IZVLEČEK
Analiziran je bil pojav periferne utrujenosti po maksimalno koncentrični in ekscentrično koncentrični vadbi. V raziskavi je sodelovalo enajst študentov Fakultete za šport, ki so izvajali 60s poskoke in kolesarjenje. Pred vadbo in po njej so bili preučevani mehanski odzivi mišice na različne parametre električne stimulacije (enojni skrček, 20 Hz in 100 Hz stimulacija). Pred poskoki in pas prišlo do statistično značilnega zmanjšanja navora v kolenu po 20 Hz stimulaciji. Navor se je zmanjšal tudi po stimulaciji z enojnim skrčkom. Pri poskokih je bil statistično značilni (P<0,01) večji kontrakcijski in polovični rekrakcijski čas. Statistično višje (P<0,001) so bile vsebnosti laktata po poskoki, kot pri vadbi. Iz rezultatov je možno sklepati, da pride po poskoki do visoko frekvenčne, po kolesarjenju pa do nizko frekvenčne utrujenosti. Glavni razlog za različno prierno mišično utrujenost, je mogoče pripisati različnemu tipu mišičnega krčenja med vadbo.

Ključne besede: visoko frekvenčna utrujenost, nizko frekvenčna utrujenost, poskoki, kolesarjenje

ABSTRACT
To analyse the occurrence of peripheral fatigue after a maximal concentric and stretch-shortening cycle exercise, 11 subjects performed maximal jumping and cycling for 60 seconds. Before and after the exercise, the vastus lateralis muscle was stimulated for single twitch and with trains of electrical stimuli delivered at 20 Hz and 100 Hz. The torque was measured during the exercise. In addition, blood lactate concentrations were measured. After the jumping, selective reduction in the 100 Hz knee torque was observed (P<0.01) while after the cycling only the 20 Hz knee torque decreased (P<0.01). The muscle twitch peak torque did not change 14.6 + 32.21% (P=0.510) after the jumping, although after the cycling it was reduced by 60.8 + 44.26% (P<0.01), while the contraction time and half-relaxation time were statistically significantly lengthened (P<0.001). Blood lactate accumulation was statistically significantly higher after the cycling (P<0.001) compared to the jumping. It was concluded that the maximal jumping produced high-frequency fatigue and the maximal cycling low-frequency fatigue. The main reason for the different peripheral fatigue was attributed to differences of the contraction type.

Key words: high-frequency fatigue, low-frequency fatigue, jumping, cycling

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INTRODUCTION

Peripheral fatigue can be related to impaired efficiency of neuromuscular transmission (so-called high-frequency fatigue) and/or alterations in excitation-contraction coupling (so-called low-frequency fatigue). These changes in muscle function depend on many factors, including exercise intensity (Enoka & Stuart 1992; Strojnik & Komi 1998, 2000), exercise duration (Tomazin et al. 2012) and contraction type (Strojnik & Komi 1998; Froyd et al. 2013).

High-frequency fatigue has been observed after a maximally intensive stretch-shortening cycle (SSC) exercise (Strojnik & Komi 1998). Since neuromuscular transmission seemed to be impaired after a maximal SSC exercise, the muscle contractile mechanism was potentiated (Strojnik & Komi 1998). When the same exercise was performed at submaximal intensity, low-frequency fatigue was observed (Strojnik & Komi 2000). Froyd et al. (2013) found low-frequency fatigue during vigorous concentric knee exercise, showing that there may be differences in the appearance of peripheral fatigue between SSC and concentric type exercises. However, the subjects and methods employed in both maximum exercise intensity experiments were different and therefore not directly comparable. The same methods were used by Tomazin et al. (2008) in a study where peripheral fatigue was measured after SSC exercise and concentric (CON) exercise; however different fatigue workout times were used in the study (the subjects performed 60 s of jumping at maximum intensity (maximum height and short contact time) and 30 s of cycling at maximum intensity).

Since the peripheral fatigue found after the maximum SSC and concentric exercise differed, the question arises of whether the contraction type affects peripheral fatigue, or the differences were simply a consequence of the different subjects and/or methods for measuring peripheral fatigue employed in the above-mentioned studies. Concentric contraction differs from SSC in many ways, including muscle mechanics (Komi 2000; Kubo et al. 1999) and activation (Voigt et al. 1995) which give space for different fatigue responses. In their study, Froyd et al. (2013) found that decreases in muscle function varied greatly with different methods of stimulation, suggesting that the extent to which muscle fatigue is documented during exercise depends considerably on the neuromuscular fatigue assessment methodology.

To test the occurrence of different types of peripheral fatigue after maximally intensive exercise, we measured the same group of subjects performing maximum drop jumps and maximum cycling (Wingate test) for 60 s with the same assessment methodology. We hypothesised that the same peripheral fatigue would be found for those exercises that were performed at the same intensity and for the same duration.

Materials and methods

Subjects. Eleven students of physical education participated in the study (age 22.9 + 3.9 years, height 176.1+4.1 cm, body mass 71.8+3.7 kg). The subjects were well informed about the procedures of the experiment. They provided informed consent, stating that they were aware of the experiment’s demands, goals and possible risks. The experiment was conducted in accordance with the Helsinki-Tokyo Declaration and approved by the National Medical Ethics Committee.

Experimental design. The subjects were informed about the experiment protocol and familiarised with the measuring equipment. Preliminary measurements were made to practise the tests. The experiment included fatigue exercises (jumping, cycling) accompanied by measurements (electric-
Peripheral fatigue after maximal concentric and stretch stimulation, response, blood samples) performed before and after the exercise. Measurements before the exercise were performed after a standardised warm-up. The time between the warm-up and the first measurement was set at 2.5 min, while the exercise started 10 min after the warm-up. The second measurements followed 1 min after the end of the exercise. The experiment took two successive weeks. Sessions were always performed on the same day and at the same time. The order of exercises was randomly chosen.

**Warm-up.** The subjects performed a warm-up, which consisted of 10 min of stepping on a 20-cm high bench with a frequency of 0.5 Hz, and a leg exchange each minute.

**Exercise.** Consecutive jumps were conducted in a laboratory environment on a force plate (model 9278, Kistler, Winterthur, Switzerland). Hands on the hips were obligatory. The first jump was performed from the mid-crouch position (squat jump), later the subject moved on to successive vertical jumps performed with maximum height and with the shortest possible contact time. The whole exercise lasted 60 s (Bosco et al. 1981c, 1983). On the basis of a force-time curve, the following parameters were calculated: work per hop, power per hop, relative power per hop, contact time, flight time, and hop height. The average load in all these parameters in each quarter of the test (Bosco et al. 1983) was calculated as well. The total number of jumps divided into four equal parts defined the quarters. A fatigue index (FI) was calculated from the relative force results of the first and last quarters of the jumping:

\[
F = 100 - \left( \frac{P_F}{P_L} \right) \cdot 100
\]

(1)

\(P_F\) = average power of the first quarter

\(P_L\) = average power of the last quarter

The Wingate test was performed in a laboratory environment on a cycle ergometer (Monark-model 818E). The height of the seat was adjusted so that the knee was slightly bent during the lowest pedal position. Body inclination during the pedalling was kept constant with stretched arms. The subjects had to cycle for 60 s at maximum intensity against resistance equal to 7.5% of their body weight (Ayalon et al. 1974). The cycling started with a flying start so that the subject reached 60 turns per minute just before the actual start of the exercise. The bicycle was fixed to the floor to ensure stable pedalling. A power-time curve was plotted on-line on a computer display in front of the subjects. They were also encouraged by the staff. The whole cycling protocol was performed in accordance with the instructions of the manufacturer (Ayalon et al. 1974). Maximum power, minimal power, and pedalling power during the 60 s exercises were calculated based on a sensor which measured the speed of a cycling wheel and took the given resistance into account (SMI, model 1000, St. Cloud, USA). Power was normalised to the body mass. A fatigue index was calculated as the ratio between the power of the first \((P_F)\) and last 15 seconds \((P_L)\) according to equation 1.

**Electrical stimulation.** Electrical stimulation started 2.5 min after the warm-up and 1 min after the exercise. The first three twitches were stimulated with three times the amplitude of the motor threshold. The duration of a single stimulus was 0.3 ms, followed by 1 s pause. After the last twitch the pause was 2 s. Then stimulation continued with a 1 s period of 20 Hz pulses followed by 1 s period of 100 Hz pulses. The sequence and timing were exactly
controlled by a computer. Measurements were performed on an isometric knee measurement device at a 45° knee joint angle. During the measurement, a subject lay supine on the table with their hips fastened and lumbar spine supported to prevent pelvis movements. On all occasions, the torque in the right knee was measured. The right leg was secured to the brace and the left one was leaning on a chair. A computer controlled current-constant stimulator (Furlan and Co, Ljubljana, Slovenia) was used for the muscle stimulation. Symmetric square biphasic impulses were employed on all occasions. The muscle stimulation was carried out through self-adhering 5x5 cm electrodes (Axelgaard, Falbrook, CA), which were placed over the vastus lateralis (VL) muscle: an anode over the distal part of the muscle's belly and a cathode over the middle part of the muscle's belly. All data were stored on-line (12 bit resolution, 1000 Hz acquisition frequency) in a PC and analysed after the measurements.

*Twisth.* From the mechanical response elicited by a single supramaximal relaxed VL electrical stimulation, the following parameters were obtained: (1) peak twitch torque (Tw), i.e. the highest value of the twitch torque curve; (2) twitch contraction time (CT), i.e. the time from when the initial torque rose above 5% of the peak Tw to the time at peak Tw; and (3) half-relaxation time (RT1/2), i.e. the time from the peak Tw to the time when the peak Tw dropped to half its value.

**High and low frequency fatigue test.** The maximum torque of the relaxed vastus lateralis muscle was measured during two consecutive trains of electrical impulses delivered at 20 Hz (F20) and 100 Hz frequency (F100). The amplitude of the electrical stimulation was three times that of the motor threshold. The motor threshold was defined as the smallest electrical current that caused the first visually observable VL muscle response at 100 Hz stimulation.

*Blood analysis.* Blood samples for blood lactate concentration analysis (20 ml) were drawn from the hyperemic ear. Blood lactate concentration was measured with a Kontron 640 Lactate Analyser (Kontron, Vienna, Austria) immediately after the drawing, which was done 2.5 min after the warm-up, and 1, 3, 5, 7 and 10 min after the exercise.

**Statistics.** The data in the text and figures are presented as mean ± SD. Normal distribution of the presented parameters was checked using the Kolmogorov-Smirnov test. Two-way ANOVAs for repeated measures with two within-subjects factors (jumping and cycling) were used to detect significant differences in muscle response to electrical stimulation with different parameters. Two-way ANOVAs were also used to detect significant differences in blood lactate concentration and also to estimate the differences in results obtained before and after the exercise. When significant main effects were found, Tukey post-hoc tests were used to locate the differences. Statistical significance was accepted at 5% alpha error. The statistical package Statistica 6.0 (StatSoft, Inc., Tulsa, USA) was used, and the level of significance for all comparisons was set at P<0.05.

**RESULTS**

The results of the mean relative power for both exercises are presented in Fig. 1. Mean power differed significantly between jumping and cycling (58.57 ± 3.35W × kg⁻¹ and 6.35 ± 0.48W × kg⁻¹, respectively, P<0.001).

No mechanical fatigue was found between the first and the last quarter of the jumping (Fig. 2). On the other hand, power in cycling decreased by about 60% (P<0.001).

Repeated Measured ANOVA analysis showed that the variables changed statistically significantly when comparing jumping and cycling (Table 1).
Fig. 1 Mean relative power during exercises. *** indicates a significant difference between exercises (P<0.001)

![Chart showing relative power during exercises](image)

Fig. 2 Mean fatigue index at jumping and cycling. ***P<0.001.

![Chart showing fatigue index at jumping and cycling](image)

Table 1 Mean differences, standard deviations and statistically significant between jumping and cycling

<table>
<thead>
<tr>
<th></th>
<th>Jumping</th>
<th>Cycling</th>
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<tr>
<td></td>
<td>FTW</td>
<td>CT</td>
</tr>
<tr>
<td>Pre</td>
<td>690.55 (254.34)</td>
<td>58.73 (5.78)</td>
</tr>
<tr>
<td>Post</td>
<td>589.73 (189.96)</td>
<td>56.18 (7.64)</td>
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<tr>
<td></td>
<td>587.00 (259.19)</td>
<td>58.55 (4.34)</td>
</tr>
<tr>
<td>Post</td>
<td>230.09 (101.84) **</td>
<td>68.27 (6.31) ***</td>
</tr>
</tbody>
</table>

FTW - twitch maximal knee torque (Nm), CT - time to reach maximum torque (ms), RT1/2 – half-relaxation time (ms), F20 - electrical stimulation with 20 Hz frequency (Nm) and F100 - electrical stimulation with 100 Hz frequency (Nm).
Average $F_{TW}$ decreased in the jumping and cycling (Fig. 3). In the jumping, $F_{TW}$ did not change statistically significantly ($P=0.510$). In the cycling, $F_{TW}$ changed statistically significantly ($P<0.01$). $F_{TW}$ was different between the jumping and cycling changes ($P=0.002$) (Table 1). After the jumping CT shortened. After the cycling, CT was prolonged statistically significantly ($P<0.001$) (Fig. 1). The differences in CT between the jumping and cycling exercises were statistically significant ($P<0.001$) (Table 1). RT$_{1/2}$ shortened after the jumping ($P=0.903$) and was prolonged after the cycling ($P<0.001$) (Fig. 1). Differences in RT$_{1/2}$ between the jumping and cycling exercises were statistically significant ($P=0.001$) (Table 1).

No differences in average knee torque at 20 Hz ES were found. At 20 Hz ES torque decreased statistically significantly ($P<0.01$) (Fig. 3) after the cycling. Differences in torque at 20 Hz ES between the jumping and cycling were statistically significant ($P<0.001$) (Table 1). The opposite happened with 100 Hz ES where the jumping caused a statistically significant ($P<0.01$) torque decrease (Fig. 3). After the cycling torque did not increase statistically significantly ($P=0.999$).
Differences in torque at 100 Hz ES between the jumping and cycling were not statistically significant (P=0.967) (Table 1).

Blood LA concentration (Fig. 4) increased after both exercises. Maximal blood LA concentration after the jumping was detected in the 3rd minute (6.48 + 2.33 mM × l⁻¹, P<0.001) and in the 7th minute (12.87 + 2.47 mM × l⁻¹, P<0.001) after the cycling (Fig. 4).

**DISCUSSION**

The aim of the present study was to analyse the occurrence of peripheral fatigue after a maximal concentric and stretch-shortening cycle exercise. The most striking difference observed between the two exercises in the present study was the high-frequency fatigue after the jumping and the low-frequency fatigue after the cycling. Other differences included higher mean power and lower blood lactate concentration after the jumping, and the opposite after the cycling. Surprisingly, the fatigue index after the jumping did not show fatigue while after the cycling a large drop in power was observed. Muscle contractile characteristics also showed a different response since they were minor after the jumping and showed substantial fatigue after the cycling.

It was a surprise that no mechanical fatigue was observed after 60 s of maximal jumping. Comparative studies (Bosco et al. 1983) always found a decrease in power. We believe that the reason for this difference was the shorter contact times in the present study. It is known that SSC is a mechanically highly efficient movement especially when performed at high intensity (Komi 2000; de Haan et al. 1993). This is due to the utilisation of elastic energy which was promoted with the subjects being instructed to have the shortest possible contact times. As a consequence, lactate concentration was fairly low after the jumping. On the other hand, power was substantially reduced after the cycling, which is a concentric activity. It was accompanied with high blood lactate concentration. The high blood lactate concentration, achieving peak lactate relatively late after the cessation of the task (7 min) (Fig. 4) revealed that the metabolic response was really substantial after the cycling and that the subjects had in fact tried their best. Interestingly, the computations showed that approximately the same amount of mechanical work was performed in both tasks. These differences suggest that the fatigue mechanisms after the two tasks might be different.

**Jumping**

Small metabolic changes after the 60 s jumping were observed. Changes in the contractile characteristics of the vastus lateralis muscle were minor as well (Fig. 3). Normally, fatigue causes a reduced twitch peak torque and prolongs twitch times, especially the half- relaxation time (Bigland-Ritchie and Woods 1984; Hainaut & Duchateau 1989). There are two concurrent mechanisms, fatigue and potentiation, working parallel to each other (Rassier & Macintosh 2000) to explain such behaviour as there were no differences in performance (Fig 2). It seems that in the present study both mechanisms were balanced after the jumping. In another study (Strojnik & Komi 1998), potentiation was found after sledge jumps performed as a maximal SSC exercise. Other mechanisms may affect muscle contractile characteristics as well. Among them is increased stiffness of serial elastic elements that reduces twitch times and has been observed after a series of near-maximal eccentric contractions (Howell et al. 1993). This could also explain our results after the 60 s jumping.

Upon a single twitch stimulation the torque decreased, CT and RT₁/₂ shortened and the torque at 20 Hz increased (Fig. 3). Measurements were done upon an unpotentiated ES twitch which
could influence the results of CT and RT1/2. There were no statistically significant changes in contractile characteristics. Torque at 100 Hz stimulation decreased statistically significantly (Fig. 3). This suggests that high-frequency fatigue had occurred. This was seen in the selective reduction of torque during the 100 Hz electrical stimulation and the increased low and high fatigue index (LHF). The selective force loss during the high frequency electrical stimulation is related to the impaired muscle action potential transmission (Stokes et al. 1989; Gibson et al. 1985; Tomazin et al. 2002), especially in T-tubules where high motor unit firing rates may build a conduction block (Balog et al. 1992). In voluntary contractions, high motor unit firing rates are observed during ballistic contractions (Enoka, 1994). In the SSC exercise increased muscle activation may be induced by a stretch reflex as well. This could explain why after the 60 s jumping no statistically significant decrease in twitch torque was found. Another reason for the high-frequency fatigue after the SSC exercise may be abnormal T-tubules observed in eccentrically stretched muscles (Takekura et al. 2001) that may reduce the exchange of ions, metabolites and fluid across the T-tubular network (Yeung et al. 2002).

Cycling

After 60 s of the cycling the muscle contractile characteristics significantly changed (Fig. 3). CT and RT1/2 were prolonged (Fig. 3), which could be a consequence of lowered intra-cellular pH. As the intra-cellular pH decreases, the concentration of Ca++ in the sarcoplasmatic reticulum increases (Nakamaru & Schwarts 1972). This is connected with a decrease in the Ca++ concentration in the sarcomere, which probably reduces the maximal stiffness of the muscle (Donaldson et al. 1978). Upon single twitch stimulation the torque decreased (Fig. 3). This could be explained by the fact that H+ binding to actin reduces a number of cross-bridges, as studied by Blanchard et al. 1984; Stryer (1991) and Kirkendall (1990). The longer CT was most probably due to the decreased speed of releasing Ca++ from the sarcoplasmatic reticulum and/or the sensitivity of myofibril Ca++ (Cooper et al. 1988; Kothhiyal & Ibramsha 1986). The lengthening of RT 1/2 could have been affected by a less efficient action of myosin ATP-ase or Ca-transport ATP-ase (Sahlin, 1986). The decrease of FTW and lengthening of CT and RT1/2 after the 60 s cycling test was also in accordance with the study of Hainaut and Duchateau (1989) who analysed 60 s long uninterrupted isometric contraction and repeated 60 one-second-long isometric contractions.

Upon single twitch stimulation the torque decreased and torque at 20 Hz also decreased (Fig. 3) (Table 1). Changes were statistically significant (Fig. 3) (Table 1). The torque did not change at 100 Hz stimulation (Fig. 3). The results could be explained by a contractile mechanism failure and LFF consequently. On the other hand, the cycling induced low-frequency fatigue, pointing to impaired excitation-contraction coupling (Bigland-Ritchie et al. 1986; Edwards et al. 1977). This degradation in the excitation-contraction coupling may reduce a Ca++ release from the sarcoplasmatic reticulum (Nakamura & Schwarts 1972; Rousseau & Pinkos 1990) and/or in a weakened tie of Ca++ with troponin due to increased H+ in the muscle (Blanchard and Woods 1984). H+, which is a product of anaerobic-lactate exercise, seemed to be a key problem in the appearance of fatigue after 60 s of maximal cycling.

CONCLUSIONS

In conclusion, maximum jumping and cycling led to different types of peripheral fatigue, although both exercises were performed at the same intensity and for the same duration and
produced approximately the same work. The main difference between tasks was of the muscle contraction type and it seems that it was the key to the differences in the appearance of peripheral fatigue. High-frequency fatigue related to voluntary actions has also been observed after other SSC exercises such as slalom in alpine skiing (Tomazin et al. 2008) and maximal sledge jumps (Strojnik & Komi 1998). However, when the exercise intensity was submaximal, SSC exercise produces low-frequency fatigue (Strojnik & Komi 2000). It therefore seems that high-frequency fatigue is specifically related to maximal SSC exercise.

REFERENCES


