, 573(2), 511-523. <https://doi.org/10.1113/jphysiol.2005.103598>

Stackhouse, S. K., Dean, J. C., Lee, S. C., & Binder-MacLeod, S. A. (2000). Measurement of central activation failure of the quadriceps femoris in healthy adults. *Muscle & nerve*, 23(11), 1706-1712. [https://doi.org/10.1002/1097-4598\(200011\)23:11<1706::AID-MUS6>3.0.CO;2-B](https://doi.org/10.1002/1097-4598(200011)23:11<1706::AID-MUS6>3.0.CO;2-B)

Taylor, J. L., & Gandevia, S. C. (2001). Transcranial magnetic stimulation and human muscle fatigue. *Muscle & nerve*, 24(1), 18-29. [https://doi.org/10.1002/1097-4598\(200101\)24:1<18::AID-MUS2>3.0.CO;2-D](https://doi.org/10.1002/1097-4598(200101)24:1<18::AID-MUS2>3.0.CO;2-D)

Taylor, J. L., & Gandevia, S. C. (2008). A comparison of central aspects of fatigue in submaximal and maximal voluntary contractions. *Journal of Applied Physiology*, 104(2), 542-550. <https://doi.org/10.1152/jappphysiol.01053.2007>

Tillin, M. N. A., & Bishop, D. (2009). Factors modulating post-activation potentiation and its effect on performance of subsequent explosive activities. *Sports Medicine*, 39(2), 147-166. <https://doi.org/10.2165/00007256-200939020-00004>

Todd, G., Taylor, J. L., & Gandevia, S. C. (2003). Measurement of voluntary activation of fresh and fatigued human muscles using transcranial magnetic stimulation. *The Journal of physiology*, 551(2), 661-671. <https://doi.org/10.1113/jphysiol.2003.044099>

Vandervoort, A. A., & McComas, A. J. (1983). A comparison of the contractile properties of the human gastrocnemius and soleus muscles. *European journal of applied physiology and occupational physiology*, 51(3), 435-440. <https://doi.org/10.1007/BF00429079>

Vandervoort, A. A., Quinlan, J., & McComas, A. J. (1983). Twitch potentiation after voluntary contraction. *Experimental neurology*, 81(1), 141-152. [https://doi.org/10.1016/0014-4886\(83\)90163-2](https://doi.org/10.1016/0014-4886(83)90163-2)

Xenofondos, A., Lapidis, K., Kyranoudis, A., Galazoulas, C., Bassa, E., & Kotzamanidis, C. (2010). Post-activation potentiation: factors affecting it and the effect on performance. *Journal of Physical Education & Sport/Citius Altius Fortius*, 28(3).

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