The VO₂ slow component for severe exercise depends on type of exercise and is not correlated with time to fatigue

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The VO₂ slow component for severe exercise depends on type of exercise and is not correlated with time to fatigue (1). A recent study (5) reported (5) that the VO₂ slow component was extremely small during suprathreshold exercise. However, the mechanism underlying the continuous rise in VO₂ during suprathreshold exercise remains poorly understood, we have recently reported (5) that the VO₂ slow component was extremely small during an 18-min exhaustive run compared with that reported during cycling (23). Indeed, in that study, all the distance runners attained only 90% of their VO₂max during the last minute before exhaustion, without ever reaching VO₂max.

PREVIOUS STUDIES PERFORMED on cycling have reported that oxygen uptake (VO₂) can attain a steady state above the lactate threshold but only in the work-rate range where lactate remains constant. Indeed, it is only above what has been termed “critical power” (17) that VO₂ continues to rise until the end of the test or until exhaustion (22, 29). Furthermore, the magnitude of this slow component increases with the level of work rate and eventually takes VO₂ to the maximal VO₂ (VO₂max), even during submaximal exercise (22, 23).

Although the mechanism underlying the continuous rise in VO₂ during suprathreshold exercise remains poorly understood, we have recently reported (5) that the VO₂ slow component was extremely small during an 18-min exhaustive run compared with that reported during cycling (23). Indeed, in that study, all the distance runners attained only 90% of their VO₂max during the last minute before exhaustion, without ever reaching VO₂max.

Data comparing the magnitude of the VO₂ slow component for different types of dynamic exercises are not available in the literature. Kyle and Caiozzo (16) reported that various types of exercise exclusively involving the legs yielded very similar power output, as long as the motion was similar and the same muscle groups were involved. However, cycling and running differ greatly in terms of muscular contraction regimen and, therefore, mechanical efficiency. For instance, the concentric work of cycling may account for a lower mechanical efficiency than running, which relies on a stretch-shortening cycle (6). The higher efficiency of stretch-shortening movements has been attributed to the elastic behavior of the muscles during contact with the ground. Cavagna et al. (8) estimated elastic contributions to be 40–50% of the total power generated during running. The gastrocnemius and soleus muscles also function during cycling on stretch-shortening cycles, although the stretching phases are not as apparent as in running or jumping (14).

In addition, it has been suggested that bicyclists could minimize peripheral muscle fatigue by pedaling at a rate that produces a higher than the optimum metabolic rate (the most economical) but that lowers crank forces (torque). Indeed, Patterson and Moreno (19) demonstrated that when the pedaling rate was increased from 60 to 120 rpm, the resultant force on the pedals averaged over a crank cycle was isometric-like and produced no external work. Their results suggested that pedaling at 90 rpm might minimize peripheral forces and therefore peripheral muscle fatigue, even though this rate might result in higher VO₂. In running, however, Cavanagh and Williams (9) reported that the freely chosen stride length allows for the most economical run.

Whether these differences between running and cycling have a potential effect on the VO₂ slow component is unclear. No studies have compared the VO₂ slow component for cycling and running in subjects trained for both exercises and with the same VO₂max and the same fraction of VO₂max at the blood lactate threshold (2).

We hypothesized that the type of exercise could influence the changes in the efficiency, i.e., the VO₂ slow component, during exhaustive suprathreshold exercise.

The purpose of this study was to examine 1) the influence of exercise, running vs. cycling, on the VO₂ slow component during exhaustive exercise in triathletes equally trained in cycling and running and 2) whether the magnitude of the VO₂ slow component...
influences the duration of exercise (time limit: \( t_{\text{lim}} \)) at a velocity (90\% \( V_{\text{O2peak}} \)) or a work rate (90\% \( WR_{V_{\text{O2peak}}} \)) corresponding to 90\% of \( V_{\text{O2max}} \). Finally, the relationship between the \( V_{\text{O2}} \) slow component and blood lactate accumulation for cycling and running exercise was analyzed.

**METHODS**

**Subjects.** Ten well-trained triathletes gave their informed consent and volunteered to participate in this study, which was approved by the Paris Ethical Committee. The physical characteristics of the subjects are presented in Table 1. All subjects were highly motivated and familiar with treadmill running, erogometer cycling, and with the sensation and symptoms of fatigue during heavy exhaustive cycling and running exercise.

**Materials.** The running tests were performed on a motorized treadmill (Gymrol 1800, Techmachine, St. Etienne, France) kept at a 0\% slope for all of the tests, the speed being controlled with a resolution of 0.5 mi/h (controller provided by the Centre d’Enseignement et de Développement pour le Montage en Surface, Université Joseph Fourier, Grenoble, France). The cycling tests were carried out on an electronically braked cycle ergometer (ERG 600 Bosch, Berlin, Germany). Respiratory and pulmonary gas exchange variables were measured by using a MedGraphics CPMax cart (Medical Graphics, St. Paul, MN), which was calibrated before each test according to the manufacturer's instructions. Breath-by-breath data were averaged every 15 s. An electrocardiograph was monitored from a three-lead configuration (Jaeger cardio-system), and the output signal was fed to the CPX Medical Graphics system for computing heart rate. The blood samples were analyzed for blood lactate concentration (YSI 27 analyzer, Yellow Springs Instruments, Yellow Springs, OH).

**Preliminary measurements.** The tests were performed on each subject at the same time of day in a climate-controlled laboratory (21–22°C). The subjects were instructed not to train hard or to ingest food and beverages containing caffeine for 3 days before testing. Each subject underwent two preliminary incremental tests on both the treadmill and the cycle-ergometer to determine 1) \( V_{\text{O2max}} \), 2) the work rate associated with \( V_{\text{O2max}} \) (\( WR_{V_{\text{O2max}}} \), and 3) the fraction of \( V_{\text{O2max}} \) at which the lactate threshold appeared. These two incremental tests (running and cycling) were performed 3 days apart and in a randomized order. Subjects performed a continuous incremental test (3-min stages) to exhaustion. Duration and workload increments were standardized for running and cycling as follows. The workload increments were estimated to demand a \( V_{\text{O2}} \) response equal to \( 2 \times \text{rest} \) (2 Mets, i.e., \( 2 \times 3.5 \) ml·kg\(^{-1}\)·min\(^{-1}\)). Each work increment ranged between 35 and 50 W for cycling, depending on the weight of the subjects [on the basis of 12 ml \( O_2 \cdot \text{min}^{-1} \cdot \text{W}^{-1} \) according to the recommendations of Astrand and Rodahl (1)]. For example, for a 60-kg subject, the workload increments were 35 W [60 (kg) \( \times 7 \) (ml·kg\(^{-1}\)·min\(^{-1}\))/12 (ml \( O_2 \cdot \text{min}^{-1} \cdot \text{W}^{-1} \)]. For running, the speed was increased by 2 km/h (33.3 m/min) at each stage, except for the last stage where the increment was only 1 km/h (3.67 m/min). The initial work was set at between 70 and 100 W for cycling and at 10 km/h for running.

**Table 1. Physical characteristics, triathlon experience, and training regimen data of 10 triathletes**

<table>
<thead>
<tr>
<th>Subject No.</th>
<th>Age, yr</th>
<th>Weight, kg</th>
<th>Height, cm</th>
<th>Triathlon Experience, yr</th>
<th>No. of Triathlon Competitions</th>
<th>Mean Training Distance, km/wk</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>25</td>
<td>61</td>
<td>172</td>
<td>6</td>
<td>20</td>
<td>60 ± 200 ± 29 ± 8</td>
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<tr>
<td>2</td>
<td>25</td>
<td>59</td>
<td>172</td>
<td>7</td>
<td>19</td>
<td>50 ± 180 ± 10 ± 8</td>
</tr>
<tr>
<td>3</td>
<td>40</td>
<td>65</td>
<td>175</td>
<td>5</td>
<td>12</td>
<td>40 ± 150 ± 8 ± 4</td>
</tr>
<tr>
<td>4</td>
<td>25</td>
<td>72</td>
<td>184</td>
<td>5</td>
<td>16</td>
<td>70 ± 240 ± 8 ± 6</td>
</tr>
<tr>
<td>5</td>
<td>40</td>
<td>66</td>
<td>176</td>
<td>4</td>
<td>10</td>
<td>60 ± 200 ± 6 ± 3</td>
</tr>
<tr>
<td>6</td>
<td>37</td>
<td>80</td>
<td>185</td>
<td>3</td>
<td>10</td>
<td>60 ± 250 ± 6 ± 2</td>
</tr>
<tr>
<td>7</td>
<td>20</td>
<td>70</td>
<td>176</td>
<td>4</td>
<td>10</td>
<td>70 ± 200 ± 6 ± 3</td>
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<tr>
<td>8</td>
<td>23</td>
<td>71</td>
<td>182</td>
<td>5</td>
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<td>40 ± 180 ± 8 ± 4</td>
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<td>9</td>
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<td>78</td>
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<td>15</td>
<td>60 ± 200 ± 12 ± 1</td>
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<td>10</td>
<td>23</td>
<td>66</td>
<td>177</td>
<td>3</td>
<td>9</td>
<td>40 ± 200 ± 8 ± 1</td>
</tr>
</tbody>
</table>

\[
\text{Mean} \pm \text{SD} \quad 29 \pm 8 \quad 69 \pm 7 \quad 177 \pm 5 \quad 5 \pm 1 \quad 12 \pm 5 \quad 55 \pm 12 \quad 200 \pm 29 \quad 8 \pm 1
\]
The $\dot{V}O_2$ slow component was computed as the difference to exhaustion were different in the cycling and running tests. Maximal values of metabolic concentration; $\dot{V}O_2$, l/min; RER, respiratory exchange ratio; HR, heart rate; [La], lactate uptake; RER, respiratory exchange ratio; HR, heart rate; [La], lactate concentration; $\dot{V}O_2_{\text{max}}$, and $P_{\dot{V}O_2_{\text{max}}}$, velocity and power associated with $\dot{V}O_2_{\text{max}}$, respectively.

The subjects ran and cycled to exhaustion at 90% WR $\dot{V}O_2_{\text{max}}$. These two tests were separated by 1 wk. After a 15-min warm-up period at 50% WR $\dot{V}O_2_{\text{max}}$, which was below the lactate threshold for all the subjects, the work rate was increased within 20 s to 90% WR $\dot{V}O_2_{\text{max}}$. All subjects were given verbal encouragement throughout each trial. For running, the time to fatigue at 90% $\dot{V}O_2_{\text{max}}$ was the time at which the subject's feet left the treadmill as he placed his hands on the guardrails. For cycling, this time corresponded to the time at which the subject was no longer able to pedal at a given power output. This time was defined as the time limit at 90% WR $\dot{V}O_2_{\text{max}}$ ($t_{\text{lim(90%)}}$).

Blood samples were obtained from the fingertip before the warm-up run, during the last 30 s of the warm-up, immediately after the end of the exercise test, and then 8 min into the recovery period. The time course of blood lactate during the all-out exercises was not analyzed.

Data analysis. Statistical analysis was performed by using t-tests for paired comparisons to determine whether $\dot{V}O_2_{\text{max}}$ blood lactate concentration, respiratory exchange ratio, heart rate, lactate threshold (in $\%\dot{V}O_2_{\text{max}}$), and times to exhaustion were different in the cycling and running tests. The $\dot{V}O_2$ slow component was computed as the difference between $\dot{V}O_2$ at the last and the third minute of the exercise. A two-way analysis of variance for repeated measurements tested the overall effect of time on cardiorespiratory and blood parameters during the first minute (onset), the minute at the mid-time to fatigue, and the last minute of $t_{\text{lim}}$ (end) during the constant-power test. Scheffé’s post hoc analysis was then used to locate the differences. The results are presented as means ± SD. Statistical significance was set at $P < 0.05$.

RESULTS

Incremental tests. Table 2 shows the cycling and running $\dot{V}O_2_{\text{max}}$, heart rate, and blood lactate values reached at the end of the incremental tests. There was no significant difference between running and cycling for $\dot{V}O_2_{\text{max}}$, maximal heart rate, blood lactate level, and lactate threshold.

Finally, the $\dot{V}O_2$ elicited at 90% WR $\dot{V}O_2_{\text{max}}$ was 90.7 ± 5.2 and 88.2 ± 3.1% of $\dot{V}O_2$ for cycling and running, respectively, which was not significantly different ($P = 0.22$). Consequently, the intensity of the exhaustive exercise (i.e., 90% WR $\dot{V}O_2_{\text{max}}$) was well above the lactate threshold, and similar for both type of exercises in absolute ($\dot{V}O_2$) and relative intensity ($\%\dot{V}O_2_{\text{max}}$). In addition, the selected warm-up period was well below the severe-exercise domain delineated by the lactate threshold. In fact, the end of the 15-min warm-up period was performed at 56 ± 2 and 54 ± 3% of $\dot{V}O_2_{\text{max}}$ for running and cycling, respectively (50% WR $\dot{V}O_2_{\text{max}}$).

Constant work rate tests. Table 3 shows the $\dot{V}O_2$ slow component, the cycling and running $\dot{V}O_2_{\text{max}}$, heart rate, and blood lactate reached at the end of the all-out constant work rate tests performed at 90% WR $\dot{V}O_2_{\text{max}}$.

Time to fatigue. The 90% $\dot{V}O_2_{\text{max}}$, and 90% WR $\dot{V}O_2_{\text{max}}$ were, respectively, 17.7 ± 1.1 km/h and 347 ± 43 W. Running and cycling times to fatigue at this velocity or power output were not significantly different at ~10 min (Table 3).

The $\dot{V}O_2$ slow component. As shown in Table 3, compared with cycling, the $\dot{V}O_2$ slow component for running was significantly lower (268.8 ± 24 vs. 20.9 ± 2 ml/min, $P = 0.02$). During cycling, $\dot{V}O_2$ at exhaustion was not significantly different from $\dot{V}O_2_{\text{max}}$ determined during the incremental test. In contrast, at the end of the exhaustive run test, the triathletes did not, on average, reach their $\dot{V}O_2_{\text{max}}$ (Fig. 2). However, examination of individual responses revealed different patterns of responses (Fig. 3, A-C). Four subjects (subjects 4, 5, 7, and 8) reached their $\dot{V}O_2_{\text{max}}$ in the cycling but not in the running test (Fig. 3A); four subjects (subjects 2, 3, 6, and 9) reached their $\dot{V}O_2_{\text{max}}$ both in cycling and running.
Blood lactate and the $\dot{V}O_2$ slow component. The subjects ended their warm-up periods with a blood lactate level of $2.9 \pm 0.9$ mmol/l for running and $2.4 \pm 0.5$ mmol/l for cycling. Blood lactate level at the end of the exhaustive exercises was not significantly different from that at the end of the incremental test, both for running ($7.2 \pm 1.9$ vs. $7.1 \pm 1.7$ mmol/l, $P = 0.79$) and cycling ($7.3 \pm 2.4$ vs. $7.7 \pm 1.3$ mmol/l, $P = 0.85$). The magnitude of the $\dot{V}O_2$ slow component and the level of blood lactate accumulation were correlated for both cycling and running ($r = 0.48$, $P = 0.03$, $n = 20$), for cycling only ($r = 0.66$, $P < 0.05$, $n = 10$) but not for running only ($r = 0.12$, $P = 0.74$, $n = 10$) (Fig. 4).

The $\dot{V}O_2$ slow component and time to fatigue. No significant correlation was found between the magnitude of the $\dot{V}O_2$ slow component and the duration tolerated in this suprathreshold exercise ($r = -0.15$ for both running and cycling combined and $r = -0.23$ and $-0.18$ for running and cycling, respectively, considered separately). However, the duration of suprathreshold exercise was positively correlated with the blood lactate accumulation for running ($r = 0.79$, $P < 0.01$) but not for cycling ($r = -0.32$, $P > 0.05$).

(Fig. 3B), the remaining two subjects (subjects 1 and 10) reaching neither their cycling nor running $V_{O2max}$ (Fig. 3C).

In other words, of the 10 triathletes studied, 8 reached their $\dot{V}O_2$ during cycling and only 4 during running.
The VO₂ slow component was higher for cycling than for running. Despite the same relative intensity of exercise, the VO₂ slow component was correlated neither with the time to fatigue nor with blood lactate accumulation, when workload (i.e., failure to sustain a required power output).

The VO₂ slow component and cardioventilatory variables. The maximal heart rate at the end of the constant test was not significantly different between cycling and running (180.4 ± 5.4 vs. 175 ± 7.1 beats/min, P = 0.81). Minute ventilation, however, was significantly higher in cycling (153.6 ± 18.6 vs. 137.2 ± 21.1/min, P = 0.002) but with a minute ventilation-to-VO₂ ratio similar to that during cycling.

**DISCUSSION**

In the present study, an exhaustive test performed at 90% WR_VO₂max was used to examine the influence of the type of exercise (cycling vs. running) on the VO₂ slow component and its relationship with the time to fatigue (i.e., failure to sustain a required power output).

Our results were twofold. First, for a similar relative and absolute intensity, the VO₂ slow component depends on the type of exercise. Second, the VO₂ slow component was correlated neither with the time to fatigue nor with blood lactate accumulation, when running and cycling were considered separately. Moreover, in contrast to cycling, the time to fatigue was unrelated to the blood lactate accumulation for running.

The VO₂ slow component depends on the type of exercise. Despite the same relative intensity of exercise, the VO₂ slow component was higher for cycling than for running. The level of work rate chosen for the test was well above each triathlete's lactate threshold because the intensity of exercise was above the blood lactate accumulation of between 3 and 5 mM (2). The constant work rate exercise corresponded to a "severe-exercise" domain, defined as the intensity at which it is no longer possible to reach a new VO₂ steady state, consistent with exercise above the critical power (12).

Most of the studies that have reported a VO₂ slow component were performed during cycling (12). However, the VO₂ slow component has also been reported during running but only for prolonged tests (20–30 min) (18, 25). No data are available on the behavior of the VO₂ slow component during a submaximal running test leading to fatigue. We observed that 8 of the 10 subjects reached their VO₂max in cycling and only 4 in running. A precise analysis of the main differences between cycling and running may help us to understand some of the mechanisms responsible for the VO₂ slow component.

By simultaneously measuring pulmonary and leg VO₂ during cycle ergometry, Poole et al. (21) demonstrated that 86% of the increment in pulmonary VO₂ beyond the third minute of exercise (i.e., the VO₂ slow component) could be accounted for by the increase in leg VO₂. These data indicate that the majority of the VO₂ slow component is attributable to factors within the working limbs (12). Different mechanisms may account for such additional increase in VO₂. It has been suggested that the VO₂ slow component may primarily be related to motor unit recruitment patterns during exercise, depending on the contribution of lower efficiency, fast-twitch motor units (15). More recently, Barstow et al. (3) and Poole et al. (20) have linked the VO₂ slow component with the type of fibers, hypothesizing that both slow- and fast-twitch fiber types are recruited simultaneously at the onset of heavy exercise. However, because of their slower kinetics, the VO₂ requirement of the fast-twitch fibers may become manifest only after several minutes.

The hypothesis that the VO₂ slow component arises from the recruitment of a fast-twitch fiber population with slow kinetics is consistent with the notion that VO₂ kinetics are limited by fiber mitochondrial content (20). Moreover, it has been shown that isolated mitochondria from type II fibers exhibit a 18% lower phosphate-to-oxygen ratio (30). Similarly, Whipp (29) considers that a, if not the, major contributor to the VO₂ excess is likely to be the high energy cost of contraction of the type II fibers recruited at a proportionally higher level of work rate and requiring a large high-energy phosphate cost for force production.

In the present study, because triathletes exercised at the same relative intensity for cycling and running (between their lactate threshold and the work rate associated with VO₂max), there was no reason to attribute the difference in the VO₂ slow component between these two types of exercises to a difference in the percentage of fast-twitch fibers recruited in cycling and in running, unless it is assumed that the contraction regimen recruits different types of fibers at a given work rate, a result actually supported by many studies. For instance, Gaesser (11) reported that the VO₂ slow component was significantly higher for cycling at 100
rpm than at 50 rpm. In our study, the subjects were free to choose their most comfortable rate and usually adopted a frequency of ~80 rpm, which may have increased the magnitude of the slow component. Recently, Takaishi et al. (27) demonstrated that the optimal pedaling rate estimated from neuromuscular fatigue in working muscles was coincident not with the pedaling rate at which the smallest $V\dot{O}_2$ was obtained but with the preferred pedaling rate of the subjects. They suggested that the reason that cyclists preferred a higher pedaling rate was closely related to the development of neuromuscular fatigue in the working muscles.

In contrast, during running, the most efficient step rate is virtually the same as the freely chosen step rate (9).

Finally, the isometric component of the contractions during cycling should be considered. Indeed, the type of muscle contraction is not homogeneous during the pedaling cycle, and an isometric-like component occurs during various phases of this cycle. This could indeed greatly affect the actual cost of pedaling in terms of $V\dot{O}_2$ at a high level of work rate.

The $V\dot{O}_2$ slow component, time to fatigue, and blood lactate. Our second finding was that the $V\dot{O}_2$ slow component was correlated neither with time to fatigue nor with blood lactate accumulation. Whipp (29) suggested that the more rapidly the slow component projects toward $V\dot{O}_2$, the shorter the tolerable duration was hypothesized that the $V\dot{O}_2$ slow component could be induced by the Hb-O$_2$ dissociation curve shifted to the right by acidosis (Bohr effect) (28).

There may be different reasons for stopping cycling and running, even if the delay of fatigue is not significantly different. However, the nature of the link between the $V\dot{O}_2$ slow component and the fatigue process remains unclear (20). The relationships between lactate and the $V\dot{O}_2$ slow component have also been the focus of attention. Barstow and Molé (4), for example, suggested that the magnitude of the $V\dot{O}_2$ slow component correlated temporally with the changes in blood lactate. Roston et al. (23) also reported a significant correlation between changes in blood lactate and the $V\dot{O}_2$ slow component during heavy exercise. It has been hypothesized that the $V\dot{O}_2$ slow component could be induced by the Hb-O$_2$ dissociation curve shifted to the right by acidosis (Bohr effect) (28). Therefore, the Bohr effect allowed further unloading of $V\dot{O}_2$ from Hb for uptake by the muscle cells at a constant (minimum) capillary PO$_2$. (26). However, the temporal relationship between blood lactate and the $V\dot{O}_2$ slow component has been convincingly shown not to be one of cause and effect (see Ref. 20 for review). Our results corroborate this conclusion because they clearly show a dissociation between blood lactate and the $V\dot{O}_2$ slow component. However, one should consider that because blood lactate concentration is the difference between rates of blood lactate production and disappearance (7), it might be possible that the same blood lactate concentration for cycling and running corresponds to a different lactate turnover reflected by the higher $V\dot{O}_2$ slow component in cycling.

In conclusion, the type of dynamic exercise performed at the same intensity ($\%WRV_{V_{max}}$) and absolute $V\dot{O}_2$ was found to significantly affect the characteristics of the $V\dot{O}_2$ response during heavy exercise. Not only was the $V\dot{O}_2$ slow component dependent on the type of exercise, it was also not correlated with the time to fatigue.

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