Oxygen Uptake Kinetics and Time to Exhaustion in Cycling and Running: a Comparison Between Trained and Untrained Subjects

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Abstract

The objective of the present study was to compare pulmonary gas exchange kinetics (VO₂ kinetics) and time to exhaustion (Tlim) between trained and untrained individuals during severe exercise performed on a cycle ergometer and treadmill. Eleven untrained males in running (UR) and cycling (UC), nine endurance cyclists (EC), and seven endurance runners (ER) were submitted to the following tests on separate days: (i) incremental test for determination of maximal oxygen uptake (VO₂max) and the intensity associated with the achievement of VO₂max (IVO₂max) on a mechanical braked cycle ergometer (EC and UC) and on a treadmill (ER and UR); (ii) all-out exercise bout performed at IVO₂max to determine the time to exhaustion at IVO₂max (Tlim) and the time constant of oxygen uptake kinetics (τ). The τ was significantly faster in trained group, both in cycling (EC = 28.2 ± 4.7 s; UC = 63.8 ± 25.0 s) and in running (ER = 28.5 ± 8.5 s; UR = 59.3 ± 12.0 s). Tlim of untrained was significantly lower in cycling (EC = 384.4 ± 66.6 s vs. UC; 311.1 ± 105.7 s) and higher in running (ER = 309.2 ± 176.6 s vs. UR = 439.8 ± 104.2 s). We conclude that the VO₂ kinetic response at the onset of severe exercise, carried out at the same relative intensity is sensitive to endurance training, irrespective of the exercise type. The endurance training seems to differently influence Tlim during exercise at IVO₂max in running and cycling.

Keywords: Aerobic training, maximal aerobic exercise, oxygen uptake kinetics, running, cycling.

Introduction

Physical activity is an effective stimulus for increasing the activity of skeletal muscle and the cardiovascular system. The ability to sustain muscular exercise is dependent in large part on the body's ability to transport oxygen from the atmosphere to be used as the terminal oxidant in the mitochondrial electron transport chain. It has been suggested that oxygen uptake (VO₂) measured at the mouth reflects the oxidative metabolism change in active tissues (Barstow, 1994). Thus, the rate of VO₂ response at the onset of exercise (VO₂ kinetics) is a valuable index that reflects the adjustment of both systemic oxygen transport and muscle metabolism.

During the transition from rest to constant-load exercise of moderate intensity (i.e., below the lactate threshold), after 15–20 s of the cardiodynamic phase (phase I), VO₂ rises in an approximately monoexponential fashion (phase II) to attain a new steady state (phase III) within 2–3 min. Some studies have demonstrated that the VO₂ kinetics adjustment [i.e., the time constant (τ) of the exponential function describing the phase II], during moderate exercise is influenced by the level of aerobic fitness (Chilibeck et al., 1996) and that it is sensitive to the detection of effects of aerobic training even in previously trained individuals (Norris & Petersen, 1998). In contrast, at exercise intensities corresponding to the severe domain (i.e., above the maximal lactate steady state or critical power), blood lactate and VO₂ increase progressively in a biexponential fashion (by the development of VO₂ slow component, in intensities below
controlled (21–22°C) laboratory. All tests were performed at the same time of day in a climate-controlled laboratory. The time constant of oxygen uptake kinetics (\(\tau\)) and the time to exhaustion (Tlim) between trained and untrained individuals during severe exercise performed on a cycle ergometer and treadmill.

**Methods**

**Subjects**

Eleven untrained males in running (UR) and cycling (UC) (26.8 ± 4.1 years, 74.9 ± 14.3 kg, 175.1 ± 5.1 cm), nine endurance cyclists (EC) (22.6 ± 2.1 years, 62.8 ± 5.4 kg, 173.8 ± 5.9 cm), and seven endurance runners (ER) (25.8 ± 6.0 years, 60.4 ± 4.1 kg, 172.1 ± 6.9 cm), volunteered to participate in this study. All subjects gave informed consent and the protocol was approved by the university’s ethics committee. The subjects were asked not to train hard during the last 2 days before each test and to report to the laboratory at least 3 h after the last meal.

**Experimental design**

The EC and ER performed 2 exercise bouts to exhaustion, on separate days, on their specific ergometer. The untrained subjects performed 4 tests, 2 exercise bouts to exhaustion in cycle ergometer (UC), and 2 exercise bouts to exhaustion on a treadmill (UR) in random order and completed on separate days within a 2 week period. The first test was an incremental exercise protocol for the determination of VO2max, the intensity corresponding at VO2max (IVO2max), and the intensity at the onset of blood lactate accumulation (OBLA). The second test was all-out exercise bout performed at IVO2max to determine the time to exhaustion at IVO2max (Tlim) and the time constant of oxygen uptake kinetics (\(\tau\)). All tests were performed at the same time of day in a climate-controlled (21–22°C) laboratory.

**Protocol of VO2max and IVO2max determination**

The subjects performed the treadmill (INBRAMED Super ATL, Porto Alegre, Brazil) incremental test, where the initial speed was set at 8 km.h\(^{-1}\) for the UR and at 14 km.h\(^{-1}\) for the ER. Velocity increments were 1 km.h\(^{-1}\) every 3 min. All stages were followed by 30 s of rest. During this period, an earlobe capillary blood samples were collected. The incremental cycle ergometer (Monark, Stockholm, Sweden) test was set at 70 W for the UC and 105 W for the EC, with increases in power output of 35 W. At the end of each stage an earlobe capillary blood samples were collected without pause. Throughout the test the pedal rate was maintained constant at 70 rpm and the grade of the treadmill set at 1%. Throughout the tests, the respiratory and pulmonary gas-exchange variables were measured using a breath-by-breath portable gas analyzer (Cosmed K4b\(^2\), Rome, Italy). These analyzers have previously been validated over a wide range of exercise intensities (McLaughlin et al., 2001). Before each test, the O2 and CO2 analysis systems were calibrated using ambient air and a gas of known O2 and CO2 concentration according to the manufacturer’s instructions, while the K4b\(^2\) turbine flowmeter was calibrated using a 3-l syringe (Cosmed K4b\(^2\), Rome, Italy). Heart rate (HR) was also monitored throughout the tests (Polar, Kempele, Finland). Breath-by-breath VO2 and HR data were smoothed using a five-step average filter, and then reduced to 15 s stationary averages for incremental test (Data Management Software, Cosmed, Rome, Italy) to reduce the noise so as to enhance the underlying characteristics. Earlobe capillary blood samples (25 µl) were collected into a capillary tube and were analyzed for lactate concentration using an automated analyzer (YSI 2300, Yellow Springs). The VO2max was defined as the highest 15 s VO2 value reached during the incremental test having a respiratory exchange ratio (R) greater than 1.1, a blood lactate concentration greater than 8 mM and peak HR at least equal to 90% of the age-predicted maximal (Taylor et al., 1955). The IVO2max was defined as the minimal velocity/power maintained for more than 1 min, which elicited VO2max (Billat & Koralsztein, 1996). OBLA was determined by linear interpolation, with a fixed lactate concentration of 3.5 mM being considered (Heck et al., 1985).

**Constant exercise at IVO2max**

The subjects subsequently performed the constant test until exhaustion at IVO2max. After a 10 min warm-up at 60% IVO2max followed by 5 min of rest, the subjects were instructed to perform the required intensity. For the treadmill test, the subjects stepped onto the moving belt and the stopwatch was stated as soon as they let go of the handrails (always within 5 s). Tests were terminated when the participants placed their hands back on the railing, signifying volitional fatigue. Tlim was measured to the nearest second. For the cycle ergometer tests, the time during which the subjects could maintain the prescribed work rate at the required pedaling frequency was considered as Tlim. As in the treadmill test, Tlim was measured to the nearest second. Breath-by-breath VO2 data were smoothed using a five-step average filter, and then reduced 5 s stationary averages (Data Management Software, Cosmed, Rome, Italy) to reduce the noise.
so as to enhance the underlying characteristics. An earlobe capillary blood samples were collected after end exercise at 3rd, 5th and 7th min.

Data modeling

Phase II response, which reflects the influence of muscle metabolic change on VO₂, was described by a mono-exponential function for all-out exercises at IVO₂max (Barstow & Mole, 1991). Data points of the phase I, which reflects the increase in cardiac output and thus pulmonary blood flow (the first 15s) were excluded from the analyses (Casaburi et al., 1992). For each constant-intensity test the VO₂ response was described using all data after the Phase I response, by an iterative non-linear regression process from the Microcal Origin 6.0 (Northampton, MA, USA) using the following equation with no delay:

$$VO₂(t) = VO₂_{basel} + A \times (1 - e^{-\frac{t}{\tau}})$$  \hspace{1cm} (1)

Where VO₂(t) is oxygen uptake at any time t; VO₂basel is oxygen uptake at the end of the rest; A is the amplitude of oxygen uptake (VO₂max - VO₂basel) and; τ is the time constant (Defined as the time required to attain 63% of the A).

For each subject, during all constant tests at IVO₂max, it was considered that the area comprised between baseline VO₂ (time-zero) and asymptotic VO₂ corresponds to the accumulated oxygen deficit (Whipp & Ozyener, 1998):

$$AOD = A \times \tau$$  \hspace{1cm} (2)

Where AOD is the accumulated oxygen deficit (ml); A is the asymptotic amplitude (ml.s⁻¹) and; τ is the time constant (seconds). Both A and τ were determined using the equation 1 for all data points (time-zero).

Statistical analysis

Data are presented as mean ± SD. A one-way analysis of variance was used to compare anthropometrics characteristics between trained and untrained groups (U × ER × EC), complement by a post-hoc Scheffe test. Differences between trained and untrained groups for VO₂max and IVO₂max were tested by non-paired t-test. A non parametric Mann-Whitney U-test was used to compare VO₂ kinetics (τ), Tlim and AOD between trained and untrained groups. Statistical significance was set at $p \leq 0.05$.

Results

Untrained subjects had presented significantly higher body mass values than the others groups (EC and ER). However, there were no significant differences for age and height between groups. Table 1 shows OBLA (expressed in percentage of IVO₂max), VO₂, HR, and power output and velocity reached at the end of the incremental cycle ergometer tests in EC and UC, and incremental treadmill tests in ER and UR. VO₂max and IVO₂max were significantly higher in EC than in UC. In running VO₂max and IVO₂max were also significantly higher in ER than in UR. HRmax was not significantly different between trained and untrained groups in both exercise modes. However, HRmax was significantly higher in UR when compared to UC. OBLA expressed in percentage of IVO₂max (%IVO₂max) was significantly higher in running than cycling for untrained groups, and significantly lower in relation to trained groups. The peak of blood lactate during the incremental tests was not significant different between all groups analyzed.

Tlim was significantly lower in UC when compared to EC. However, Tlim was significantly higher in UR when compared to ER (Table 2). Analyzing the exercise mode, Tlim was significantly higher in UR when compared to UC. The τ was significantly different between trained and untrained groups in both ergometers (Table 2 and Figure 1). There was no significant difference in τ between cycling and running for untrained group. AOD and lactate peak were not significantly different between all groups analyzed.

Discussion

The aim of this study was to determine, in a cross-sectional design, the influence of aerobic training on Tlim and on VO₂ kinetic at the same relative intensity (100% IVO₂max). The main finding of the present study was that training status

| Table 1. Data from the incremental test for all groups analyzed. |
|-----------------|-------------|-------------|-------------|-------------|-------------|
| Subject         | VO₂max (ml.Kg⁻¹.min⁻¹) | IVO₂max   | HR max (bpm) | OBLA % IVO₂max | Lactate peak mmol.L⁻¹ |
| EC (n = 9)       | 67.6 ± 7.6          | 332.2 ± 41.3* | 191.0 ± 8.4 | 85.1 ± 4.2 | 10.0 ± 1.8 |
| UC (n = 11)      | 36.7 ± 5.6*         | 200.0 ± 36.2* | 186.2 ± 6.8* | 61.6 ± 5.9* | 10.3 ± 1.4 |
| ER (n = 7)       | 68.8 ± 6.3          | 19.7 ± 1.7* | 195.4 ± 5.7 | 82.0 ± 6.6 | 9.4 ± 1.7 |
| UR (n = 11)      | 43.5 ± 7.0b         | 12.8 ± 1.0b | 199.1 ± 7.1 | 76.6 ± 6.4b | 9.1 ± 1.9 |

Values are mean ± SD. EC, endurance cyclist; UC, untrained cyclist; ER, endurance runner; UR, untrained runner; VO₂max, maximal oxygen uptake; IVO₂max, velocity and power output at VO₂max values obtained at the end of incremental; HR, heart rate; OBLA, velocity or power output at the onset of blood lactate accumulation expressed as percent of VO₂max; *p ≤ 0.05 when compared with EC; *p ≤ 0.05 when compared with ER; ‡p ≤ 0.05 when compared with UC; *Units are km.h⁻¹; *Units are watts.
seems to differently influence Tlim during severe exercise at the same relative intensity in running and cycling. Second, in agreement with literature data regarding moderate domain intensities, an acceleration in VO2 kinetics is observed in subjects with better aerobic fitness, irrespective of the exercise type.

The VO2max and IVO2max values obtained for the EC and ER groups were compatible with those reported in the literature for individuals classified as well trained (Jeukendrup et al., 2000; Billat et al., 2002a). Thus, even without interfering with the training of these athletes, we can infer from the association between VO2max and IVO2max, that our subjects suffered adaptations of long-term aerobic training (Jeukendrup et al., 2000). With respect to the untrained individuals, both VO2max and IVO2max values were similar to data reported in the literature for sedentary individuals (Astrand & Saltin, 1961), thus indicating low aerobic fitness of these subjects.

In the present study, both EC and ER individuals showed lower τ values than untrained subjects, demonstrating a possible effect of endurance training on initial VO2 adjustment. This decrease was similar for the two exercise types, suggesting that the VO2 kinetics responded similarly to training adjustments in the two modalities studied. Data in the literature are highly contradictory with respect to the main limiting factor of VO2 kinetics at the onset of exercise, which includes a mechanism responsible for oxygen delivery (convection and diffusion), or a metabolic inertia (cellular metabolic controllers and/or enzymatic activation) (Grassi, 2001; Hughson et al., 2001). At submaximal intensities, the mechanism responsible for this faster increase in VO2 after training seems to result from a more rapid increase in cardiac output and/or skeletal muscle blood flow during the first minute of exercise (Shoemaker et al., 1996). These alterations in VO2 kinetics at submaximal intensities have been shown to parallel changes in heart rate kinetics after training (Phillips et al., 1995). In contrast, according to Grassi (2001), the ventilatory threshold (VT) might discriminate intensities at which oxygen supply would (above VT) or would not be (below VT) one of the limiting factors of VO2 kinetics. Increases in oxidative enzyme concentration and in the size and number of mitochondria are observed after prolonged

Table 2. Responses at constant load exercise at IVO2max.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Tlim (s)</th>
<th>τ (s)</th>
<th>AOD (ml)</th>
<th>AOD (ml.kg⁻¹)</th>
<th>AOD (% AO2)</th>
<th>Lactate peak mmol.L⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>EC (n = 9)</td>
<td>384 ± 66</td>
<td>28.2 ± 4.7</td>
<td>1975 ± 598</td>
<td>31.8 ± 10.7</td>
<td>8.7 ± 2.4</td>
<td>10.9 ± 1.7</td>
</tr>
<tr>
<td>UC (n = 11)</td>
<td>311 ± 105a</td>
<td>63.8 ± 25.0a</td>
<td>2247 ± 705</td>
<td>30.0 ± 7.5</td>
<td>21.7 ± 7.0a</td>
<td>11.0 ± 2.4</td>
</tr>
<tr>
<td>ER (n = 7)</td>
<td>309 ± 176</td>
<td>28.5 ± 8.5</td>
<td>1705 ± 568</td>
<td>28.5 ± 10.5</td>
<td>12.1 ± 5.8</td>
<td>10.7 ± 2.6</td>
</tr>
<tr>
<td>UR (n = 11)</td>
<td>439 ± 104b</td>
<td>59.3 ± 12.0b</td>
<td>2195 ± 707</td>
<td>29.6 ± 9.9</td>
<td>12.1 ± 2.6</td>
<td>9.9 ± 1.5</td>
</tr>
</tbody>
</table>

Values are mean ± SD. EC, endurance cyclist; UC, untrained cyclist; ER, endurance runner; UR, untrained runner; Tlim, time to exhaustion; τ, time constant of VO2 kinetics; AOD, accumulated oxygen deficit; AO, accumulated oxygen; *p ≤ 0.05 when compared with EC; †p ≤ 0.05 when compared with ER; ‡p ≤ 0.05 when compared with UR.

Fig. 1. Example of the 4 typical oxygen uptake patterns observed in the subjects of this study during the constant-intensity test. Individual data points are 5-s average values. The curves were fitted by a mono-exponential function. In the upper panel, (▲) endurance runner – ER, and (○) untrained runner – UR; the bottom panel (○) untrained cyclist – UC and (▲) endurance cyclist – EC; τ, time constant of oxygen uptake kinetics.
endurance training, which might also contribute to an acceleration of VO₂ kinetics (Phillips et al., 1995). Even considering all of these contradictions, it is logical to assume that aerobic training has an influence on all these possible limiting factors, permitting accelerated VO₂ kinetics irrespective of the intensity and exercise type, as demonstrated in the present investigation at IVO₂max and in other longitudinal studies, carried out at different submaximal intensities (Phillips et al., 1995; Norris & Petersen, 1998; Demarle et al., 2001; Billat et al., 2002b).

Tlim at IVO₂max has been used as an index of anaerobic capacity, to prescribe, in an individualized manner, the duration of stimuli during interval training, and to predict performance in athletes (Billat & Koralsztein, 1996). However, Tlim values have shown wide intra- and inter-study variability, preventing a possible comparison between studies (Billat & Koralsztein, 1996).

To our knowledge, no study has yet compared Tlim at IVO₂max between sedentary and trained individuals exercising on a bicycle ergometer and treadmill. High-intensity interval training might reduce (Demarle et al., 2001), or not modify (Billat et al., 1999b), Tlim during severe exercise carried out at the same relative intensity (93 and 100% IVO₂max, respectively) in trained runners. Billat et al. (1994) have found an inverse correlation between Tlim and VO₂max and between Tlim and IVO₂max in long-distance elite runners. Furthermore, Billat et al. (2000) reported that during running at IVO₂max, the time necessary to reach VO₂max was positively correlated (r = 0.94) with the time during which exercise was sustained (Tlim). Thus, the higher Tlim values during running observed for the UR group compared to the ER group, agree with the studies cited earlier and suggest that the higher the aerobic power, the lower Tlim during running at IVO₂max. The significance of the Tlim at IVO₂max still needs consideration. In fact, it is not clear whether the large interindividual differences, are caused by a higher aerobic endurance, or as suggested by some studies, by individual differences in anaerobic capacity (Faina et al., 1997; Renoux et al., 1999). In the present study, AOD was not different between all groups analyzed. Therefore, we cannot attribute the difference between UR and ER in the Tlim to AOD.

For cycling, we did not find any data about the effects of training on Tlim at IVO₂max. Our data, however, suggest that cycling endurance training may provoke effects different on Tlim from those observed for running. Part of these differences might be explained by the biomechanical characteristics of the exercises analyzed in the present study. Cavanagh & Kram (1985) have provided evidence that the mechanical efficiency of running exceeds that predicted from simple conversion of chemical energy to kinetic energy by muscles. The stretch-shortening cycle in running allows for storage of elastic energy during the eccentric phase and its subsequent release during the concentric phase of the action, thereby enhancing force production for a given neural input. It is possible that the greater eccentric muscle action in running may in some way offset or delay the onset of peripheral fatigue and/or reduce the recruitment of type II motor units during running compared with cycling for the same relative exercise intensity. In addition, during cycling high intramuscular pressures developed during the pedaling cycle can lead to partial occlusion of the femoral artery (Edwards et al., 1972), reduce oxygen supply and cause greater recruitment of type II fibers. Messonnier et al. (2002) observed in sedentary individuals that the Tlim at IVO₂max during cycling was positively correlated with the lactate exchange and removal abilities. In these individuals, the lactate exchange ability was moderately correlated with capillary density and with the number of capillaries per type I fiber area (Messonnier et al., 2002). It is possible that endurance training modifies these factors, increasing the maximal duration of cycling exercise at IVO₂max.

Finally, simultaneous analysis of the effects of training and the exercise type on Tlim permits us to propose that a slower VO₂ kinetic alone does not seem to determine a lower Tlim during exercise at IVO₂max, particularly during running. However, further studies are necessary to investigate possible factors that might influence Tlim during exercise carried out at IVO₂max.

**Conclusions**

We conclude that the VO₂ kinetic response at the onset of severe exercise carried out at the same relative intensity is sensitive to endurance training, irrespective of the exercise type. The training status seems to differently influence Tlim during exercise at IVO₂max in running and cycling. In addition, a slower VO₂ kinetic alone does not seem to determine a lower Tlim during exercise at IVO₂max, particularly during running.

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