Relative importance of aerobic and anaerobic energy release during short-lasting exhausting bicycle exercise

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Medbo, Jon Ingulf, and Izumi Tabata. Relative importance of aerobic and anaerobic energy release during short-lasting exhausting bicycle exercise. J. Appl. Physiol. 67(5): 1881–1886, 1989.—Anaerobic energy release is of great importance for shortlasting exercise but has been difficult to quantify. In order to determine the amount of anaerobic energy release during shortlasting exercise we let 17 healthy young males exercise on the ergometer bike to exhaustion. The power during exercise was kept constant and selected to cause exhaustion in \~30 s, 1 min, or 2–3 min. The \( \text{O}_2 \) uptake was measured continuously during the exercise, and the anaerobic energy release was quantified by the accumulated \( \text{O}_2 \) deficit. The work done as well as the total energy release rose linearly with the exercise duration and was therefore a sum of a component proportional to time plus a constant addition. The accumulated \( \text{O}_2 \) deficit increased from \( 1.86 \pm 0.07 \) (SE) mmol/kg for 30 s exercise to \( 2.25 \pm 0.06 \) mmol/kg for 1 min exercise and further to \( 2.42 \pm 0.08 \) mmol/kg for exercise lasting 2 min or more \( (P < 0.01) \). The accumulated \( \text{O}_2 \) uptake increased linearly with the duration, and as a consequence of this the relative importance of aerobic processes increased from 40% at 30 s duration to 50% at 1 min duration and further to 65% for exercise lasting 2 min. These results show that both aerobic and anaerobic processes contribute significantly during intense exercise lasting from 30 s to 3 min.

Physiological activity results in splitting of ATP in the exercising muscles. Because the ATP stores are very limited, the ATP broken down must be resynthesized continuously at the same rate as it is used. At moderate exercise intensities this resynthesis is accomplished by aerobic processes. High intensity exercise where the ATP-turnover rate exceeds the maximal power of the \( \text{O}_2 \) transporting system (that is supramaximal exercise intensity) is in addition heavily dependent on anaerobic ATP-forming processes. The ability to exercise at high intensities is therefore dependent on the capacities of both aerobic and anaerobic processes. In the present study the following questions are addressed: 1) How large is the anaerobic energy release during exhausting bicycling? 2) What is the relative contribution from anaerobic processes during shortlasting exercise?

Anaerobic ATP-production is closely linked to lactate production and to creatine phosphate (CrP) breakdown. The amount of CrP available and the amount of lactate that can accumulate in muscle and blood is limited (9, 10, 13, 19, 21). There must therefore be a maximum amount of anaerobic energy release during exercise. This maximum is called the anaerobic capacity. Whereas the metabolic pathways underlying anaerobic ATP-production have been well known for many years, it has been difficult to quantify the anaerobic energy release during exercise (7, 12, 14–16). We have found that the accumulated \( \text{O}_2 \) deficit is a useful measure of the anaerobic energy release for the whole body during running (17). The principle of the method is that at moderate intensities a linear relationship between exercise intensity and \( \text{O}_2 \) demand (estimated rate of energy release) is found. For supramaximal intensities the \( \text{O}_2 \) demand is estimated by an extrapolation of this relationship, and the rate of anaerobic contribution is taken as the \( \text{O}_2 \) demand less the \( \text{O}_2 \) uptake (that is the \( \text{O}_2 \) deficit) (17). In this study the method is applied to bicycling.

Some studies have suggested that the anaerobic capacity can be exhausted in \(<30 \text{ s} \) (3, 7, 24) or 40 s (16). If this is correct, the work done and the amount of energy released during exercise of 30 s or more may be modeled as the sum of two components, one aerobic component proportional to the duration plus a constant anaerobic addition. Moreover, measurements of the \( \text{O}_2 \) debt suggest that the amount of aerobic energy release equals the anaerobic energy release for exhausting exercise lasting 2 min (2), but the \( \text{O}_2 \) debt may overestimate the anaerobic component (7). We have therefore reexamined the relative importance of aerobic and anaerobic processes for exhausting exercise of different durations with the use of the accumulated \( \text{O}_2 \) deficit as a measure of the anaerobic component.

Subjects and Methods

Subjects. Seventeen healthy men aged 25 ± 1 (SE) yr (19–35 yr), 1.80 ± 0.02 m tall (1.65–1.97 m), weighing 75 ± 2 kg (62–95 kg), and with a maximal \( \text{O}_2 \) uptake of 41 ± 1 \( \mu \text{mol} \cdot \text{kg}^{-1} \cdot \text{s}^{-1} \) (32–46 \( \mu \text{mol} \cdot \text{kg}^{-1} \cdot \text{s}^{-1} \)) underwent a medical examination before they gave their written consent to participate in the experiments. The subjects were randomly assigned to one or more experimental groups (see below). The maximal \( \text{O}_2 \) uptake was 42 \( \mu \text{mol} \cdot \text{kg}^{-1} \cdot \text{s}^{-1} \) in the 30 s group compared with 39 \( \mu \text{mol} \cdot \text{kg}^{-1} \cdot \text{s}^{-1} \) in the 1- and 2-min groups \( (P = 0.05) \). Apart from this there were no significant differences in the above mentioned characteristics between the three groups of subjects. Most of the subjects were physically active students.
Power each subject could keep for ~30 s, 1 min, or 2-3 min, respectively, was established on separate tests. On separate days 10 subjects underwent additional experiments. The maximal O2 uptake was determined by the leveling-off criterion (8, 23). We measured the steady state O2 uptake (O2 demand) from 8 to 10 min exercise was a steady-state value equaling the O2 demand (total rate of energy release). We therefore conclude that the O2 demand increased linearly with power for all subjects in the examined range.

The subjects were randomly assigned to a 30-s group, a 1-min group, or a 2- to 3-min group, and the maximum power each subject could keep for ~30 s, 1 min, or 2-3 min, respectively, was established on separate tests. On separate days 10 subjects underwent additional experiments so that altogether the 17 subjects did 40 exhausting bouts of exercise.

Experiments. After a 10 min warm-up at 50% of the maximal O2 uptake and a 10 min rest, the subject exercised at the predetermined power to exhaustion. The O2 uptake was measured from the expired air collected in Douglas bags throughout the whole exercise period.

Analytic methods. Fractions of O2 and CO2 in the expired air were measured on a Scholander gas analyzer (22) or on an automatic system (CO2: CO2 analyzer, Simrad Optronics, Oslo, Norway; O2: S 3A/I AMETEK, Pittsburgh, PA), and the gas volumes were measured in a wet spirometer.

Calculations. The O2 demand of the exhausting bouts was estimated individually by extrapolating the linear relationship between the power and the O2 demand established on the pretests. The accumulated O2 uptake and the accumulated O2 demand were taken as the O2 demand integrated over the whole exercise period (17). The accumulated O2 deficit is the accumulated O2 deficit divided by the exercise duration. The work of the exercise was measured by multiplying the numbers of revolutions of the flywheel with the work done per revolution, and the power during exercise was calculated as the ratio between work and duration.

The accumulated O2 deficit is used as a measure of the total anaerobic energy release in the body. However, during exercise the blood gives off O2 to the exercising muscles. O2 is replenished in the lungs, and the measured O2 uptake is the rate of O2 replenishment in the blood. Because it takes ~10 s to pass blood from the muscles to the lungs even during exercise, there is a lag from the onset of O2 consumption in the muscles to the increase in the O2 uptake level through the mouth (14). During this interval O2 stored in the venous blood is used. This amount of O2 is ~0.25 mmol/kg body weight [a reduction of 5 mmol O2/l venous blood which is 5% of the body mass (1, 8, 12)]. This is an aerobic contribution to the energy release but is a part of the accumulated O2 deficit. Therefore, when stated explicitly in the text, the anaerobic energy release given in this paper is the accumulated O2 deficit less 0.25 mmol/kg, whereas the aerobic energy release is the accumulated O2 uptake plus 0.25 mmol/kg (Fig. 3).

Statistics. The data are given as individual results or means ± SE and range. Paired and two-sample t tests (1-sided or 2-sided whenever appropriate) were used for tests for statistically significant differences. Levels of statistical significance were calculated by Asyst (MacMillan Software, Rochester, NY). Linear regressions were calculated as the geometric mean (18), and the scatter around the regression line (Sxy) was used as a measure of the fit.

RESULTS

Power and work. All bouts of exercise were carried on until exhaustion. The power therefore had to be reduced from 9.1 ± 0.2 W/kg for the bouts lasting 30 s to 5.0 ± 0.1 W/kg for the 2- to 3-min bouts (Fig. 1A, Table 1). In spite of the reduction in power with increasing duration the work increased linearly at a rate of 3.95 ± 0.09 J·kg⁻¹·s⁻¹ (Fig. 1B).

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<th>TABLE 1. Work and accumulated O2 demand, uptake, and deficit, and their mean rates for exhausting bouts of different durations</th>
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<td>VO2max, % of VO2max</td>
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<td>Mean O2 uptake, μmol·kg⁻¹·s⁻¹</td>
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Values are means ± SE. VO2max, O2 uptake; VO2max, maximal O2 uptake.
Energy release. Because the work increased with duration, the total energy release during exercise, expressed as the accumulated O2 demand, increased linearly with the duration at a rate of 37.7 ± 1.2 μmol·kg⁻¹·s⁻¹ [92% of the mean maximal oxygen uptake (VO2 max), Fig. 2A].

The accumulated O2 uptake increased roughly linearly at a rate of 34.8 ± 1.0 μmol·kg⁻¹·s⁻¹ (85% of the mean VO2 max) after an estimated delay of 15 s (Fig. 2B).

The accumulated O2 deficit increased when the duration of the exhausting bouts was increased from 30 s to 1 min (P = 0.004), and a further small increase was found when the duration was increased from 1 min to >2 min (P = 0.008, Table 1). This means that both the accumulated O2 uptake and the accumulated O2 deficit increased with the duration. However, the relative contribution from the accumulated O2 deficit decreased from 70 ± 1% for 30 s duration to 35 ± 2% for 2-3 min duration (Fig. 3, Table 1); by interpolation the accumulated O2 uptake was estimated to equal the accumulated O2 deficit for exercise lasting 80 s.

Stored O2 used during exercise was subtracted from the accumulated O2 deficit and added to the accumulated O2 uptake to give better estimates of the aerobic and anaerobic energy releases during exercise (see METHODS). These corrections suggest that the aerobic and anaerobic energy releases were equal for 60 s duration (Fig. 3). The corrections also show that this amount of O2 is of significance for shortlasting bouts, while for bouts lasting several minutes the relative importance is quite small. This means that for exercise lasting only 30 s the aerobic contribution was 40% of the energy release,

![Graphs showing energy release during bicycling](https://example.com/graphs)

**Fig. 1.** Power (A) and work (B) vs. duration of the exhausting bout of exercise. The line in B was calculated by linear regression, and the hyperbolic fit in A was calculated by dividing the equation in B by the exercise duration.

**Fig. 2.** The accumulated O2 demand (A), accumulated O2 uptake (B), accumulated O2 deficit (C), O2 demand (D), O2 uptake (E), and O2 deficit (F) vs. duration. The two lines in A and B were calculated by linear regression. The hyperbolas in D and E were calculated as explained in the legend to Fig 1. The hyperbola in F is the difference between the two curves in D and E.
and for exercise lasting 2 min there is a 2:1 relationship in favor of aerobic processes.

Rates of energy release. Dividing the accumulated $O_2$ demand, the accumulated $O_2$ uptake, and the accumulated $O_2$ deficit by the duration of each bout shows that the $O_2$ demand and the mean $O_2$ deficit both decreased with increasing duration ($P < 0.001$, Fig. 2, bottom). The mean $O_2$ uptake rose with each increase in the duration ($P < 0.001$).

Another important result is that for the 30 s group the estimated rate of anaerobic energy release ($O_2$ deficit corrected for reduced $O_2$ stores) was 47.7 ± 1.2 μmol · kg$^{-1}$·s$^{-1}$ (117% of the $V_O_2$ max). Hence, the peak aerobic and anaerobic rates of energy release were comparable in size.

Curve fits. The work, the accumulated $O_2$ demand, and the accumulated $O_2$ uptake increased linearly with duration. The corresponding rates could accordingly be fitted to hyperbolic curves (Fig. 1A and Fig. 2, bottom). These curves fit the data very well with one exception. The accumulated $O_2$ uptake for the 30 s group was 0.18 ± 0.03 mmol/kg (21%) above the regression line ($P < 0.001$), and the mean $O_2$ uptake for this group was therefore >5 μmol·kg$^{-1}$·s$^{-1}$ above the hyperbola (Fig. 2E). This observation suggests that the $O_2$ uptake increases in proportion to the power at the onset of exercise.

DISCUSSION

This study quantifies the aerobic and anaerobic energy turnovers during short-lasting exhausting bicycling, and it was found that both aerobic and anaerobic energy releases are of great importance for exercise lasting from <30 s to >3 min. The amount of both aerobic and anaerobic energy releases increased with the duration, but in relative terms the importance of the anaerobic processes declined with duration. The contribution from the two processes was found to be equal for exhausting exercise lasting 60 s.

The accumulated $O_2$ deficit is a measure of anaerobic energy release. This study estimated the anaerobic energy release during intense exercise by the accumulated $O_2$ deficit determined by an extrapolation procedure. Energy is released anaerobically by lactate production and splitting of CrP. Our accumulated $O_2$ deficit compares with changes in muscle metabolite concentration provided the exercising muscle mass is 25% of the body weight (6a, 17; Tabata et al., unpublished data), and two former studies have reported that the muscle mass engaged during cycling is ~25% of the body weight (4, 20). The latter study measured the accumulated $O_2$ deficit and the muscle lactate and CrP concentrations during the first minutes of submaximal exercise where anaerobic processes contribute. Because the exercise intensity was below the maximal $O_2$ uptake, the $O_2$ demand could be measured as the steady state $O_2$ uptake, and no extrapolation was involved. The two measurements of the anaerobic energy release in that study are equal, provided the active muscle mass was 25% of the body weight. Finally, a recent study on intense one-leg cycling has shown that the accumulated $O_2$ deficit in the exercising leg energetically equaled the lactate production and CrP breakdown (21). We therefore conclude that the accumulated $O_2$ deficit can be used as a measure of the anaerobic energy release for bicycling.

We found a small increase in the accumulated $O_2$ deficit when the duration was increased from 1 min to >2 min. Hence, no leveling off with increasing duration was found. However, we have shown that for treadmill running a maximal value is found for exhaustive exercise lasting 2 min or more (17). A maximal lactate concentration is reached within 2 min exercise (Tabata et al., unpublished data). Further lactate production is therefore dependent on transfer of lactate to other compartments, but the lactate efflux is at most 10% of the lactate production even for exercise lasting several minutes (25). Therefore, there is no reason to assume a larger anaerobic energy release for longer durations. Thus, we conclude that the accumulated $O_2$ deficit found for 2–3 min exercise reflects the anaerobic capacity for bicycling.

Relative importance of aerobic and anaerobic processes. We found that for a typical subject the aerobic energy release during 30 s, 1 min, and 2 min of exhausting exercise provided ~40, 50, and 65% of the total energy release, respectively. This conflicts with the current idea that 2 min duration is needed for equal contribution from aerobic and anaerobic processes (2). Both studies have measured the accumulated $O_2$ uptake, and the cause of the difference is due to the different ways the anaerobic contribution was established. Åstrand and Rodahl (2) estimated the anaerobic energy release from Hermansen’s data on the increased $O_2$ uptake ($O_2$ debt) accumulated in the recovery after exhaustive running (7), and the anaerobic energy release was taken to be 5.5 mmol $O_2$/kg body weight (36 mmol ATP/kg) (2). During exhausting exercise there is an accumulation of 25–30 mmol lactate/kg wet weight muscle and a splitting of 15–20 mmol CrP + ATP/kg muscle. The total anaerobic ATP turnover is therefore around 60 mmol/kg muscle (9, 10, 13, 19, 21). The anaerobic energy release of 36 mmol ATP/kg body weight, as indicated by the $O_2$ debt method (2), should be compared with the anaerobic ATP.
turnover of 60 mmol/kg muscle. These values disagree because the exercising muscle mass would have to be 60% of the body weight [1.5 times the total muscle mass (4)] to match the estimate by the O2 debt approach. We therefore conclude that the O2 debt overestimates the anaerobic energy release at least twofold.

**Significance of aerobic energy release.** Our data show a large relative contribution from aerobic sources for all durations, and there are two reasons for this. First, the accumulated O2 uptake increased linearly at a rate of 85% of the maximal O2 uptake after an estimated delay of 15 s. Hence, there was a large O2 uptake in absolute terms for all durations. Second, former studies seem to overestimate the anaerobic and therefore also the total energy release considerably (2).

Our data showed that aerobic processes provide as much as 40% of the total energy release even for exercise lasting only 30 s. This conclusion is supported by a recent study where changes in muscle lactate and CrP concentrations were measured during 30 s of sprinting (6a). Assuming an active muscle mass of 25% of the body weight shows that anaerobic processes accounted for 60% of the total energy release in that study, leaving 40% for aerobic processes.

Finally, we emphasize that our estimated rate of anaerobic energy release (O2 deficit corrected for use of stored O2) during the 30 s bouts was only 17% more than the maximal O2 uptake. Hence, the peak aerobic and anaerobic rates in our study seem similar in size.

**Linear increase with duration.** It has been suggested that the amount of anaerobic energy released during exercise is independent of the exercise duration (7, 16, 24). If this is correct, the energy release during exercise could be viewed as the sum of an aerobic component proportional to the duration plus a constant anaerobic addition; the work and accumulated O2 demand should then increase linearly with the duration. However, our data on the accumulated O2 deficit were not constant but significantly less for exercise lasting <1 min, in conflict with the hypothesis above. It may therefore seem surprising that the work and the accumulated O2 demand did indeed increase linearly with the duration. The disproportionately large accumulated O2 uptake for the 30 s group compensates for the lower anaerobic contribution. Therefore, it is justifiable to conclude that for exhausting exercise lasting between 30 s and 3 min, the work done and the total energy release is the sum of a component proportional to time plus a constant addition. However, it is not correct to say that the constant part is only anaerobic and that the component proportional to duration is only aerobic.

Because the work and accumulated O2 demand increased linearly with duration, we conclude that the highest mean power and rate of energy release that can be maintained for exercise lasting from 30 s to 3 min decrease hyperbolically with duration.

**Tests of anaerobic capacity and power.** Our peak power and rate of energy release were found for 30 s exercise, and there was no clear leveling off. Other studies have found that the power (5, 6, 11) as well as the anaerobic ATP-regeneration (5, 11) are higher during the initial 5–10 s than the mean for the whole 30 s period. Hence, tests of peak power and rates should last for 10 s or less.

Our data showed a significant increase in the accumulated O2 deficit with duration, and it is not correct to say that the aerobic capacity test should last 2–3 min and be exhausting. This means that exercise tests lasting 20–45 s, as used in several studies of aerobic capacity (3, 7, 16, 24), do not exhaust the aerobic capacity.

The Wingate test is a 30-s all-out test where the work done is used as a measure of the anaerobic capacity. Our measurements showed a significant aerobic energy release even during 30 s exercise. Because a 30-s test does not exhaust the anaerobic capacity, and because the Wingate test does not consider the significant aerobic contribution (3), the Wingate test may not be a proper anaerobic capacity test.

**Bicycling vs. treadmill running.** We have found that the accumulated O2 deficit for running at the 10% inclined treadmill was 1.7 mmol/kg and 3.2 mmol/kg for 30 s and 2 min exhausting exercise. The values for 30 s exercise are similar for running and bicycling, whereas the values for 2 min running are 30% larger than for cycling. The anaerobic energy release depends mainly on the muscle mass engaged and the extent to which lactate can accumulate in the muscles (17, 21). The observed difference between treadmill and bicycle exercise may reflect different use of the leg muscles. A further discussion of this matter is deferred to a separate study.

To sum up, the accumulated O2 deficit is a valid measure of the anaerobic energy release during intense bicycling. Aerobic and anaerobic processes contribute equally for exercise lasting 1 min.

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AEROBIC AND ANAEROBIC ENERGY RELEASE DURING BICYCLING


