POST-ACTIVATION POTENTIATION AND FATIGUE IN QUADRICEPS FEMORAL MUSCLE AFTER A 5 S MAXIMAL VOLUNTARY ISOMETRIC CONTRACTION

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ABSTRACT

Following an acute physical exercise, both post-activation potentiation and fatigue of the neuromuscular apparatus may occur. The voluntary recruitment of motor units occurs with frequencies that elicit incompletely fused tetanic contractions and these frequencies are most susceptible for post-activation potentiation as well as low-frequency fatigue. Therefore, the goal of the present study was to investigate which of the processes post-activation potentiation or low-frequency fatigue will be prevalent after 5 s maximal voluntary contraction (MVC).

Eight healthy untrained men (age 24—35 years, mass 81.2 ± 5.1 kg) performed maximal sustained isometric knee extension for 5 s at a knee angle of 90 degrees. The contractile properties of quadriceps muscle evoked by electrical stimulation at 1, 7, 10, 15, 20, 50 Hz and 100 Hz, were recorded before and immediately after the exercise and 3, 5, and 10 min following the exercise. The rest interval between muscle electrical stimulation was 3 s.

A significant raise of force evoked by 1—15 Hz stimulation was observed immediately after the 5 s MVC exercise (p < 0.01). Later in recovery (at 10 min) the contraction force at 15 Hz and 20 Hz significantly decreased (p < 0.05). Tetanic force at 50 Hz and 100 Hz demonstrated a significant decrease immediately after the exercise and remained depressed up to 3 min (p < 0.01). The ratio of 20 / 50 Hz recorded immediately after the 5 s MVC increased significantly (p < 0.05), however 10 min after the exercise there was a significant decrease compared to its initial level (p < 0.05).

The simultaneous occurrence of post-activation potentiation at low stimulation frequencies and suppressed forces at high stimulation frequencies suggests that potentiation and fatigue mechanisms were acting concurrently. Moreover, when post-activation potentiation is lost (in 10 min after the 5 s MVC exercise), the contraction force at low stimulation frequencies decreases resulting in significant low-frequency fatigue.

Keywords: isometric exercise, electrical stimulation, low-frequency fatigue, recovery.

INTRODUCTION

Following an acute stimulus, both post-activation potentiation (PAP) and fatigue of the neuromuscular apparatus may occur (Baudry, Duchateau, 2004; Masiulis et al., 2006). In contrast to fatigue, which serves to impair force production, there is evidence that the contractile activity of skeletal muscle may facilitate the production of force — this phenomenon is known as post-activation potentiation (PAP). Few mechanisms have been proposed to explain this phenomenon. These mechanisms are phosphorylation of the regulatory light chains on the myosin head (Sweeney et al., 1993), elevation of Ca^{2+} in the cytosol (Allen et al., 1989), and reflex potentiation in the spinal cord (Hodgson et al., 2005).

A particular type of fatigue referred to as low-frequency fatigue (LFF) is observed by a reduction in force observed at low frequencies of stimulation

(Edwards et al., 1977). During voluntary muscle contractions in vivo individual motor units usually fire at rates between 5 Hz and 30 Hz (De Ruiter et al., 2004) which is exactly within the range of frequencies that LFF manifests itself when electrical stimulation is applied (Edwards et al., 1977; Ratkevicius et al., 1998). Therefore, the production of LFF may have significant implications for muscular function.

Stimulation at high frequencies, as used in other experiments (e. g. Tubman et al., 1996; O'Leary et al., 1997), elicits a tetanic contraction resulting from a sustained increase in intracellular Ca^{2+} that is maintained throughout the period of stimulation (Tubman et al., 1996). These studies demonstrated that elevation of intracellular Ca^{2+} can apparently activate myosin light chain kinase during sustained muscle contraction. However, this type of tetanus rarely, if ever, occurs *in vivo*.

Considering that voluntary recruitment of motor units occurs with frequencies that elicit incompletely fused tetanic contractions (De Ruiter et al., 2004) and these frequencies are most susceptible for PAP as well as LFF, we hypothesize that contractility of skeletal muscle during and after brief high intensity exercises is determined by interaction between the mechanism mediating PAP and fatigue. Therefore, the goal of the present study was to investigate which of the phenomenon's PAP or LFF will be prevalent during and after a brief (5 s) MVC.

METHODS

Subjects. Eight healthy untrained men (age 24—35 years, mass 81.2 ± 5.1 kg) gave their informed consent to participate in this study. The subjects were physically active but did not take part in any formal physical exercise or sport program. Each subject read and signed written informed consent form consistent with the principles outlined in the Declaration of Helsinki.

Force Measurements. The equipment and technique used for measuring force were the same as used in the previous studies (Skurvydas, Zachovajevas, 1998; Masiulis et al., 2006). Briefly, before the performing explosive strength training session the subjects were seated in a steel framed straight-backed adjustable chair and appropriate adjustments were made to ensure an optimal riding position. A seatbelt attached to the side of the chair passed around the subject's waist and chest to firmly secure the pelvis and upper body

for minimizing uncontrolled movements. The right leg was clamped in a force-measuring device with the knee kept at an angle of 90° (full extension being 180°) during the whole experiment. A 6-cm-wide plastic cuff, placed around the right leg just proximal to the malleoli, was tightly attached to a linear variable differential transducer. The output of the transducer, proportional to isometric knee extension force, was amplified and digitized at a sampling rate of 1 kHz by a 12-bit analogue-to-digital converter incorporated in a personal computer. The digitized signal was stored on a hard disk for subsequent analysis. The output from the force transducer was also displayed on a voltmeter in front of the subject. Maximal voluntary contraction (MVC) force was determined.

Electrical Stimulation. A high-voltage stimulator (MG 440, Medicor, Budapest, Hungary) was used to deliver electrical stimuli to the quadriceps muscle through surface electrodes (9×18 cm) padded with cotton cloth and soaked in saline solution. One stimulation electrode was placed just above the patella, while another one covered a large portion of the muscle belly in the proximal third of the thigh. The electrical stimulation was always delivered in trains of square wave pulses of 1 ms duration (voltage 150 V, which induces approximately 60—80 percent of MVC). To maximize recruitment of fibres, the highest possible stimulation voltage was employed. The subjects were familiarized with electrical stimulation during the introductory visit before the onset of experiments. We measured the contractile force of the quadriceps muscle, evoked by electrical stimulation at 1 (P 1), 7 (P 7), 10 (P 10), 15 (P 15), 20 (P 20), 50 (P 50) and 100 Hz (P 100) (the duration of each electrical stimulation series was 1 s). The rest interval between muscle electrical stimulation was 3 s.

Experimental Protocol. After 5 min rest in the experimental chair, the subject performed three MVC, separated by 1 min. The best try was taken for evaluation. Five minutes later, the protocol of electrical stimulation was applied consisting of a 1 s train of pulses interspaced with 3 s rest. The employed frequencies of electrical stimulation were recorded in the following sequence: P 1, P 7, P 10, P 15, P 20, P 50 and P 100. The recorded parameters were considered to be initial (Ini) ones. Two min later the subject was encouraged to perform 5 s MVC. Immediately after 5-s MVC (0 min), 3, 5 and 10 min following the exercise, the stimulation protocol was repeated.

Statistics. The results obtained have been processed using the methods of mathematical statistics by calculating the means ($\overline{x}$) and standard deviations of mean ($\pm$ SD). The differences for repeated measures in mean values were evaluated by using Student's t-test for paired data. The level of significance of the difference between arithmetic means was considered relevant when the p value was less than 0.05. The analyses were done making use of the Microsoft Excel 2000.

RESULTS

During the recovery after 5 s MVC, a significant potentiation of P 1—P 15 was observed (Fig. 1—2). P 1 was potentiated ($p < 0.01$) immediately after the exercise, then it decreased slightly, but remained augmented at 3 and 5 min of recovery period (both, $p < 0.05$) (Fig. 1). Similarly, the P 7, P 10 (Fig. 1) and P 15 (Fig. 2) were augmented immediately after the exercise (all, $p < 0.01$) but potentiation persisted up to 3 min after exercise only for P 7 and P 10 (both, $p < 0.05$). The contraction force at P 15 and P 20 were reduced at 10 min ($p < 0.05$) (Fig. 2).

Tetanic force at P 50 and P 100 demonstrated a significant decrease immediately after the exercise and remained depressed up to 3 min ($p < 0.01$) (Fig. 3). Data analysis showed that the ratio of P 20 / P 50 recorded immediately after the 5 s MVC (Fig. 4) increased significantly ($p < 0.05$), however 10 min after the exercise there was a significant decrease compared to its initial level ($p < 0.05$).

DISCUSSION

Our main finding was that after 5 s MVC muscle fatigue and PAP occurred simultaneously while after 10 min of recovery low-frequency fatigue (LFF) was observed. It was unexpected to find that after 5 s MVC exercise LFF can occur. Our results were in agreement with H. Green and S. Jones (1989) who observed that after more strenuous isometric exercises, when potentiation is lost, LFF becomes conspicuous. However, it has to be taken into account that even after 5 s MVC simultaneous PAP and fatigue at high stimulation frequencies and later in recovery LFF can occur.

It has been shown, that the force at low stimulation frequencies is increased following a sustained
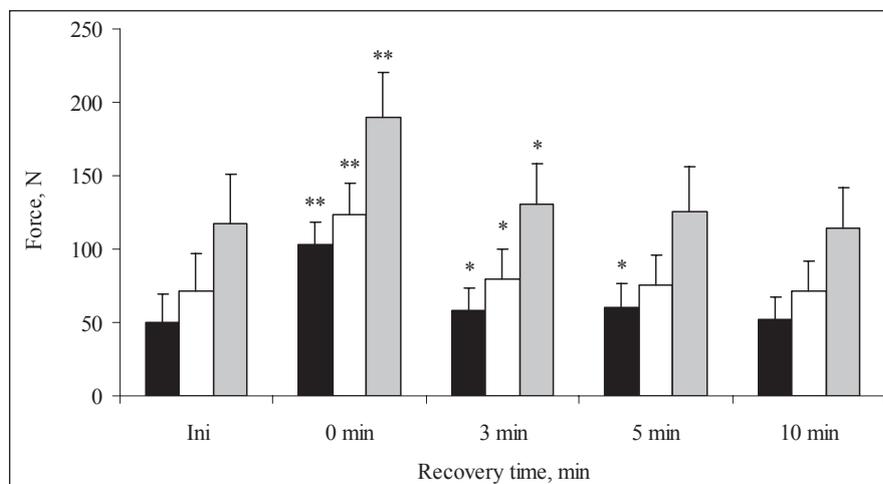

Fig. 1. **The time-course of changes in P 1, P 7 and P 10 (black, white and grey bars, respectively) after sustained MVC for 5 s before the experiment (Ini), right after (0 min) and following 3, 5 and 10 min of recovery**

Note. P 1, P 7, P 10, muscle contraction force at a stimulation rate of 1, 7 and 10 Hz, respectively; Values are means $\pm$ SD. Statistically significant differences from initial mean level (Ini) are indicated as: * — $p < 0.05$; ** — $p < 0.01$ (n = 8).
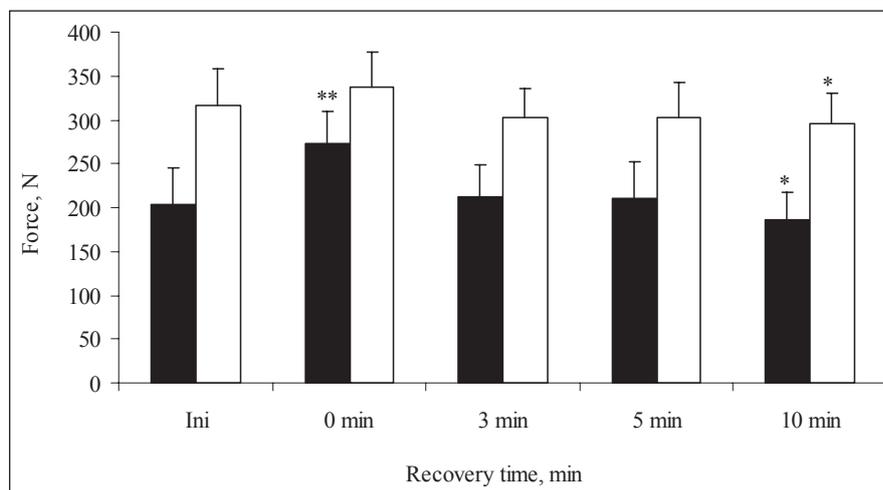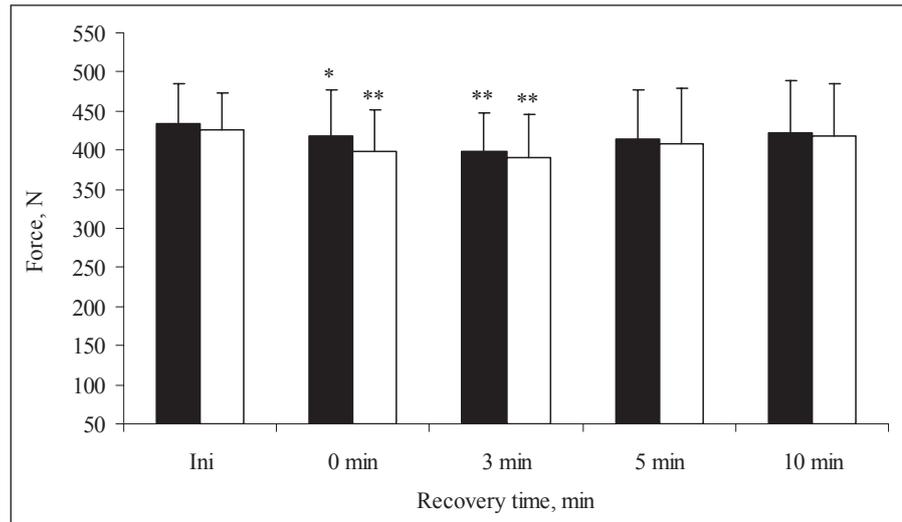

Fig. 2. **The time-course of changes in P 15 and P 20 (black and white bars, respectively) after sustained MVC for 5 s before the experiment (Ini), right after (0 min) and following 3, 5 and 10 min of recovery**
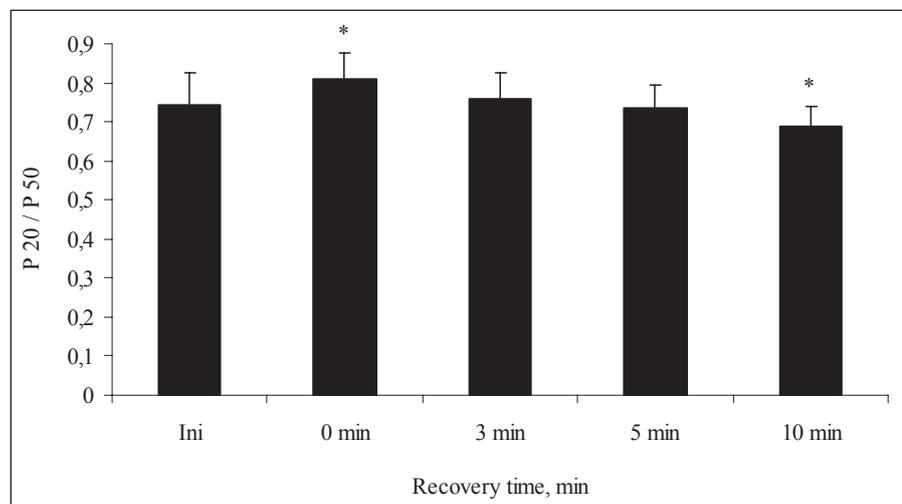
Note. P 15, P 20, muscle contraction force at a stimulation rate of 15 and 20 Hz, respectively; Values are means $\pm$ SD. Statistically significant differences from initial mean level (Ini) are indicated as: * — $p < 0.05$; ** — $p < 0.01$ (n = 8).

Fig. 3. **The time-course of changes in P 50 and P 100 after sustained MVC for 5 s before the experiment (Ini), right after (0 min) and following 3, 5 and 10 min of recovery**

Note. P 50, P 100, muscle contraction force at a stimulation rate of 50 and 100 Hz, respectively; Values are means ± SD. Statistically significant differences from initial mean level (Ini) are indicated as: * — p < 0.05; ** — p < 0.01 (n = 8).

Fig. 4. **The time-course of changes in P 20 / P 50 ratio after sustained MVC for 5 s before the experiment (Ini), right after (0 min) and following 3, 5 and 10 min of recovery**

Note. P 20 and P 50, muscle contraction force at a stimulation rate of 20 Hz and 50 Hz respectively; Values are means ± SD. Statistically significant differences from initial mean level (Ini) are indicated as: * — p < 0.05 (n = 8).

MVC (Skurvydas, Zachovajevas, 1998; Baudry, Duchateau, 2004). Our results are in agreement with this observation, as, after brief MVC, we found potentiation in contractile responses up to 15 Hz of electrical stimulation (Fig. 1—2).

Some authors observed potentiation with intermittent contractions at 40 Hz in rat gastrocnemius muscle (MacIntosh, Willis, 2000), cat tibialis posterior muscle (Bevan et al., 1993), and cat gastrocnemius muscle (Burke et al., 1976). However, in their case, fatigue was not a limiting factor for potentiation. While in our case, we did not see potentiation of contractions elicited with 20 Hz stimulation, but the fatigue that was evident immediately and following 3 min after 5 s MVC at high stimulation frequencies (Fig. 3) may have masked potentiation that otherwise might have been evident at P 20 (Fig. 2).

Notably, the force loss at 50 Hz and 100 Hz (Fig. 3) without depression of force at low-frequencies is considered a marker of attenuated sarcolemma excitability, which has been associated with depletion of Na^+ and accumulation of K^+ in the extracellular spaces impairing membrane depolarization especially at high frequencies (Strojnik, Komi, 1998).

When the contractile response to low-frequency stimulation is diminished (P 15 and P 20 at 10 min) while at the same time the response to high-frequency stimulation is not affected, LFF is present (Edwards et al., 1977). After 5 s MVC, LFF was identified as a decrease in the P 20 / P 50 ratio (Fig. 4). A close relationship was observed between the depressions in Ca^{2+} release with the extent of LFF examined after fatiguing isometric contractions of the quadriceps (Binder-Macleod, Russ, 1999). When trains of impulses arrive in quick succession, the Ca^{2+} is thought to accumulate in the sarcoplasm so that full cross-bridge interaction can take place once more. Although the LFF became obvious only in the later phase of recovery, a decrease in P20/P50 ratio following the 5 s MVC indicates that the onset of it occurs as early as 10 min after the exercise (Fig. 4).

However, previously LFF was observed after much more strenuous isometric exercises (Edwards

et al., 1977; Ratkevicius et al., 1998). There is a possibility that in the isometric exercise with maximal intensity, the sarcomeres of the end of fibre overextend and it leads to damage. In this situation the active sarcomeres would be working at a shorter length than predicted from the overall fibre length and the force-frequency curve will be shifted to the right (Jones, 1996). We suppose that rising LFF during and after isometric exercises of maximal intensity may be linked to the damage of sarcomeres. Therefore, the reduction of P 7 and P 10 forces would be expectable in the case of LFF. However, with the present data (Fig. 1) we cannot state it clearly. This discrepancy possibly can be explained, that P 7 and P 10 forces are augmented because of PAP, while P 15 and P 20 forces are less dependent on PAP.

Three different segments in the range of stimulation frequencies may be separated according to the changes in the contraction force after 5 s MVC. Segment *A* (P 1—P 10) (Fig. 1) appeared to be the most sensitive to 5 s MVC. In segment *B* (P 15—P 20) (Fig. 2) there still persisted a tendency of force to potentiate when the studies with 10-s MVC showed the reduction of force (Green, Jones, 1989). We speculate that P 20 force is susceptible for both PAP and LFF, while P 15 is more sensitive to PAP then P 20, and, therefore, LFF in P 15 can be less evident. However, if potentiation would not be present, P 15 would be more depressed comparing to P 20. In segment *C* (P 50—P 100) (Fig. 3), there was a significant force attenuation. Besides, the reduction of P 50 may be partly explained by stimulation history (P 50 was recorded as the last contraction in the stimulation sequence) in addition to 5 s MVC. It was shown that even the sprint of 6-s duration significantly affects metabolite pattern that may account for fatigue (Dawson et al., 1978).

We speculate that segmentation is related to different net output of the effects of PAP- and fatigue-related mechanisms at distinct ranges of stimulation frequency. However, this notion will need additional research to be verified.

Summing up, the present study showed that immediately after the 5 s MVC, the simultaneous occurrence of PAP at very low and low stimulation frequencies and suppressed forces at high stimulation frequencies suggests that potentiation and fatigue mechanisms were acting concurrently. It has been shown that when potentiation is lost, LFF becomes conspicuous (Green, Jones, 1989). This finding is in agreement with our results whereas when PAP is lost the contraction force at P 15 and P 20 appears to reduce at 10 min resulting in significant LFF.

CONCLUSION

Simultaneous occurrence of post-activation potentiation at very low and low stimulation frequencies and increased fatigue at high stimulation frequencies suggest that potentiation and fatigue mechanisms are acting concurrently immediately after brief 5 s MVC. Moreover, when post-activation potentiation is lost, the contraction force at low stimulation frequencies decreases resulting in significant low-frequency fatigue.

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KETURGALVIO ŠLAUNIES RAUMENS POSTAKTYVACINĖ POTENCIACIJA IR NUOVARGIS ATLIKUS 5 SEKUNDŽIŲ TRUKMĖS MAKSIMALAUS INTENSYVUMO IZOMETRINĮ KRŪVĮ

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SANTRAUKA

Po trumpų ir intensyvių fizinių pratimų gali pasireikšti postaktyvacinė potenciacija (PAP) ir raumenų nuovargis. Valingo raumenų susitraukimo metu motoriniai vienetai rekrutuojami dažnių, sukeliančių nelygųjį tetanusą. Būtent šie dažniai yra labiausiai veikiami postaktyvacinės potenciacijos, taip pat mažų dažnių nuovargio (MDN). Todėl ir norima šiuo tyrimu nustatyti, kuris iš fenomenų PAP ar MDN bus vyraujantis po 5 s trukmės maksimaliosios valingos jėgos (MVJ) krūvio.

Tirti sveiki aktyviai nesportuojantys vyrai (amžius 24—35 m., svoris 81,2 ± 5,1 kg) (n = 8). Tiriamieji atliko 5 s trukmės maksimalų izometrinį krūvį — kojos tiesimą per kelio sąnarį. Krūvio metu koja per kelio sąnarį fiksuota 90 laipsnių kampu. Keturgalvio šlaunies raumens susitraukimo jėga, sukelta 1, 7, 10, 15, 20, 50 Hz ir 100 Hz stimuliavimo dažniu, buvo registruojama iš karto atlikus krūvį ir praėjus 3, 5 ir 10 min po jo. Poilsio intervalai tarp stimulų — 3 s.

Raumenų susitraukimo jėga, sukelta 1—15 Hz dažnio elektrostimuliavimo, iš karto po 5 s trukmės MVJ krūvio buvo reikšmingai didesnė nei prieš krūvį (p < 0,01). Atsigavimo metu mažais dažniais sukelta jėga mažėjo. Praėjus 10 min po krūvio 15 ir 20 Hz dažnio sukelta jėga buvo reikšmingai mažesnė, lyginant su reikšme prieš krūvį (p < 0,05). Raumenų susitraukimo jėga, sukelta 50 Hz ir 100 Hz dažnio, reikšmingai sumažėjo tuoj pat po 5 s trukmės MVJ krūvio ir išliko sumažėjusi 3 min (p < 0,01). P 20 / P 50 santykis tuoj pat po 5 s MVJ krūvio reikšmingai padidėjo (p < 0,05), tačiau praėjus 10 min po krūvio buvo reikšmingai mažesnis, palyginti su jo pradine reikšme (p < 0,05).

Tyrimo rezultatai rodo, kad po 5 s trukmės maksimalaus valingo jėgos krūvio konkuruoja du mechanizmai: nuovargis, mažinantis mažais ir dideliais stimuliavimo dažniais sukeltą raumenų susitraukimo jėgą, ir postaktyvacinė potenciacija, didinanti mažų stimuliavimo dažnių sukeltą raumenų susitraukimo jėgą. Išnykus postaktyvacinei potenciacijai (per 10 min po MVJ krūvio), sumažėja mažų stimuliavimo dažnių sukelta raumenų susitraukimo jėga, atsiranda mažų dažnių nuovargis.

Raktažodžiai: izometrinai pratimai, elektrostimuliacija, mažų dažnių nuovargis, atsigavimas.

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