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ORIGINAL ARTICLE

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Influence of ultra-long-term fatigue on the oxygen cost of two types of locomotion

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Abstract The aim of this study was to examine the effects of fatigue induced by a 65-km ultramarathon on the oxygen cost of running (C_r) and cycling (C_{cycl}). The day before and immediately after the race, a group of nine well-trained male subjects performed two submaximal 4-min exercise bouts: one cycling at a power corresponding to 1.5 $W \cdot kg^{-1}$ body mass on an electromagnetically braked ergometer, and one running at 11 $km \cdot h^{-1}$ on a flat asphalt roadway. Before oxygen cost determinations, the subjects performed 12 "ankle" jumps at a given frequency that was fixed by an electronic metronome (2.5 Hz). From the non-fatigued to the fatigued condition, there was a significant increase in minute ventilation for both running ($P < 0.01$) and cycling ($P < 0.0001$). Significant changes were also found in respiratory exchange ratio both for running ($P = 0.01$) and cycling ($P < 0.0001$). However, running and cycling differed in that C_{cycl} increased significantly by [mean (SD)] 24.2 (11.5)% ($P < 0.001$), suggesting an alteration of muscle efficiency, while C_r did not change with fatigue [186.8 (14.1) $mlO_2 \cdot kg^{-1} \cdot km^{-1}$ vs 186.8 (18.7) $mlO_2 \cdot kg^{-1} \cdot km^{-1}$]. In addition, contact times during hopping increased significantly from 0.173 (0.019) ms to 0.194 (0.027) ms ($P < 0.01$). Analysis of the factors that determine C_r indicate that the subjects modified their movement pattern in order to decrease the mechanical cost of running in such long-term fatigue conditions.

Key words Fatigue · Oxygen cost · Running · Contact time · Cycling

Introduction

Fatigue is a complex phenomenon that is characterised by a decrease in performance. It has been reported that fatigue induces an increase in energy expenditure per unit of distance travelled, that is the energy cost, in running (Brueckner et al. 1991; Hausswirth et al. 1996; Nicol et al. 1991b; Sproule 1998; Xu and Montgomery 1994) and walking (Brisswalter et al. 1996). However, conflicts exist in the literature regarding the causes of the increase in energy cost during both high- and low-intensity fatigue, namely the slow component of oxygen uptake ($\dot{V}O_2$) and oxygen drift, respectively. It has been suggested that mechanical (e.g. Candau et al. 1998) as well as physiological modifications such as higher muscular temperature (Willis and Jackman 1994), higher free fatty acid oxidation (Hausswirth et al. 1996), or an increase in pulmonary ventilation ($\dot{V}_E$; Candau et al. 1998), reduce economy with the appearance of fatigue. One explanation of this discrepancy in the literature is the fact that the determinants of elevations in $\dot{V}O_2$ may be multi-factorial. For exercises leading to exhaustion in about 10 min, it has nevertheless been suggested that most of the elevation in $\dot{V}O_2$ is attributable to the working muscle (Poole et al. 1991). Since a similar study does not exist for low-intensity exercise, one cannot be sure that the same factors are implied in exercises leading to exhaustion in more than 2 h. In fact, the factors involved in the increase in energy cost with fatigue may vary with the type of contraction, subject characteristics, training history, and exercise duration and intensity.

In this sense, it must be noted that the energetics of long-distance locomotion have been studied extensively for exercise durations lower than (Sproule 1998; Xu and Montgomery 1994) or equivalent to a marathon run (Brueckner et al. 1991; Hausswirth et al. 1996; Nicol et al. 1991b). Most of the experiments studying fatigue after exercises lasting more than 3 h have focussed on tissue damage (e.g. Crenshaw et al. 1993; Koller et al. 1998). For example, Koller et al. (1998) have shown that

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skeletal muscle damage was higher after a 67-km running race than after a cycling competition of 230 km. With the exception of Davies and Thompson (1986), who studied energy expenditure during 4 h of treadmill running, very few experiments have tested the energetic modifications that occur in such long-distance events. The purposes of this study were therefore to (1) examine the alteration in energy cost with extreme fatigue, and (2) to test the hypothesis that the changes in energy cost depend upon the type of locomotion (i.e. running vs cycling).

Methods

Subjects

Nine healthy male subjects [mean (SD) age 40.1 (6.8) years; mass 69.2 (7.1) kg; height 178.3 (10.3) cm; body fat 10.6 (2.5)%] completed the study. All subjects regularly participated in competitions either in running or triathlon and were especially trained for the ultramarathon supporting the study (65 km, altitude difference of 2500 m). Before participating, each subject received an explanation of the procedures and gave its informed consent.

Experimental protocol

All subjects underwent two sets of tests, the first during the day preceding the race (non-fatigued state), and the second immediately after the race (fatigued state). Each set of tests consisted of vertical and rebound jumps and determinations of the metabolic cost of cycling (C_{cycl}) and running (C_r).

Vertical jumps

The subjects performed two squat jumps (SJ) and two countermovement jumps (CMJ) on a contact mat (Ergo Test, Globus, Codogne, Italy), and in a randomised order. In order to minimise trunk movements, the position of the upper body was standardised and controlled by the main experimenter. The subjects were asked to jump as high as possible and the best SJ and CMJ performance were analysed. A 1-min rest period was allowed between the four jumps. Then the subjects performed one set of rebound jumps (RJ) at a frequency of 2.5 Hz, which was paced by an electronic metronome. The subjects were instructed to keep their knees as stiff as possible ("ankle jumps") and to have as brief a contact time as possible. Once they were able to follow the required frequency, the contact time and flight time of 12 jumps were recorded. For all RJs, the actual frequencies ranged between 2.41 and 2.55 Hz. During both single jumps and RJs, the subjects were instructed to keep their hands on their hips.

Metabolic cost

For each testing session, the subjects performed two 4-min exercises in a randomised order at an intensity that was chosen to allow all subjects to be comfortable after the race. The physiological parameters were determined during the last 30 s of each bout of exercise using a portable system (KB1-C, Aerosport, Ann Arbor, USA) less than 15 min after the end of the race. These parameters included: $\dot{V}O_2$, carbon dioxide output ($\dot{V}CO_2$), $\dot{V}_E$, ventilatory equivalent for oxygen ($\dot{V}_E/\dot{V}O_2$) and respiratory exchange ratio (R, where $R = \dot{V}CO_2/\dot{V}O_2$).

The $\dot{V}O_2$ of the respiratory muscles ($\dot{V}RMO_2$, in ml · min^{-1}) was calculated from the work of breathing (W_B, in kg · m · min^{-1}), using the equations proposed by Coast et al. (1993):

$$W_B = -0.251 + 0.0382 \times \dot{V}_E + 0.00176 \times \dot{V}_E^2 \quad (1)$$

$$\dot{V}RMO_2 = 34.9 + 7.45 \times W_B \quad (2)$$

One test was performed with the subject cycling at a power corresponding to 1.5 W · kg^{-1} body mass on an electromagnetically braked ergometer (Excalibur, Lode, Groningen, The Netherlands) for which the seat and handlebars are fully adjustable both vertically and horizontally. The same position was kept for a given subject during the two tests. C_{cycl} (mlO$_2$ · min^{-1} · W^{-1}) was calculated by dividing the overall $\dot{V}O_2$ (in ml · min^{-1}) by mechanical power (in W). For the purpose of clarity, the term C_{cycl} was preferred to cycling efficiency. Indeed, the fact that a potential decrease in economy would have resulted an increase in running energy cost and decrease in cycling efficiency would have been confusing. However, because C_{cycl} is expressed in a non-usual unity, cycling gross efficiency (η), that is the ratio of power output to total energy expended, was also determined.

The other 4-min bout consisted of running at 11 km · h^{-1} on a flat asphalt roadway. The runner was paced by an investigator riding approximately 3 m in front of him on a bicycle that was equipped with a calibrated electronic speedometer. C_r (mlO$_2$ · kg^{-1} · km^{-1}) was calculated by dividing the overall $\dot{V}O_2$ (in ml · min^{-1} · kg^{-1}) by velocity (m · min^{-1}).

Statistical analysis

Each study variable was compared between conditions with a paired Student's *t*-test. Correlation coefficients were calculated to determine the relationships between selected parameters. For all statistical analyses, a P value of 0.05 was accepted as the level of significance, and the data are presented as the mean (SD).

Results

The time of the winner of the race supporting the study was 355.4 min and the average time of our subjects was 489.3 (96.3) min; the average velocity of the subjects was 8.2 (1.5) km · h^{-1}. This low speed can be explained by the distance and the altitude difference as well as the type of trail encountered. C_{cycl} was 24.2 (11.5)% higher in the fatigued state than in the non-fatigued state ($P < 0.001$; Fig. 1A), which means that η decreased from 25.5 (2.2)% to 21.3 (1.8)%, whereas C_r did not change between the two conditions (Fig. 1B). As shown in Fig. 2A, $\dot{V}_E$ increased from the non-fatigued to the fatigued condition for both running ($P < 0.01$) and cycling ($P < 0.0001$). Similarly, $\dot{V}_E/\dot{V}O_2$ increased significantly with fatigue in running [from 24.9 (1.9) to 30.4 (2.6); $P < 0.001$] and cycling [from 27.7 (3.7) to 30.3 (1.7); $P < 0.05$]. In addition, significant changes were found in R both for running ($P = 0.01$) and cycling ($P < 0.0001$; Fig. 2B).

Vertical jump performances decreased significantly with fatigue for both the SJ and CMJ ($P < 0.01$; Fig. 3). The contact time during hopping at 2.5 Hz was significantly shorter in the non-fatigued condition than in the fatigued condition [from 0.173 (0.019) to 0.194 (0.027) ms; $P < 0.01$]. In addition, there was a positive correlation between the changes in contact time and the changes in C_r ($r = 0.66$; $P < 0.05$).

The C_r in the fatigued condition was significantly correlated ($r = 0.70$; $P < 0.05$; Fig. 4B) with perfor-

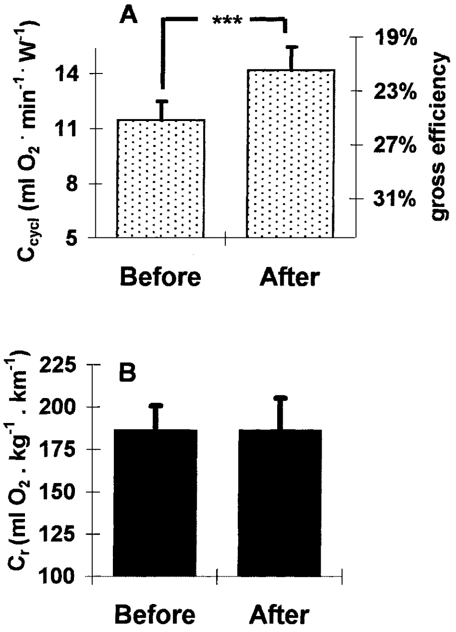

Fig. 1 Comparison of the oxygen cost of cycling (C_{cycl}, **A**) and running (C_r, **B**) before and after the fatiguing exercise. *Brackets* represent 1 SD. ***Significant difference at the $P < 0.001$ level

mance expressed as a percentage of the winner's average velocity. There was also a tendency for this relationship when considering C_r in the non-fatigued condition, but the correlation failed to reach the level of statistical significance ($r = 0.51$; $P = 0.15$; Fig. 4A).

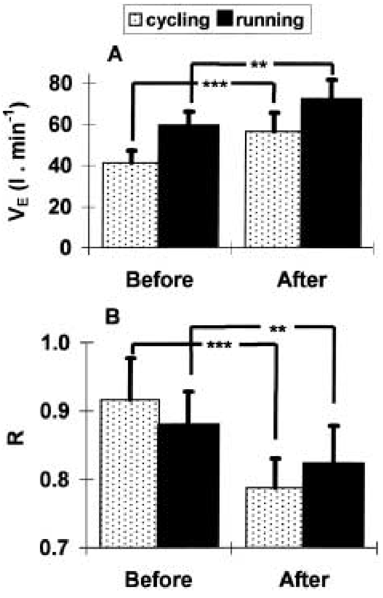

Fig. 2 Comparison of minute ventilation ($\dot{V}_E$, **A**) and respiratory exchange ratio (R, **B**) before and after the fatiguing exercise (*speckled bars* cycling, *black bars* running). *Brackets* represent 1 SD. ** Significant difference at the $P < 0.01$ level; ***significant difference at the $P < 0.001$

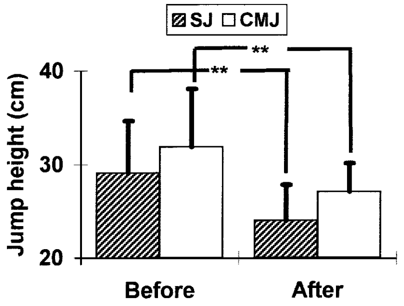

Fig. 3 Comparison of jump performance for squat jump (*SJ*, *hatched bars*) and counter-movement jump (*CMJ*, *black bars*) before and after the fatiguing exercise. *Brackets* represent 1 SD. ** Significant difference at the $P < 0.01$ level

Discussion

The most important finding of this study is that C_r did not change with the fatigue evoked by an ultramarathon, despite the altered neuromuscular capacities, the lower R and the higher $\dot{V}_E$ found in the fatigued state.

It has been suggested previously that pulmonary diffusion limitation due to interstitial oedema may occur during prolonged strenuous exercise (Manier et al. 1991). This could explain part of the raise in $\dot{V}_E/\dot{V}O_2$ found in the present study for both running and cycling. For cycling, the equations proposed by Coast et al. (1993, Eqs 1, 2) enabled estimation of the increase in $\dot{V}RMO_2$ due to the higher $\dot{V}_E$, to account for approximately 7% of the elevation in C_{cycl}. Similarly, part of the increase in the C_{cycl} (when expressed in $mlO_2 \cdot W^{-1}$) could be attributed to the higher oxidation of free fatty

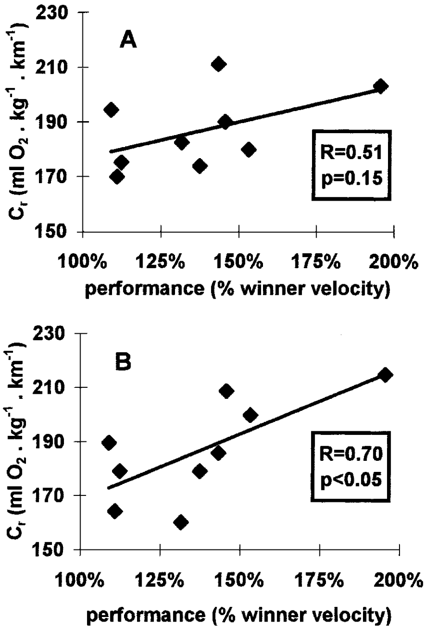

Fig. 4 Relationship between the level of performance and the oxygen cost of running (C_r) in non-fatigued (**A**) and fatigued conditions (**B**)

acids evidenced by the lower R in the fatigued state. This modification of substrate oxidation, which was probably due to glycogen depletion, is in line with previous studies (Bosch et al. 1990; Davies and Thompson 1986). For instance, it has been shown that after 4 h of running at 65% of $\dot{V}O_{2max}$, glycogen stores were 37–53% of the resting values (Davies and Thompson 1986). However, the decrease in R found for cycling in the present study accounted for only 4% of the increase in C_{cycl}. Since C_{cycl} increased by 24.2 (11.4)%, changes in $\dot{V}_E$ and R do not explain the entire economy alteration. As a result, it can be suggested that muscular efficiency was altered.

In contrast to C_{cycl}, C_r did not change with fatigue. This latter result differs from previous findings (Brueckner et al. 1991; Davies and Thompson 1986; Hausswirth et al. 1996; Nicol et al. 1991b, Xu and Montgomery 1994). In the present study, $\dot{V}_E$, R and muscular efficiency were altered such that C_r should have increased. One can also observe that the changes in neuromuscular activation with fatigue (i.e. the decrease in lower-limb stiffness) should have induced an increase in C_r. In fact, it has been suggested recently that C_r is influenced by the stiffness of the lower limbs (Dalleau et al. 1998). Dalleau et al. (1998) observed a negative relationship between C_r and stiffness, as measured with a kinematic arm. Indirect evidence of the beneficial effects of stiffness on running economy can also be found in the study of Paavolainen et al. (1999), who showed that 9 weeks of lower-limb strength training decreased the contact time of athletes running at sub-maximal velocity. This shorter contact time was associated with a lower C_r. In the present study, contact times were measured during a non-specific movement pattern (i.e. hopping), but at a frequency close to the step frequency that is used during running at low speed. Contact times were longer in the fatigued condition and, interestingly, we observed a significant relationship between the changes in contact time and the changes in C_r. Contact times during running or hopping depend upon both the stiffness of the tendon-muscle complex and neural command. Even if alterations in the series elastic component cannot be ruled out, we speculate that the longer contact time is mainly due to neuromuscular activation failure. The factors responsible for such neuromuscular alterations could be related to a decreased central drive, disfacilitation of the stretch reflex, and/or inhibition of activation through type III and IV afferent fibres, which are sensitive to inflammation (Avela et al. 1999). In the present study, the observed significantly longer contact time in the fatigued state is also in line with previous experiments showing that a marathon can induce a reduced tolerance to stretch load (Avela and Komi 1998; Nicol et al. 1991a).

C_r depends upon a number of mechanical and physiological parameters. Mechanical factors include primarily (1) potential and kinetic energy changes due to oscillations of the centre of mass of the body in the vertical plane and to its acceleration at each stride, and (2) internal work (Di Prampero 1986). Several physiological factors such as myotypology (Bosco et al. 1987), the ability to store and re-use elastic energy, heart rate and $\dot{V}_E$ (Morgan and Craib 1992) have also been discussed in the literature as potential factors affecting economy. In the present study, the increased contact times and $\dot{V}_E$, as well as the decreased muscular efficiency and R should have induced a raise in C_r. Since C_r did not change, it can be speculated that the subjects modified their running pattern in order to improve the mechanical cost of running. This modification could involve a decrease in internal and/or external work. The present results are in opposition with previous experiments studying the effects of fatigue for exercise lasting less than 3 h, where no kinematic changes were observed (Hausswirth et al. 1996; Nicol et al. 1991b), or where an increase in the external mechanical work was observed (Candau et al. 1998). The running pattern modification observed with fatigue suggested by the present results could also involve other factors such as lower co-contraction or higher relaxation of the muscles contracted for maintaining balance and posture. To the best of our knowledge, no previous study has tested the influence of ultra-long-term fatigue on the economy of different types of locomotion. In addition, only one experiment has studied C_r alteration with fatigue due to running exercise longer than 3 h (Davies and Thompson 1986). Why our results are in opposition with those of this study is unclear. It must be noted that the fatiguing exercise used in the present experiment [489.3 (96.3) min] is much longer than that considered by Davies and Thompson (240 min). Also, it can be argued that the velocity chosen to measure C_r in the present study ($11\ \mathrm{km \cdot h^{-1}}$) is unfamiliar for trained subject, so that C_r in the non-fatigued condition was higher than in the real one. However, it is important to note that the C_r measured in the present study [186.8 (14.1) $\mathrm{mlO_2 \cdot kg^{-1} \cdot km^{-1}}$] is not higher than the usual C_r for athletes having a body mass similar to our subjects (Bourdin et al. 1993).

$\dot{V}O_{2max}$ (not measured in the present experiment) is known to be a key factor for performance in aerobic activities. However, the longer the duration, the more important are two other factors that are involved in performance, endurance and economy. In the present study, a significant relationship was observed between performance and C_r in the fatigued state, while a tendency existed for this correlation in the non-fatigued state. Thus, in line with previous studies (e.g. Sjödin and Svedenhag 1985), it seems that good ultramarathoners are able to run with a good economy and especially to maintain a low C_r while in a fatigued condition.

In conclusion, the results of this study show that the energy cost alterations that are associated with the extreme fatigue evoked by running differ between running and cycling. An ultramarathon lasting more than 6 h does not seem to change the C_r at low speed despite (1) elevations in both $\dot{V}_E$ and free fatty acid oxidation,

(2) increases in contact time during hopping, and (3) decreases in muscular efficiency. Taken together, these results suggest that in the present study the runners were able to modify their running patterns to decrease their mechanical cost at a low velocity. Since only one submaximal speed was tested in the present experiment, further studies are needed to confirm these findings.

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