©Journal of Sports Science and Medicine (2006) **5,** 440-448
http://www.jssm.org

Research article

MUSCLE FATIGUE INCREASES METABOLIC COSTS OF ERGOMETER CYCLING WITHOUT CHANGING VO_2 SLOW COMPONENT

Aivaras Ratkevicius [1]✉, Arvydas Stasiulis [2], Loreta Dubininkaite [2] and Albertas Skurvydas [2]

[1] School of Medical Sciences, College of Life Sciences & Medicine, Institute of Medical Sciences, Forresterhill, University of Aberdeen, Aberdeen AB25 2ZD, UK
[2] Department of Applied Physiology and Health Education, Lithuanian Academy of Physical Education, Sporto 6, Kaunas 3000, Lithuania

Received: 10 May 2006 / Accepted: 26 July 2006 / Published (online): 01 September 2006

ABSTRACT
The aim of the present study was to investigate effects of muscle fatigue on oxygen costs of ergometer cycling and slow component of pulmonary oxygen uptake (VO_2) kinetics. Seven young men performed 100 drop jumps (drop height of 40 cm) with 20 s of rest after each jump. After the subsequent hour of rest, they cycled at 70, 105, 140 and 175 W, which corresponded to 29.6 ± 5.4, 39.4 ± 7.0, 50.8 ± 8.4 and 65.8 ± 11.8 % of VO_2peak, respectively, for 6 min at each intensity with 4-min intervals of rest in between the exercise bouts. The VO_2 response to cycling after the exercise (fatigue condition) was compared to ergometer cycling without prior exercise (control condition). From 3rd to 6th min of cycling at 105, 140 and 175 W, VO_2 was higher ($p < 0.05$-0.01) when cycling in the fatigue compared to the control condition. Slow component of VO_2 kinetics was observed when cycling at 175 W in the control condition (0.17 ± 0.09, $l \cdot min^{-1}$, mean ± SD), but tended to decrease in the fatigue condition (0.13 ± 0.15 $l \cdot min^{-1}$). In summary, results of the study are in agreement with the hypothesis that muscle fatigue increases oxygen costs of cycling exercise, but does not affect significantly the slow component of pulmonary oxygen uptake (VO_2) kinetics.

KEY WORDS: Muscle fatigue, energy cost, oxygen uptake, oxygen consumption slow component.

INTRODUCTION

In spite of intensive research, factors determining metabolic costs of cycling remain unclear. It is known that mass of legs and rate of pedalling can affect the pulmonary oxygen uptake (VO_2) which reflects the energy metabolism in aerobic exercise (Martin et al., 2001; McDaniel et al., 2002; Neder et al., 2000). A slow and continuous increase in VO_2 is often observed after 3 min of ergometer cycling at intensities exceeding 60% VO_2max (Whipp, 1994). It has been hypothesized that this slow component of VO_2 kinetics reflects an increase in metabolic costs of cycling associated with recruitment of less efficient type II fibres (Saunders et al., 2000).

Concentric muscle contractions are impaired following exhaustive eccentric exercise which is known to induce muscle fatigue and damage (Horita et al., 2003). It is not clear if metabolic costs of ergometer cycling increase as well. An elevated

minute ventilation, breathing frequency, blood lactate, respiratory exchange ratio, heart rate, and rating of perceived exertion have been reported during ergometer cycling after eccentric exercise (Gleeson et al., 1995; 1998). However, VO_2 at submaximal intensities did not change. It has been also shown that eccentric exercise did not alter or had only a marginal effect on gross cycling efficiency in presence of marked muscle soreness (Moysi et al., 2005). At the same, there is a clear evidence that eccentric exercise reduces concentric contraction economy in the muscle of the mouse (Warren et al., 1996). It has been also demonstrated that VO_2 increased during ergometer cycling after exercise induced depletion of glycogen in type I fibres as well as during repetitive fatiguing isometric contractions (Krustrup et al., 2004; Vollestad et al., 1990). There is some evidence that muscle fatigue intensifies recruitment of less efficient type II fibres during exercise (Nakagawa et al., 2005; Krustrup et al., 2004). Overall, however, findings on the metabolic costs of ergometer cycling after fatiguing exercise are controversial and we decided to re examine them. We could not find any study investigating effects of fatiguing stretch shortening exercise on slow component of VO_2 kinetics during exercise.

The main of the present study was to investigate effects of drop jump exercise on VO_2 during ergometer cycling at several submaximal intensities. Repetitive drop jumps induce muscle fatigue of long duration with signs of muscle damage (Murfet et al., 2003; Skurvydas et al., 2000). It could be expected that this would increase metabolic costs of ergometer cycling at least in part due to intensified recruitment of less efficient type II muscle fibres (Nakagawa et al., 2005). The first hypothesis of the study was that during ergometer cycling after the drop jump exercise the plateau level of VO_2 will be higher in the fatigue compared to the control condition. The second hypothesis was that the slow component of VO_2 kinetics would increase in amplitude and appear at lower exercise intensities during muscle fatigue. It is believed that progressive recruitment of type II muscle fibres can be associated with a gradual increase in metabolic cost of ergometer cycling even at 50% VO_2max (Krustrup et al., 2004).

METHODS

Subjects and experiments

Seven young men (age 24.1 ± 0.7 years, stature 1.79 ± 0.02 m, body mass 71.9 ± 3.9 kg) took part in the study that was approved by the local Ethics Committee. The subjects were students of physical education and participated in aerobic activities two-three times a week (3-5 h per week). All of them were familiar with the procedures of the study. After a detailed explanation, informed consent was obtained, and the participants took part in three different experiments. In experiment I, peak VO_2 was determined. Experiments II and III were designed to study VO_2 during ergometer cycling in rested and fatigue conditions, respectively.

Ergometer cycling and data collection

The mechanically braked cycle ergometer (Monark 818E, Monark-Crescent AB, Sweden) was used. The cadence was 70 revolutions per minute. Subjects breathed through low resistance mouthpiece and gas exchange was measured breath-by-breath using miniaturised telemetric gas analysis system (Cortex, Leipzig, Germany). Heart rate was recorded simultaneously (Polar Electro Oy, Kempele, Finland). Data values for these measurements were averaged over 1-min periods for statistical comparison of the exercise in the control and fatigue condition. Analysis of VO_2 kinetic was performed using the initial breath-by-breath data. A fingertip blood sample was collected into a capillary tube at the end of each 6-min bout of exercise and subsequently analysed for blood lactate concentration as described previously (Kulis et al., 1988).

Experimental protocols

In experiment I, peak VO_2 (VO_2peak) was evaluated using a ramp exercise test (21 $W \cdot min^{-1}$). The test was started at 70 W and continued until the intensity of cycling could not be maintained at the required level for longer than 10 s. The volunteers exercised for 12.0 ± 1.85 min^{-1} and the average value of VO_2 over the last 30 s of cycling is referred to as peak VO_2.

In experiments II and III, the participants cycled for 6 min at intensities of 70, 105, 140 and 175 W with 4-min intervals of rest in between the exercise bouts. Capillary blood samples were collected during the last 30 s of cycling at each of the four intensities. Firstly, participants cycled without any prior exercise (experiment II, control condition). Then, after at least three days, the ergometer cycling was repeated 60 min after the repetitive drop jump exercise (experiment III, fatigue condition). It has been previously demonstrated that the employed protocol of repetitive drop jumps induces depression of force lasting at least 24 hours in the knee extensor muscles (Skurvydas et al., 2000). At the same time 60 min of rest after repetitive exercise would allow a recovery

Table 1. Expiratory pulmonary ventilation (V_E), heart rate (HR) and pulmonary oxygen uptake (VO_2) after subtraction of oxygen uptake of cardiac and respiratory muscles (see methods for details). All the data are averages over the last 3 min of cycling at each intensity in control and fatigue conditions. Values are means (±SD).

Workload	V_E (l·min^{-1})		HR (beats·min^{-1})		Corrected VO_2 (l·min^{-1})	
(W)	Control	Fatigue	Control	Fatigue	Control	Fatigue
70	24.1 (4.7)	26.6 (1.9)	109 (14)	113 (7)	1.00 (.12)	1.09 (.08)
105	33.1 (5.6)	37.7 (5.6)	125 (16)	131 (8)	1.34 (.13)	1.50 (.15) *
140	43.3 (7.6)	51.2 (10.7) *	140 (19)	149 (13)	1.71 (.18)	1.90 (.24) *
175	60.7 (11.8)	71.5 (17.5) **	158 (20)	165 (13)	2.23 (.28)	2.41 (.25) **

* and ** denote significant ($p < 0.05$ and $p < 0.01$, respectively) differences between control and fatigue conditions.

of muscle temperature and metabolites which could interfere with VO_2 responses to exercise (Ratkevicius et al., 1998b; Saugen and Vøllestad,1995; Tordi et al., 2003).

Drop jump exercise

The drop jump exercise was performed as previously described (Skurvydas et al., 2000). The jumps were performed on a standard jump mat that displayed jump heights after each jump (Powertimer Testing System, Newtest, Tampere, Finland). Before repetitive jumping, each subject performed warming up exercise that consisted of 5-min running on the spot with an intensity that corresponded to 130-150 heart beats min^{-1}. Then the subjects performed 10 squat-stands. Thereafter, the subject performed 100 drop jumps from a height of 40 cm to an approximately 90-degree angle in the knees, followed by a countermovement jump. One jump was performed every 20 s. The subjects received feedback about their performance and were instructed to jump as high as possible. This protocol of exercise is known to induce a prolonged loss of muscle force accompanied with signs of muscle damage (Murfet et al., 2003; Skurvydas et al., 2000). All these procedures, including the warming up exercise and 100 drop jumps, lasted approximately 50 min.

VO_2 components

The amplitude of the slow component of VO_2 kinetics was calculated as the difference between the mean value of VO_2 over the last 30 s of the 6th min of exercise and that of the last 30 s of the 3rd min of the test (Whipp et al., 1994). This was apparently the most reliable method of assessment, as mathematical modelling of the slow component did not produce reliable results.

Oxygen uptake of heart and respiratory muscles contributes to VO_2, and changes in pulmonary ventilation and heart rate could have a significant impact on VO_2 response to repetitive exercise. An attempt was made to evaluate importance of these factors to VO_2 (Table 1). The oxygen costs of cardiac work were assumed to be 0.2 ml·beat^{-1} (Kitamura et al., 1972), while oxygen uptake of respiratory muscles was calculated as previously described (Carra et al., 2003). For this particular correction, work of breathing was calculated at first:

$$W_B = -0.251 + 0.0382V_E + 0.00176\ V_E^2$$

where W_B is work of breathing, and V_E is expiratory pulmonary ventilation.

Then oxygen uptake of respiratory muscles was estimated as:

$$V_{RM}O_2 = 34.9 + 7.45\ W_B$$

where $V_{RM}O_2$ is O_2 uptake of the respiratory muscles, W_B is work of breathing.

Statistical analysis

Two-factor repeated measures analyses of variances

Table 2. Blood lactate and slow component of VO_2 kinetics (s. c. VO_2) when cycling in control and fatigue conditions. Values are means (±SD).

Workload	Blood lactate (mM)		s. c. VO_2 (l min^{-1})	
(W)	Control	Fatigue	Control	Fatigue
70	2.33 (.71)	2.15 (1.02)	.04 (.10)	.07 (.09)
105	2.22 (.47)	2.15 (.77)	.06 (.08)	.08 (.03)
140	2.42 (.73)	2.75 (.95)	.08 (.07)	.11 (.11)
175	3.93 (1.39) #	3.15 (1.13) #	.17 (.09) #	.13 (.15)

Significant ($p < 0.05$) differences from the values at 70 W.

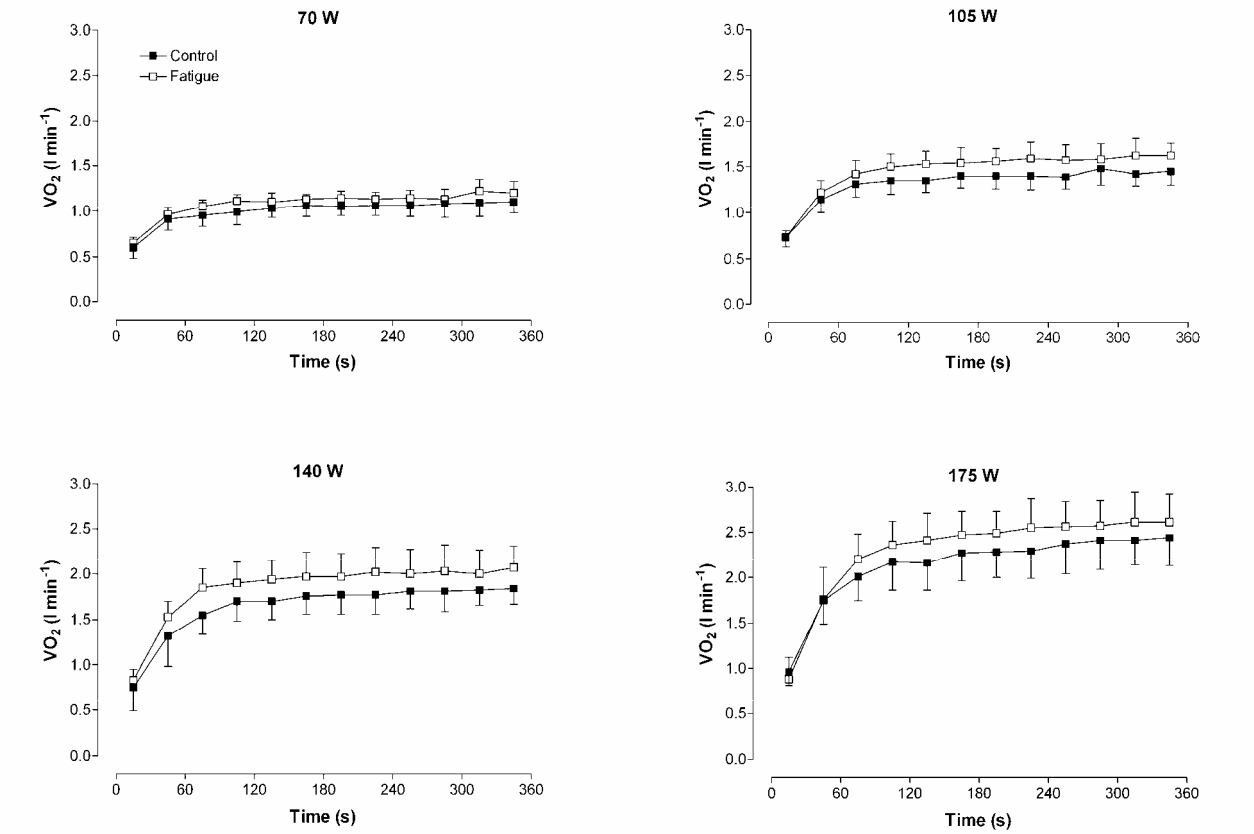

Figure 1. Pulmonary oxygen uptake (VO_2) during ergometer cycling at 70 W, 105 W, 140 W and 175 W. Value are means with standard deviations (SD) indicated by the bars.

(ANOVAs) were used when evaluating effects of exercise time and repetition of exercise bout. The F ratios were considered statistically significant when $p < 0.05$. If significant effects were found, post hoc testing was performed applying paired t- tests with Bonferroni correction for multiple comparisons. Statistical significance of all tests was set at $p < 0.05$. The results are presented as means ± standard deviations (SD).

RESULTS

VO_2 in repetitive exercise

The VO_2 peak of the volunteers was 51.7 ± 5.6 $ml \cdot min^{-1} \cdot kg^{-1}$. All the participants cycled at 70, 105, 140 and 175 W in the control and fatigue conditions, respectively. The VO_2 data from these experiments are presented in Figure 1. In the control condition, VO_2 increased with exercise intensity ($p < 0.001$) reaching 29.6 ± 5.4, 39.4 ± 7.0, 50.8 ± 8.4 and 65.8 ± 11.8 % of VO_2peak at 70, 105, 140 and 175 W, respectively. The prior drop jump exercise tended to amplify the VO_2 response to exercise. From 3rd to 6th min of cycling at 105, 140 and 175 W, VO_2 was higher ($p < 0.05$-0.01) in the fatigue compared to the control condition. This could be due to changes in pulmonary ventilation (V_E) and heart rate (HR). Data on V_E, HR and VO_2 corrected for oxygen uptake of cardiac and respiratory muscles are presented in Table 1. Indeed, V_E and HR tended to increase when cycling was performed in the damage condition. However, this increase in V_E and HR could account for only up to 10% of the overall increase in VO_2 during cycling in the fatigue relative to the control condition. At 105, 140 and 175 W of cycling, VO_2 remained higher ($p < 0.05$-0.01) in the fatigue compared to the control condition even when oxygen uptake of cardiac and respiratory muscles was subtracted from the VO_2 values.

Slow component of VO_2 kinetics and blood lactate

Data on blood lactate and the amplitude of slow component of VO_2 kinetics are presented in Table 2. The two-way ANOVA revealed a significant effect of the drop jump exercise neither on the blood lactate nor on the amplitude of the slow component of VO_2. The blood lactate increased significantly ($p < 0.05$) only when exercise was performed at the highest intensity (175 W) in the control condition. Similar results were noted for the amplitude of the slow component of VO_2. In the control condition, the slow component of VO_2 kinetics was significant ($p < 0.05$) at 175 W as all seven subjects showed an increase in VO_2 from 3rd min to 6th min of cycling. However, it tended to decrease in the fatigue condition.

Respiratory exchange ratio (RER)

The data on RER during exercise are presented in Table 3. The two-way ANOVA showed that RER increased with exercise intensity ($p < 0.05$), but there were no differences between experiments in the control and fatigue conditions**.**

Table 3. Respiratory exchange ratio (RER) during the last 3 min of cycling in control and fatigue conditions. Values are means (±SD).

Workload (W)	Control	Fatigue
70	.83 (.06)	.82 (.05)
105	.86 (.04)	.83 (.04)
140	.86 (.04)	.84 (.03)
175	.88 (.04)	.86 (.05)

Drop jump exercise

Drop jump exercise was used to induce muscle fatigue which would lead to a change in oxygen costs of the subsequent cycling exercise. During repetitive jumping, VO_2 increased over initial 3 min and then was maintained at the level of 1.38 ± 0.22 l min^{-1} or approximately 38% of VO_2peak recorded during cycling in experiment I. Data on heights of these jumps are presented in Figure 2. The jump heights tended to decrease during the exercise, but the decrease did not reach the significance level.

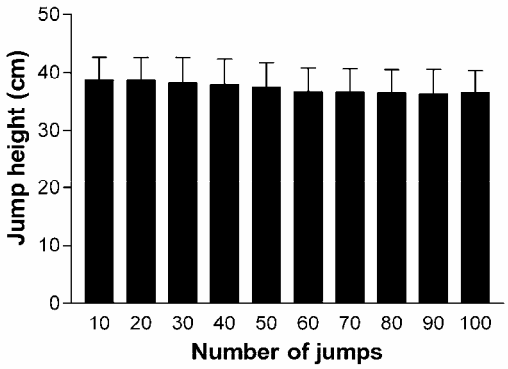

Figure 2. Jump heights during repetitive drop jumps. Averages of each ten consecutive jumps are presented. Values are means with standard deviations (SD) indicated by the bars.

DISCUSSION

The study was designed to investigate effects of muscle fatigue on metabolic costs of ergometer cycling. A protocol of repetitive drop jumps was employed to induce muscle fatigue and stimulate recruitment of motor units during the subsequent ergometer cycling exercise. Overall, VO_2 increased to higher plateau levels when ergometer cycling was repeated in the fatigue condition. It is argued that compensatory recruitment of type II fibres and impaired force transmission due to damage of structural proteins contributed to this phenomenon. On the other hand results of the study fail to link muscle fatigue and damage to the slow component of VO_2 during cycling exercise.

After the drop jump exercise, VO_2 increased significantly when ergometer cycling was performed at the three highest intensities and a similar tendency was observed at the lowest intensity as well. Each subject cycled under the two conditions on separate occasions. Thus it is unlikely that the increase in VO_2 was accidental. An increase in O_2 costs of cycling at 50% VO_2max has been observed after 3 days of exhaustive combat exercise and 65 km running (Bahr et al., 1991; Millet et al., 2000, respectively). In our study, however, volunteers performed a drop jump exercise of rather limited duration. Our calculations show that changes in heart rate and pulmonary ventilation could account for only up to 10 % of the increase in VO_2 and the largest increase in VO_2 must have occurred in skeletal muscles. This is agreement with direct measurements of oxygen uptake in knee extensor muscles that show a significant increase in oxygen uptake during fatiguing exercise at high intensity (Poole et al., 1991). Repetitive stretching of contracting muscles might be of importance in our study. An exercise with repetitive cycles of stretch and shortening induces muscle fatigue and damage (Lieber et al., 1996; Lieber and Frieden, 1999; Strojnik et al., 2000).

It has been previously demonstrated, that after the protocol of drop jumps applied in the present study, muscle force generating capacity decreases by ~30% as measured 20 min after the exercise and still shows ~15% deficit 24 hours after the exercise (Skurvydas et al., 2000, Streckis et al., 2005). In addition, there is also evidence of a significant increase in plasma creatine kinase (CK) activity 24 hours after the exercise (Murfet et al., 2003). These are typical signs of muscle fatigue and damage after exercise (Clarkson and Hubal, 2002; Lieber and Frieden, 1999). Changes in force generating capacity of skeletal muscles were not measured in this study, but our experiments were performed using the same equipment with participation of similar volunteers as in previous studies (Skurvydas et al. 2000, Streckis et al. 2005). Changes in height of repetitive jumps also followed a similar pattern. Other authors employing similar protocols of exercise also reported muscle fatigue and damage (Strojink et al., 2000). Thus, it is reasonable to assume that muscle fatigue was induced in the present study. It is also likely that some degree of muscle damage was present. Our volunteers did report a mild pain in their muscles when walking the stairs for a few days after the experiment.

Cycling exercise was performed at 70, 105, 140 and 175 W which corresponded to approximately 30, 40, 50 and 65% VO_2peak. Primarily type I fibres are recruited at intensities below 50% VO_2max and recruitment of type II fibres increases progressively at higher intensities (Greig et al., 1985, Krustrup et al., 2004). This is in agreement with our data on blood lactate that showed a significant increase only during exercise at the highest intensity (see Table 2). After the drop jump exercise, recruitment of type II fibres is expected to intensify at lower intensities of ergometer cycling compared to the exercise performed in the control condition (Ratkevicius et al., 1995; 1998a). Studies on single fibre preparation and whole muscles suggest that type II fibres have significantly higher ATP costs of isometric force generation than type I fibres (Horrowitz et al., 1994; Nakagawa et al., 2005; Stienen et al. 1996). Thus increased involvement of type II could lead to an increase in average metabolic costs of work. Muscle damage per se might also contribute to metabolic costs of exercise. It could be hypothesized that damaged muscle fibres act as an additional mechanical loading on the contracting fibres (Lieber et al., 1996; Sandercock, 2000). In addition, indirect evidence suggests that mechanical interactions between motor units are involved in reducing ATP costs of force production during isometric contractions (Nakagawa et al., 2005). Damage to structural proteins is likely to impair such interactions and increase metabolic costs of muscle work in addition to the possible effects of type II fibre recruitment.

Exercise induced muscle pain and soreness could also be associated with increased metabolic costs of exercise though evidence is contradictory (Moysi et al., 2005). There was no attempt to quantify muscle pain in the present study, but exercise was performed one hour after repetitive drop jumps. Muscle pain and inflammation are mild at this time point of recovery and become marked 1-3 days after muscle damage inducing exercise (Clarkson and Newham, 1995). Thus it is unlikely that muscle pain was a significant factor in this study.

Muscle temperature could also potentially affect metabolic costs of cycling exercise (Edwards et al., 1972). Muscle temperature was not measured in our study. However, a moderate increase in muscle temperature did not increase VO_2 when ergometer cycling was performed at similar exercise intensities (Koga et al., 1997). In this study, cycling exercise was carried out 1 hour after the drop jump exercise when major recovery of muscle temperature should have occurred (Saugen and Vøllestad, 1995). Furthermore, VO_2 did not differ significantly between control and fatigue conditions in the first bout of cycling when the largest differences in muscle temperature are expected. In view of all these considerations, it is unlikely that temperature was the major factor in our study.

It appears also that 1 hour of rest is sufficient for a major metabolic recovery since repetitive jumping can be considered as an exercise of moderate intensity (<40% VO_2peak). RER was similar during exercise in the control and fatigue conditions, and differences in VO_2 between exercise in the control and fatigue conditions could hardly be due to differences in the metabolic state and blood flow at the beginning of exercise.

The slow component of VO_2 response to exercise was evaluated in this study as there was a slow increase in VO_2 during the forth bout of exercise at 175 W (~ 65% VO_2peak). The protocol of ergometer cycling was possibly not optimal for full manifestation of this phenomenon as higher exercise intensities (75% VO_2max) are associated with a larger drift in VO_2 during exercise (Pringle et al., 2003). Incomplete metabolic recovery between repeated exercise bouts could also affect VO_2 kinetics (Tordi et al., 2003). However, exercise bouts at 70, 105 and 140 W were associated with little accumulation of blood. There is evidence that recovery of ATP, phospocreatine and intracellular pH are essentially complete within 4 min even after exercise of much higher intensity (Ratkevicius et al., 1998b). Thus it seems unlikely that prior exercise compromised VO_2 slow component to a significant degree as it appeared in all seven subjects. Interestingly, the drop jump exercise did not increase the amplitude of the slow component of VO_2. If anything, it became smaller. This suggests that recruitment of type II fibres is not always linked to appearance of the slow component of VO_2 kinetics during exercise. This agrees well with the findings of Scheuerman et al. (2001) who did not observe any link between changes in EMG, an indicator of motor unit recruitment, and VO_2 during the continuous high intensity cycling. However, findings on the slow component of VO_2 are contradictory. Pringle et al. (2003) showed an increase in amplitude of slow component of VO_2 when ergometer cycling was performed at high pedal rates that could be associated with greater involvement of type II fibres. The major concern here is a possible increase in activity of muscles for postural stabilization at high pedal rates. However, slow component of VO_2 appeared also during ergometer cycling at ~50% VO_2max when the exercise was performed after a significant depletion of muscle glycogen in slow twitch muscle fibres

(Krustrup et al., 2004). Under these exercise conditions, slow component of VO_2 was linked to recruitment of type II muscle fibres that showed metabolic evidence of increased activity. Results of our results do not necessarily contradict findings of Krustrup et al. (2004). Glycogen depletion and muscle damage after repetitive drop jumps could produce different patterns of muscle fibre recruitment. Glycogen depletion is likely to increase fatigue rate in the affected muscle fibres and compensatory recruitment of type II fibres would accelerate after a few minutes of exercise. Muscle damage is expected to cause a failure to produce any force in a number of fibres and a larger number of type II fibres would be recruited right from the beginning of exercise.

CONCLUSIONS

In summary, results of the study support the hypothesis that muscle fatigue and possibly damage induces an increase in metabolic costs of ergometer cycling, but fail to link these impairments with the slow component of VO_2 kinetics.

ACKNOWLEDGEMENT

All the experiments of this study comply with the current laws of Lithuania where the study was performed. Authors would like to thank volunteers who enthusiastically participated in this study.

REFERENCES

Bahr, R., Opstad, P.K., Medbø, J.I. and Sejersted, O.M. (1991) Strenuous prolonged exercise elevates resting metabolic rate and causes reduced mechanical efficiency. *Acta Physiologica Scandinavica* **141,** 555-563.

Burnley, M., Doust, J.H., Ball, D. and Jones, A.M. (2002) Effects of prior heavy exercise on VO_2 kinetics during heavy exercise are related to changes in muscle activity. *Journal of Applied Physiology* **93,** 167-174.

Campbell-O'Sullivan, S.P., Constantin-Teodosiu, D., Peirce, N. and Greenhaff, P.L. (2002) Low intensity exercise in humans accelerates mitochondrial ATP production and pulmonary oxygen kinetics during subsequent more intense exercise. *Journal of Physiology* **538,** 931-939.

Carra, J., Candau, R., Keslacy, S., Giolbas, F., Borrani, F., Millet, G.P., Varray, A. and Ramonatxo, M. (2003) Addition of inspiratory resistance increases the amplitude of the slow component of O_2 uptake kinetics. *Journal of Applied Physiology* **94,** 2448-2455.

Clarkson, P.M. and Hubal, M.J. (2002) Exercise-induced muscle damage in humans. *American Journal of Physical Medicine and Rehabilitation* **81, Issue 11 Supplement,** S52-S69.

Clarkson, P.M. and Newham, D.J. (1995) Associations between muscle soreness, damage, and fatigue. *Advances in Experimental Medicine and Biology* **384**, 457-469.

Edwards, R.H.T., Harris, R.C., Hultman, E., Kaijser, L., Koh, D. and Nordsjö, L-O. (1972) Effects of temperature on muscle energy metabolism and endurance during successive isometric contractions, sustained to fatigue, of the quadriceps muscle in man. *Journal of Physiology* **220,** 335-352.

Horita, T., Komi, V., Hamalainen, I. and Avela, J. (2003) Exhausting stretch-shortening cycle (SSC) exercise causes greater impairment in SSC performance than in pure concentric performance. *European Journal of Applied Physiology* **88,** 527-534.

Horowitz, J.F., Sidossis, L.S. and Coyle, E.F. (1994) High efficiency of type I muscle fibres improves performance. *International Journal of Sports Medicine* **15,** 152-157.

Gleeson, M., Blannin, A.K., Zhu, B., Brooks, S. and Cave, R. (1995) Cardiorespiratory, hormonal and haematological responses to submaximal cycling performed 2 days after eccentric or concentric exercise bouts. *Journal of Sports Sciences* **13,** 471-479.

Gleeson, M., Blannin, A.K., Walsh, N.P, Field, N.E. and Pritchard, JC. (1998) Effects of exercise-induced muscle damage on the blood lactate response to incremental exercise in humans *European Journal of Applied Physiology* **77,** 292-295.

Greig, C.A., Sargeant, A.J. and Vøllestadt, N. (1985) Muscle force and fibre recruitment during dynamic exercise in man. *Journal of Physiology* **371,** 176P.

Jones, DA. (1996) High-and low-frequency fatigue revisited. *Acta Physiologica Scandinavica* **156,** 265-270.

Kitamura, K., Jorgensen, C.R., Gobel, F.L., Taylor, H.L. and Wang, Y. (1972) Hemodynamic correlates of myocardial oxygen consumption during upright exercise. *Journal of Applied Physiology* **32,** 516-522.

Koga, S., Shiojiri, T., Kondo, N. and Barstow, T.J. (1997) Effects of increased muscle temperature on oxygen uptake kinetics during exercise. *Journal of Applied Physiology* **83,** 1333-1338.

Krustrup, P., Söderlund, K., Mohr, M. and Bangsbo, J. (2004) Slow-twitch fibre glycogen depletion elevates moderate-exercise fast-twitch fibre activity and O_2 uptake. *Medicine and Science in Sports Exercise* **36,** 973-982.

Kulis, Y., Laurinavichyus, V., Firantas, A. and Kurtinaitienė, B. (1988) Determination of lactic acid with an Exan-G analyser. *Journal of Analytical Chemistry of USSR* **43,** 1521–1523. (In Russian: English Abstract)

Lieber, R.L., Thornall, L.-E. and Friden, J. (1996) Muscle cytoskeleton disruption occurs within the first 15 min of cyclic eccentric contraction. *Journal of Applied Physiology* **80,** 278-284.

Lieber, R.L. and Friden, J. (1999) Mechanisms of muscle injury after eccentric contraction. *Journal of Science and Medicine in Sport* **2,** 253-265.

Martin, J.C. and Spiriduso, W.W. (2001) Determinants of maximal cycling power: crank length, pedalling rate and pedal speed. *European Journal of Applied Physiology* **84,** 413-418.

McDaniel, J., Durstine, J.L., Hand, G.A. and Martin, J.C. (2002) Determinants of metabolic cost during submaximal cycling. *Journal of Applied Physiology* **93,** 823-828.

Millet, G., Lepers, R., Lattier, G., Martin, V., Babault, N, and Maffiuletti, N. (2000) Influence of ultra-long-term fatigue on the oxygen cost of two types of locomotion. *European Journal of Applied Physiology* **83,** 376-380.

Moysi, J.S., Garcia-Romero, J.C., Alvero-Cruz, J.R., Vicente-Rodriguez, G., Ara, I., Dorado, C. and Calbet, J.A. (2005) Effects of eccentric exercise on cycling efficiency. *Canadian Journal of Applied Physiology* **30,** 259-275.

Mole, P. and Hoffman, J.J. (1999) VO_2 kinetics of mild exercise are altered by RER. *Journal of Applied Physiology* **87,** 2097-2106.

Murfet, F., Higgins, S., Ratkevicius, A., Fletcher, S. and Malkova, D. (2003) Markers of muscle damage, muscle soreness and lipid peroxidation after eccentric exercise: effects of vitamin C supplementation. *12th International Biochemistry of Exercise Conference (IBOEC 2003), July 16-10, 2003, Maastricht-Holland.* Book of Abstract. 205.

Nakagawa, Y., Ratkevicius, A., Mizuno, M. and Quistorff, B. (2005) ATP economy of force maintenance in human tibialis anterior muscle. *Medicine and Science in Sports Exercise* **37,** 937-943.

Neder, J.A., Nery, L.E., Andreoni, S., Sachs, A. and Whipp, B.J. (2000) Oxygen cost for cycling as related to leg mass in males and females, aged 20 to 80. *International Journal of Sports Medicine* **21,** 263-269.

Poole, D.C., Schaffartzik, W., Knight, D.R., Derion, T., Kennedy, B., Guy H.J., Prediletto, R. and Wagner, P.D. (1991) Contribution of exercising leg to the slow component of oxygen uptake kinetics in humans. *Journal of Applied Physiology* **71,** 1245-1253.

Pringle, J.S., Doust, J.H., Carter, H., Tolfrey, K. and Jones, A.M. (2003) Effect of pedal rate on primary and slow-component oxygen uptake responses during heavy-cycle exercise. *Journal of Applied Physiology* **94,** 1501-1507.

Ratkevicius, A., Mizuno, M., Povilonis, E. and Quistorff, B. (1998b) Energy metabolism of the gastrocnemius and soleus muscles during isometric voluntary and electrically induced contractions in man. *Journal of Physiology* **507,** 593-602.

Ratkevicius, A., Skurvydas, A. and Lexell, J. (1995) Submaximal-exercise-induced impairment of human muscle to develop and maintain force at low frequencies of electrical stimulation. *European Journal of Applied Physiology* **70,** 294-300.

Ratkevicius, A., Skurvydas, A., Povilonis, E., Quistorff, B. and Lexell, J. (1998a) Effects of contraction duration on low-frequency fatigue in voluntary and electrically induced exercise of quadriceps muscle in humans. *European Journal of Applied Physiology* **77,** 462-468.

Sandercock, T.G. (2000) Nonlinear summation of force in cat soleus muscle results from stretch of the common-elastic elements. *Journal of Applied Physiology* **89,** 2206-2214.

Saugen, E. and Vøllestad, N.K. (1995) Nonlinear relationship between heat production and force during voluntary contractions in humans. *Journal of Applied Physiology* **79,** 2043-2049.

Saunders, M.J., Evans, E.M., Arngrimsson, S.A., Allison, J.D., Warren, G.L. and Cureton, K.J. (2000) Muscle activation and the slow component rise in oxygen uptake during cycling. *Medicine and Science in Sports and Exercise* **32,** 2040-2045.

Scheuermann, B.W., Hoelting, B.D., Noble, M.L. and Barstow, T.J. (2001) The slow component of O_2 uptake is not accompanied by changes in muscle EMG during repeated bouts of heavy exercise in humans. *Journal of Physiology* **531,** 245-256.

Skurvydas, A., Jascaninas, J. and Zachovajevas, P. (2000) Changes in height of jump, maximal voluntary contraction force and low-frequency fatigue after 100 intermittent or continuous with maximal intensity. *Acta Physiologica Scandinavica* **169,** 55-62.

Stienen, G.J.M., Kiers, J.L., Bottinelli, R. and Reggiani, C. (1996) Myofibrillar ATPase activity in skinned human skeletal muscle fibres: fibre type and temperature dependence. *Journal of Physiology* **493,** 299-307.

Streckis, V., Skurvydas, A. and Ratkevicius, A. (2005) Twelve- to thirteen-year-old boys are more resistant to low-frequency fatigue than young men. *Pediatric Exercise Science* **17,** 399-416.

Strojnik, V. and Komi, P.V. (2000) Fatigue after submaximal intensity stretch-shortening cycle exercise. *Medicine and Science in Sports and Exercise* 32: 1314-1319.

Tordi, N., Perrey, S., Harvey, A. and Hughson, R.L. (2003) Oxygen uptake kinetics during two bouts of heavy cycling separated by fatiguing sprint exercise in humans. *Journal of Applied Physiology* **94,** 533-541.

Vøllestad, N.K., Wesche, J. and Sejersted, O.M. (1990) Gradual increase in leg oxygen uptake during repeated submaximal contractions in humans. *Journal of Applied Physiology* **68,** 1150-1156.

Warren, G.L. 3rd, Williams, J.H., Ward, C.W., Matoba, H., Ingalls, C.P., Hermann, K.M. and Armstrong, R.B. (1996) Decreased contraction economy in mouse EDL muscle injured by eccentric contractions. *Journal of Applied Physiology* **81,** 2555-2564.

Whipp, B. (1994) The slow component of VO_2 uptake kinetics during heavy exercise. *Medicine and Science in Sports and Exercise* **26,** 1319-1326.

KEY POINTS

- Repetitive fatiguing exercise induce an increase in metabolic costs of ergometer cycling exercise.
- It is argued that muscle pain, muscle temperature, elevated pulmonary ventilation and heart rate, shift towards from carbohydrate to fat metabolism are of minor importance in this phenomenon.
- Increased recruitment of type II fibres and impaired force transmission between muscle fibres due to damage of structural proteins appear to play the major role in reducing efficiency of ergometer cycling.

AUTHORS BIOGRAPHY

Aivaras RATKEVICIUS
Employment
Lecturer, School of Medical Sciences, College of Life Sciences & Medicine, Institute of Medical Sciences (IMS), Forresterhill, University of Aberdeen, U.K.
Degree
PhD
Research interests
Energy costs of exercise, molecular mechanisms of muscle adaptation to exercise.
E-mail: a.ratkevicius@abdn.ac.uk

Arvydas STASIULIS
Employment
Professor, Department of Applied Physiology and Health Education, Lithuanian Academy of Physical Education
Degree
PhD
Research interests
Aerobic capacity and its changes under different conditions including neuromuscular fatigue
E-mail: a.stasiulis@lkka.lt

Loreta Dubininkaite
Employment
Lector, Department of Applied Physiology and Health Education, Lithuanian Academy of Physical Education
Degree
MSc
Research interests
Cardiorespiratory responses to repeated exercise bouts
E-mail: l.dubininkaite@lkka.lt

Albertas SKURVYDAS
Employment
Professor, Department of Applied Physiology and Health Education, Lithuanian Academy of Physical Education
Degree
PhD
Research interests
Complex and dynamic adaptations in human motor system
E-mail: a.skurvydas@lkka.lt

✉ **Dr. A. Ratkevicius**
School of Medical Sciences, College of Life Sciences & Medicine, Institute of Medical Sciences, Forresterhill, University of Aberdeen, Aberdeen AB25 2ZD, U.K.