

# Fat Oxidation Rates Are Higher During Running Compared With Cycling Over a Wide Range of Intensities

Juul Achten, Michelle C. Venables, and Asker E. Jeukendrup

The aim of the present study was to compare the intensity that elicits maximal fat oxidation ( $\text{Fat}_{\text{max}}$ ) determined using a cycle-ergometer and a treadmill-based protocol. Twelve moderately trained male subjects ( $66.9 \pm 1.8 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) performed 2 graded exercise tests to exhaustion. One test was performed on a cycle ergometer while 1 test was performed on a motorized treadmill; stage duration during both trials was 3 minutes. Gas exchange measurements and heart rate (HR) recordings were performed throughout exercise. Fat oxidation rates were calculated using stoichiometric equations. Maximal fat oxidation rates were significantly higher during running compared with cycling ( $0.65 \pm 0.05 \text{ v } 0.47 \pm 0.05 \text{ g} \cdot \text{min}^{-1}$ ). However, the intensity, which elicited maximal fat oxidation, was not significantly different between the cycle ergometer and treadmill test ( $62.1 \pm 3.1 \text{ v } 59.2 \pm 2.8\% \text{ Vo}_{2\text{max}}$ , respectively). Fat oxidation rates were significantly higher during the treadmill test compared with the cycle ergometer test from 55 to 80%  $\text{Vo}_{2\text{max}}$ . Maximal oxygen uptake and maximal HR were significantly higher during the treadmill test. It was concluded that fat oxidation rates were higher during walking compared with cycling. Maximal fat oxidation was 28% higher when walking compared with cycling, but the intensity, which elicits maximal fat oxidation, is not different between these 2 exercise modes.

© 2003 Elsevier Inc. All rights reserved.

**I**N STUDIES investigating the physiologic effects of endurance exercise, running and cycling have been the most commonly used exercise modes. There are, however, a number of different physiologic, metabolic, and ergogenic responses to cycling and running. For instance, it has been suggested that substrate oxidation during cycling and running exercise at the same relative intensity is different. The main body of evidence for this statement arises from studies investigating the effects of carbohydrate (CHO) feedings during exercise on glycogen utilization. While no reduction in muscle glycogenolysis was found during constant-load cycling with CHO feedings,<sup>1-4</sup> Tsintzas et al<sup>5</sup> reported a glycogen-sparing effect of CHO feedings during constant-load running. It was suggested by Tsintzas and Williams<sup>6</sup> that differences in the glycemic and insulinemic responses to CHO ingestion could explain some of the observed differences during running and cycling.

In fasted conditions, there also appear to be differences in substrate utilization between running and cycling at the same relative exercise intensity. In a study by Thomas et al,<sup>7</sup> 5 subjects, who were familiar to both cycling and running exercise, performed two 1-hour exercise bouts at 57%  $\text{Vo}_{2\text{max}}$ , 1 on a cycle ergometer and 1 on a motorized treadmill. After 10 minutes of exercise, the respiratory exchange ratio (RER) was significantly lower during running than during cycling (0.90 v 0.93, respectively) and the difference remained for the rest of the exercise bouts. However, these results have not been consistently reproduced. Houmard et al<sup>8</sup> reported similar RER values during running and cycling exercise at the same relative intensity.

It has been shown that exercise intensity is one of the main factors that influence substrate utilization during exercise. The relative contribution of CHO increases and the relative contribution of fat to energy expenditure decreases with increasing intensity. In absolute terms, CHO oxidation shows a gradual increase with increasing exercise intensity, while it has been shown that fat oxidation increases from low to moderate intensities and then decreases from moderate to high exercise intensities.<sup>9</sup> The exercise intensity at which the transition from increasing to decreasing fat oxidation rates occurs has recently been determined in a large group of moderately trained men.

Achten et al<sup>10</sup> demonstrated that during a graded exercise test fat oxidation increased until an intensity of  $64\% \pm 4\% \text{ Vo}_{2\text{max}}$ , after which a rapid decrease was seen. The protocol used in that study was cycle-ergometer-based and because substrate utilization might be affected by exercise mode, it is possible that the results would be different when a treadmill-based protocol is used.

There are many ways to express exercise intensity, and it is therefore not surprising that there has been debate about the best way to compare different exercise modalities. To standardize the exercise intensity, some have argued that exercise should be compared at the same percentage of  $\text{Vo}_{2\text{max}}$ ; others have argued that it should be related to lactate threshold. The best comparison can, however, be obtained if substrate utilization is measured over a wide range of intensities. The aim of the present study was to compare the intensity, which elicits maximal fat oxidation, determined using a cycle-ergometer and a treadmill-based protocol and to compare fat oxidation over a wide range of intensities in running and cycling.

## METHODS

### Subjects

Twelve healthy, moderately trained men (age,  $22.9 \pm 1.9$  years; body mass,  $74.3 \pm 1.3$  kg;  $\text{Vo}_{2\text{max}} 66.9 \pm 1.8 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) participated in this study, which was approved by the Ethics Committee of the School of Sport and Exercise Sciences of The University of Birmingham, UK. Each volunteer gave his written informed consent after explanations of the experimental procedures, possible risks, and

---

*From the Human Performance Laboratory, School of Sport and Exercise Sciences, University of Birmingham, Birmingham, United Kingdom.*

*Submitted August 15, 2002; accepted January 31, 2003.*

*Supported by a research grant from Polar Electro Oy, Finland.*

*Address reprint requests to Asker Jeukendrup, PhD, School of Sport and Exercise Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, United Kingdom.*

© 2003 Elsevier Inc. All rights reserved.

0026-0495/03/5206-0016\$30.00/0

doi:10.1016/S0026-0495(03)00068-4

benefits. The subjects were all club/county standard endurance cyclists with a training background of at least 3 years.

### General Design

Twelve subjects performed a graded exercise test to exhaustion on a cycle ergometer and on a treadmill; the results of this test were used to measure fat oxidation over a wide range of intensities for each subject during 2 different modes of exercise. The data were then used to determine whether the maximal rate of fat oxidation and the intensity at which it occurs were different when walking or cycling. The order of the trials was assigned to the subjects in a randomized cross-over design, and the tests were performed 5 to 7 days apart.

### Experimental Design

Before the start of the experiments, the subjects were familiarized with the equipment and the procedures. Experiments were always performed in the morning (start of exercise between 8 and 10 AM) and at the same time to avoid circadian variance. Subjects were asked to fill in a 1-day food diary on the day before their first test, and they were asked to repeat this diet before the second test. Furthermore, subjects were asked to avoid strenuous exercise the day before the tests; the time between the last exercise bout and the test was standardized. Subjects reported to the laboratory after a 10- to 12-hour overnight fast, and body mass and height were determined. On the first visit, body fat was estimated from skin fold thickness measurements at 4 sites according to the methods of Durnin and Womersley.<sup>11</sup> A teflon catheter (Quickcath; Baxter, Norfolk, UK) was introduced into an antecubital arm vein and connected to a 3-way stopcock (Sims Portex, Kent, UK) and a lectrocath extension line and an initial blood sample was collected. The catheter was maintained patent with isotonic saline (Baxter).

On the cycle ergometer (Lode Excalibur, Groningen, The Netherlands), subjects started cycling at 95 W, and the work rate was increased by 35 W every 3 minutes until exhaustion as described in detail by Achten et al.<sup>10</sup> The cycle ergometer protocol used in the present study has been validated by comparing the fat oxidation rates during each stage of the graded exercise test with fat oxidation rates determined when subjects cycled on each of the intensities on a separate day for a prolonged period of time.<sup>10</sup> It was concluded that the stage duration of 3 minutes, as well as the incremental nature of the test, did not affect the maximal rate of fat oxidation or the determination of the intensity at which this occurred.<sup>10</sup> On the treadmill, subjects walked at  $5.5 \text{ km} \cdot \text{h}^{-1}$  and  $6.5 \text{ km} \cdot \text{h}^{-1}$  at a gradient of 1% for 3 minutes to accustom their legs to the fairly brisk walking speed of the test. The test was then started at  $7.5 \text{ km} \cdot \text{h}^{-1}$  at 1% and the gradient of the treadmill was increased with 2% until an RER of 1.0 was reached. The subjects then started running at a speed of  $10 \text{ km} \cdot \text{h}^{-1}$  at 10% and speed was further increased by  $2 \text{ km} \cdot \text{h}^{-1}$  every 3 minutes until exhaustion. The aim of this second part of the test was to obtain a measure of  $\text{Vo}_2\text{max}$  in a relatively short period of time. For the determination of the fat oxidation, only the values during the gradient-increase phase of the protocol were used.

During the last 30 seconds of each exercise intensity, a blood sample ( $\sim 1 \text{ mL}$ ) was collected. Heart rate (HR) was recorded continuously during the test using a radio telemetry HR monitor (Polar Vantage NV; Polar Electro Oy, Kempele, Finland). Breath-by-breath measurements were performed throughout exercise using an Oxycon Alpha (Jaeger, Wuerzburg, Germany) gas analysis system. The volume and gas analyzers of the system were calibrated using a 3-L calibration pump and calibration gas (15.12%O<sub>2</sub>; 5.10%CO<sub>2</sub>), respectively. Maximal work rate reached during the cycle-ergometer test was calculated from the last completed work rate, plus the fraction of time spent in the final noncompleted work rate multiplied by the work rate increment. Oxygen uptake was considered to be maximal when at least 2 of the following three criteria were met: (1) a leveling off of  $\text{Vo}_2$  with increasing work

rate (increase of no more than  $2 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ), (2) a HR within 10 beats  $\cdot \text{min}^{-1}$  of the predicted maximum (220 beats  $\cdot \text{min}^{-1}$  minus age), (3) a RER  $>1.05$ .  $\text{Vo}_2\text{max}$  was calculated as the average oxygen uptake over the last 60 seconds of the test.

### Indirect Calorimetry and Calculations

Average values for  $\text{Vo}_2$  and  $\text{VCO}_2$  were calculated over the last 2 minutes of every stage of both tests. Fat and carbohydrate oxidation and energy expenditure were calculated using stoichiometric equations<sup>12</sup> and appropriate energy equivalents, with the assumption that the urinary nitrogen excretion rate was negligible.

For each individual, the results of the graded exercise test were used to construct a curve of fat oxidation rate versus exercise intensity, expressed as  $\text{Vo}_2$  and HR. The curve was used to determine the following variables.  $\text{Fat}_{\text{max}}$ : the exercise intensity at which the highest rate of fat oxidation was observed.  $\text{Fat}_{\text{min}}$ : the exercise intensity at which fat oxidation becomes negligible (ie RER  $\geq 1.0$ ).

If the economy of the subjects during a stage of the  $\text{Fat}_{\text{max}}$  test was below an arbitrary  $3.35 \text{ kJ} \cdot \text{L}^{-1}$ , the fat oxidation rates at that stage were not taken into consideration for the  $\text{Fat}_{\text{max}}$  determination.<sup>10</sup>

To quantify  $\text{Fat}_{\text{max}}$ , the results of the graded exercise tests were used to compose an average fat oxidation curve. The specific points on the graph were determined for each individual. In addition to the exercise intensity at  $\text{Fat}_{\text{max}}$  and  $\text{Fat}_{\text{min}}$ , exercise intensities for fat oxidation rates 5%, 10%, and 20% below the peak rate were determined for each subject.

### Lactate Analysis and Threshold Determination

Blood samples were collected in prechilled tubes with  $100 \mu\text{L}$  0.2 mol/L EDTA (Sigma, Dorset, UK). The samples were centrifuged immediately at  $4^\circ\text{C}$  for 10 minutes at 3,500 rpm and aliquots of plasma were frozen at  $-70^\circ\text{C}$ . Plasma lactate concentration was determined enzymatically (Lactate reagent, Sigma Diagnostics) on a semiautomatic analyzer (Cobas Bio, Roche, Switzerland). Plasma lactate concentration was plotted against exercise intensity to determine the intensity at which the first increase in lactate concentration above baseline occurred (as described by Hagberg and Coyle<sup>13</sup>). This intensity was individually determined. To construct an average lactate curve for the entire group, the intensity at lactate concentrations 0.5, 1.0, 2.0, and  $3.0 \text{ mmol} \cdot \text{L}^{-1}$  above baseline concentration and at maximal performance were determined for each individual.

### Statistical Analysis

Experimental data are presented as means  $\pm$  SEM unless stated otherwise. Significant differences in  $\text{Vo}_2\text{max}$ ,  $\text{Fat}_{\text{max}}$ ,  $\text{Fat}_{\text{min}}$ , and the fat oxidation rate at  $\text{Fat}_{\text{max}}$  between the walking and cycling test were identified using a student *t* test for paired observations. For all statistical analyses, significance was accepted at  $P < .05$ .

## RESULTS

Average oxygen uptake, RER, and HR for each stage of the 2 graded exercise protocols during which the RER was below 1.0 is displayed in Table 1. All 3 variables were equal during the first stage of the 2 trials ( $1.94 \pm 0.04$  v  $1.96 \pm 0.04 \text{ L} \cdot \text{min}^{-1}$ ;  $0.84 \pm 0.02$  v  $0.84 \pm 0.01$ ;  $108 \pm 3$  v  $105 \pm 3 \text{ beats} \cdot \text{min}^{-1}$  for cycle ergometer v treadmill, respectively). The average increase in oxygen uptake with each increment during the cycle-ergometer test was  $0.39 \pm 0.02 \text{ L} \cdot \text{min}^{-1}$ , while it was  $0.31 \pm 0.02 \text{ L} \cdot \text{min}^{-1}$  during the treadmill test. HR did increase with  $11 \pm 1$  beats/min during every stage of both tests. The  $\text{V}_E$  versus  $\text{Vo}_2$  curves were similar during both trials (data not shown).  $\text{Vo}_2\text{max}$  and HR were significantly higher during

Table 1. Oxygen Uptake, RER, and HR During Stages of the Cycle-Ergometer and Treadmill Tests

Cycle-Ergometer Protocol	95	130	165	200	235	270	305	
$\dot{V}O_2$	1.94 ± 0.04	2.30 ± 0.06	2.69 ± 0.05	3.04 ± 0.05	3.48 ± 0.08	3.91 ± 0.07	4.28 ± 0.09	
RER	0.84 ± 0.02	0.88 ± 0.01	0.90 ± 0.02	0.93 ± 0.02	0.95 ± 0.02	0.97 ± 0.01	1.01 ± 0.01	
HR	108 ± 3	118 ± 2	128 ± 2	137 ± 2	153 ± 2	163 ± 2	172 ± 3	
Treadmill Protocol	1%	3%	5%	7%	9%	11%	13%	15%
$\dot{V}O_2$	1.96 ± 0.04	2.29 ± 0.05	2.49 ± 0.06	2.83 ± 0.07	3.14 ± 0.07	3.49 ± 0.07	3.85 ± 0.09	4.11 ± 0.10
RER	0.84 ± 0.01	0.87 ± 0.01	0.87 ± 0.01	0.88 ± 0.01	0.89 ± 0.01	0.91 ± 0.01	0.93 ± 0.01	0.97 ± 0.01
HR	105 ± 3	116 ± 3	125 ± 3	137 ± 4	148 ± 5	159 ± 5	170 ± 6	174 ± 5

NOTE. Values are mean ± SEM.

Abbreviations:  $\dot{V}O_2$ , oxygen uptake in  $L \cdot min^{-1}$ ; RER, respiratory exchange ratio; HR, heart rate in beats  $\cdot min^{-1}$ ; n = 12.

the treadmill test compared with the cycle ergometer test ( $65.9 \pm 1.6$  v  $64.1 \pm 1.6$   $mL \cdot min^{-1} \cdot kg^{-1}$  and  $186 \pm 3$  v  $181 \pm 3$  beats  $\cdot min^{-1}$ , respectively).

Figure 1 shows the relationship between fat oxidation rates and exercise intensity, expressed as a percentage of  $\dot{V}O_{2max}$ . To construct the curves, the exercise intensities at which the subjects had maximal fat oxidation rates and where the subjects had rates, which were 95%, 90%, and 80% of the peak rate, were determined individually. The 2 curves represent the cycle-ergometer and treadmill test. During the cycle-ergometer test, the maximal fat oxidation rate was  $0.47 \pm 0.05$   $g \cdot min^{-1}$ , which was found at  $62.1\% \pm 3.1\% \dot{V}O_{2max}$ . During the treadmill trial,  $\dot{V}O_{2max}$  was  $59.2\% \pm 2.8\% \dot{V}O_{2max}$  and the maximal rate  $0.65 \pm 0.05$   $g \cdot min^{-1}$ . The maximal fat oxidation rate was significantly lower between the 2 modes of exercise, but the intensity at which it occurred was not different.

Because the graph in Fig 1, does not allow for direct comparison in fat oxidation rates between the 2 protocols at the same absolute exercise intensity ( $\dot{V}O_2$ ), a second graph (Fig 2) was constructed, which presents the fat oxidation rates during both trials at absolute oxygen uptakes calculated at regular intervals. From  $2.75 L \cdot min^{-1}$  onwards, fat oxidation rates were significantly higher during the treadmill test compared with the cycle ergometer test.

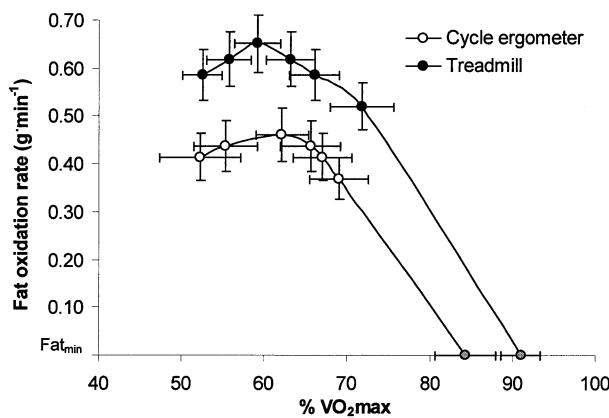


Fig 1. Fat oxidation v exercise intensity, expressed as a percentage of maximal oxygen uptake ( $\dot{V}O_{2max}$ ) during cycle-ergometer-based and treadmill-based protocol. Values are mean ± SEM; n = 12.

Due to technical problems, blood samples were collected from only 6 subjects during the treadmill tests. The graphs in Fig 3A and 3B, therefore only display the plasma lactate concentration and fat oxidation rates of these 6 subjects. During the cycle ergometer test, the onset of the decrease in fat oxidation and the initial increase in plasma lactate concentration occurred at the same intensity (Fig 3A). The lactate concentration then increased gradually till  $\sim 75\% \dot{V}O_{2max}$ , after which a steep increase was observed. The maximal lactate concentration at the end of the cycle-ergometer test was  $12.3 \pm 0.8$   $mmol \cdot L^{-1}$ . During the treadmill test, the lactate concentration increased gradually during the entire test. The maximal lactate concentration reached during the treadmill test was  $8.2 \pm 0.8$   $mmol \cdot L^{-1}$ . The lactate concentrations at the submaximal intensities were not significantly different between the 2 exercise modes; the maximal concentration was however significantly higher at the end of the cycle-ergometer test compared with the treadmill test.

## DISCUSSION

The main finding of the present study was that although the maximal rate of fat oxidation was significantly higher when determined using a treadmill-based compared with a cycling-

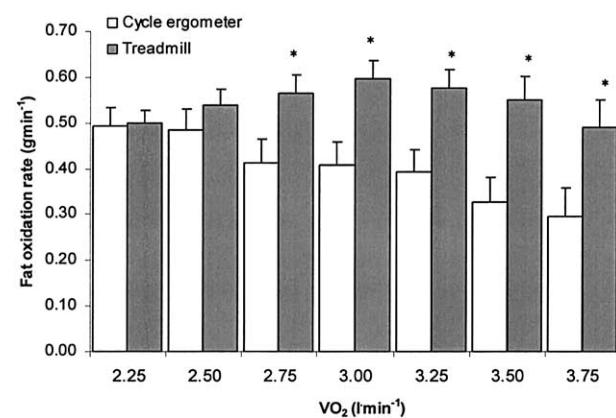
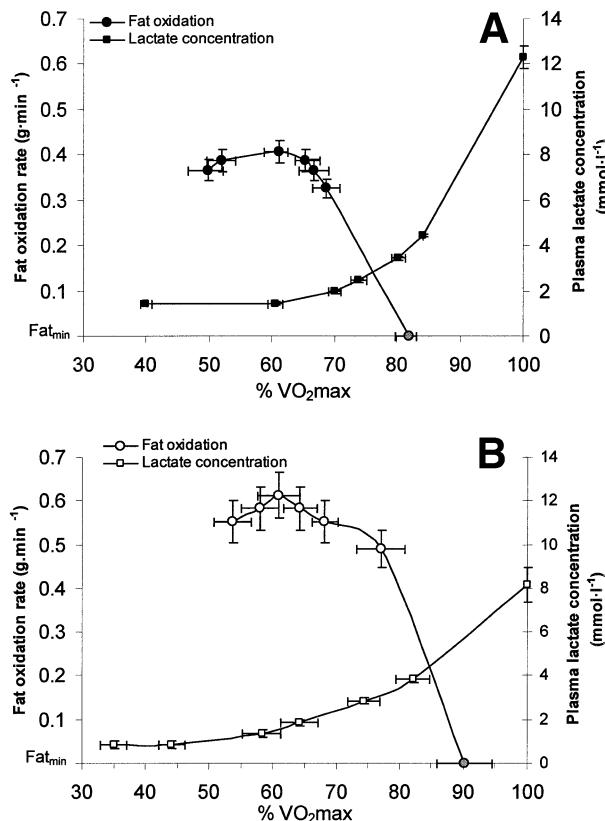


Fig 2. Average fat oxidation rates during cycle-ergometer and treadmill test at intensities between 50% and 80% of the maximal oxygen uptake ( $\dot{V}O_{2max}$ ). Values are mean ± SEM; n = 12; \*significantly different from cycle-ergometer test.



**Fig 3.** (A) Fat oxidation rates and plasma lactate concentrations during graded exercise test on cycle-ergometer. Values are mean  $\pm$  SEM;  $n = 6$ . (B) Fat oxidation rates and plasma lactate concentrations during graded exercise test on treadmill. Values are mean  $\pm$  SEM;  $n = 6$ .

based protocol, the exercise mode did not affect the intensity at which it occurred. A second important finding was that fat oxidation rates are higher during treadmill exercise compared with cycle ergometer exercise over a wide range of intensities.

Exercise intensity is one of the main factors affecting fat oxidation rates. The majority of studies investigating the effects of exercise intensity on fat metabolism have been performed using cycle-ergometer-based protocols. The intensity, which elicited maximal fat oxidation rates during the cycle-ergometer protocol in the present study, was  $61.2 \pm 3.1\%$   $\text{Vo}_{2\text{max}}$ , which is similar to  $\text{Fat}_{\text{max}}$  determined in an earlier study using cycle-ergometer-based protocols.<sup>10</sup> On the treadmill, maximal fat oxidation was reached at  $59.2\% \pm 2.8\%$   $\text{Vo}_{2\text{max}}$ . As far as we are aware, only 1 study<sup>14</sup> investigated fat oxidation rates during different exercise intensities on a treadmill. Unfortunately, in this study, subjects only performed exercise on 2 different intensities, thereby making it impossible to determine  $\text{Fat}_{\text{max}}$ .<sup>14</sup>

The intensity, which elicited maximal fat oxidation rates, was not different between the 2 different exercise modes used in the present study. Most studies that have made direct comparisons between substrate oxidation rates during running and cycling protocols have used 1 exercise intensity, thereby not allowing any comparison of changes, which occur with increasing exercise intensity.<sup>8,15-17</sup> However, in a study by Snyder et

al,<sup>17</sup> 2 male and 9 female subjects performed four 4-minute exercise bouts on a cycle ergometer at different intensities and five 4-minute exercise bouts at different intensities on a motorized treadmill. Regrettably, the data of this study is presented in a graph in which a regression line of  $\text{Vo}_2$  against RER is given. Without individual data points, it is difficult to calculate fat oxidation rates and therefore to determine  $\text{Fat}_{\text{max}}$ .

The maximal rate of fat oxidation was significantly higher during uphill walking compared with cycling in the present study ( $0.65 \pm 0.05$  v  $0.47 \pm 0.05$   $\text{g} \cdot \text{min}^{-1}$ ). In addition, it was found that not only the maximal rate of fat oxidation was different; it appeared that the rates were significantly different over a wide range of intensities. This is in agreement with the results of the study by Snyder et al,<sup>17</sup> who showed that over a range of intensities (30% to 90%  $\text{Vo}_{2\text{max}}$ ), fat oxidation rates were higher on the treadmill compared with the cycle-ergometer when measured. Furthermore, in studies that only compared fat oxidation rates on 1 intensity,<sup>8,15-18</sup> fat oxidation rates were significantly higher during running compared with cycling. Thomas et al<sup>7</sup> measured fat oxidation rates during steady state exercise at 57%  $\text{Vo}_{2\text{max}}$  on a cycle-ergometer and a motorized treadmill. After 10 minutes of exercise, fat oxidation rates were 21% higher during the treadmill exercise compared with cycling exercise.<sup>7</sup>

It has been suggested that the observed differences in fat oxidation rates in these studies are caused by the comparison of 2 different exercise intensities rather than 2 different exercise modes. Traditionally, it has been accepted that  $\text{Vo}_{2\text{max}}$  values for cycling are 7% to 10% lower than for running.<sup>19,20</sup> To be able to compare substrate oxidation at similar intensities in running and cycling, previous studies were often performed at a percentage of the mode-specific  $\text{Vo}_{2\text{max}}$ .<sup>8,15-17,21</sup> As a consequence of the difference in maximal oxygen uptake, exercise was performed at a higher absolute  $\text{Vo}_2$  and HR while running than while cycling. Houldard et al<sup>8</sup> studied 10 moderately-trained triathletes during 1 hour of running and 1 hour of cycling at 75% of their mode-specific  $\text{Vo}_{2\text{max}}$ . During the running trial, subjects'  $\text{Vo}_2$  was  $46.7 \text{ mL} \cdot \text{kg}^{-1} \text{ min}^{-1}$ , while it was  $41.3 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$  during the cycling trial. The RER was 0.93 during both trials, giving fat oxidation rates of 0.40 and  $0.35 \text{ g} \cdot \text{min}^{-1}$  for the running and cycling trial, respectively. Although in absolute terms the fat oxidation rates appear to be higher during running compared with cycling, the contribution of fat oxidation to total energy expenditure was similar (~21%) for both modes.

Even though these results suggest that part of the difference between running and cycling is caused by differences in absolute exercise intensity, there are an equal number of studies showing that apart from differences in  $\text{Vo}_2$ , RER is also significantly different between exercise modes.<sup>15-17</sup> In a study by Nieman et al,<sup>15</sup> subjects had an RER of 0.85 during a treadmill exercise bout and an RER of 0.87 during cycling exercise. Together with the slightly higher rates of oxygen uptake in running, this lead to 16% higher fat oxidation rates during running. So it is likely that the differences found in fat oxidation rates in previous studies are not just the result of different absolute exercise intensities.

In an attempt to compare substrate utilization at a normalized exercise intensity, subjects in a study by Arkinstall et al<sup>18</sup>

performed 60 minutes of running and cycling exercise at their respective lactate thresholds. Throughout exercise, no differences were detected in RER or fat oxidation rates between the cycling and running trials. These results suggest that during submaximal exercise at lactate threshold, substrate oxidation is not influenced by exercise mode. These results are however not in agreement with the results of the present study. At the lactate threshold, determined using the same procedure as in the study by Arkinstall et al (intensity at  $1 \text{ mmol} \cdot \text{L}^{-1}$  above baseline plasma lactate concentration<sup>13</sup>), fat oxidation rates were  $0.28 \pm 0.10 \text{ g} \cdot \text{min}^{-1}$  during cycling and  $0.54 \pm 0.04 \text{ g} \cdot \text{min}^{-1}$  during running. In addition, plasma lactate concentrations during the present study were similar over a wide range of submaximal intensities in the 2 different trials (Fig 3A and 3B); while the fat oxidation rates were significantly different, so there appeared to be no relationship between the plasma lactate concentration and fat oxidation. Therefore, it appears that the studies available at the moment cannot provide a clear picture of possible differences in substrate utilization during cycle-ergometer compared with treadmill exercise. The results of the present study however suggest that over a wide range of intensities, fat oxidation rates appear to be higher during treadmill than during cycling exercise.

Several possible reasons have been suggested for the higher rates of fat oxidation during running than cycling. It is generally believed that during cycling a smaller muscle mass is being recruited than during cycling.<sup>20</sup> Because it has been shown that the release of catecholamines during exercise is proportional to the exercising muscle mass,<sup>22</sup> it is likely that catecholamine concentrations are higher during running compared with cycling. Catecholamines are potent activators of lipolysis during exercise, and it would be logical to assume that catecholamine stimulation of lipolysis was higher during running than cycling. Only 1 study<sup>16</sup> determined catecholamine levels during running and cycling in the same subjects. In this study, 10 moderately trained subjects cycled and ran for 2.5 hours at 75% of their mode-specific  $\text{Vo}_{2\text{max}}$ . Catecholamine concentration was determined on cessation of exercise, and no differences were found in epinephrine or norepinephrine concentration between the 2 exercise modalities.<sup>16</sup> Therefore, the results of this study do not support the suggestion that higher fat oxidation rates during running are the result of catecholamine-induced increased lipolytic rates. However, the results in the study by Nieman et al<sup>16</sup> are gathered after 2.5 hours of steady state exercise; this might not be representative of the present study in which subjects performed graded exercise for 25 to 30 minutes.

A second hypothesis is also related to the muscle mass recruited during exercise. During cycling, the work rate will be divided over a smaller number of muscle fibers than during running. The metabolic stress per muscle fiber may be greater as a greater amount of energy per fiber is required. It is possible that this increased stress level and energy requirement per fiber can only be met by an increased CHO oxidation. Deschenes et al<sup>23</sup> have recently investigated the physiologic effect to different muscle recruitment patterns. Ten men cycled for 30 minutes at 55%  $\text{Vo}_{2\text{max}}$  while maintaining a cadence of either 40 or 80 rpm. Electromyograph (EMG) data showed that muscle recruitment was significantly greater during the 40-rpm trial compared with the 80-rpm trial, indicating more intense muscle contraction at the lower cadence. It was found that HR and cortisol were significantly higher when cycling at the low cadence, however, no differences were found in RER. Although these results suggest that substrate utilization is not affected by muscle recruitment pattern, it should be kept in mind that the differences between running and cycling are far greater than the differences observed between cycling at 2 different pedalling rates.

In a previous study, we investigated the reproducibility of the estimation of  $\text{Fat}_{\text{max}}$  using a cycling-based protocol.<sup>24</sup> In this study, it was found that there was a fairly large day-to-day variability in this specific intensity. It was concluded that a difference of 10 beats  $\cdot \text{min}^{-1}$  between 2 conditions would be necessary to obtain significantly different results. It is possible that if the day-to-day variability of the estimation of  $\text{Fat}_{\text{max}}$  was smaller, differences between the cycling- and running-based protocol were found. However, the absolute HR and oxygen uptake at  $\text{Fat}_{\text{max}}$  in the present study were very similar between exercise modalities ( $130 \pm 5$  v  $135 \pm 6$  beats  $\cdot \text{min}^{-1}$  and  $2.93 \pm 0.14$  v  $2.96 \pm 0.11 \text{ L} \cdot \text{min}^{-1}$  for cycle ergometer and treadmill exercise, respectively), suggesting that it is not likely that there are any differences.

In summary, the maximal rate of fat oxidation, as well as fat oxidation rates over a wide range of intensity are significantly higher during treadmill exercise compared with cycle-ergometer exercise. However, there appears to be no difference between the intensity, which elicited maximal fat oxidation rates ( $\text{Fat}_{\text{max}}$ ) determined after an overnight fast between the 2 exercise modalities. The exact mechanisms behind the differences in substrate metabolism between treadmill and cycling exercise remain to be determined.

#### REFERENCES

1. Bosch AN, Dennis SC, Noakes TD: Influence of carbohydrate loading on fuel substrate turnover and oxidation during prolonged exercise. *J Appl Physiol* 74:1921-1927, 1993
2. Coyle EF, Coggan AR, Hemmert MK, et al: Muscle glycogen utilization during prolonged strenuous exercise when fed carbohydrate. *J Appl Physiol* 61:165-172, 1986
3. Fielding R, Costill D, Fink D, et al: Effect of carbohydrate feeding frequencies and dosage on muscle glycogen use during exercise. *Med Sci Sports Exerc* 17:472-476, 1985
4. Flynn M, Costill D, Hawley J: Influence of selected carbohydrate drinks on cycling performance and glycogen use. *Med Sci Sports Exerc* 19:37-40, 1987
5. Tsintzas K, Williams C, Boobis L, et al: Carbohydrate ingestion and glycogen utilisation in different muscle fibers in man. *J Physiol* 81:801-809, 1995
6. Tsintzas K, Williams C: Human muscle glycogen metabolism during exercise. Effect of carbohydrate supplementation. *Sports Med* 25:7-23, 1998
7. Thomas TR, Feiok CW, Araujo J: Metabolic responses associated with four modes of prolonged exercise. *J Sports Med Phys Fitness* 29:77-82, 1989
8. Houshard JA, Egan PC, Johns RA, et al: Gastric emptying during 1 h of cycling and running at 75%  $\text{Vo}_{2\text{max}}$ . *Med Sci Sports Exerc* 23:320-325, 1991

9. Romijn J, Coyle E, Sidossis L, et al: Regulation of endogenous fat and carbohydrate metabolism in relation to exercise intensity and duration. *Am J Physiol* 265:E380-E391, 1993
10. Achten J, Gleeson M, Jeukendrup AE: Determination of the exercise intensity that elicits maximal fat oxidation. *Med Sci Sports Exerc* 34:92-97, 2002
11. Durnin JV, Womersley J: Body fat assessed from total body density and its estimation from skinfold thickness: Measurements on 481 men and women aged from 16 to 72 years. *Br J Nutr* 32:77-97, 1974
12. Frayn KN: Calculations of substrate oxidation rates in vivo from gaseous exchange. *J Appl Physiol* 55:628-634, 1983
13. Hagberg JM, Coyle EF: Physiological determinants of endurance performance as studied in competitive racewalkers. *Med Sci Sports Exerc* 15:287-289, 1983
14. Broeder CE, Brenner M, Hofman Z, et al: The metabolic consequences of low and moderate intensity exercise with or without feeding in lean and borderline obese males. *Int J Obes* 15:95-104, 1991
15. Nieman DC, Nehls-Cannarella SL, Fagoaga OR, et al: Influence of mode and carbohydrate on the cytokine response to heavy exertion. *Med Sci Sports Exerc* 30:671-678, 1998
16. Nieman DC, Nehls-Cannarella SL, Fagoaga OR, et al: Effects of mode and carbohydrate on the granulocyte and monocyte response to intensive, prolonged exercise. *J Appl Physiol* 84:1252-1259, 1998
17. Snyder AC, O'Hagan KP, Clifford PS, et al: Exercise responses to in-line skating: Comparisons to running and cycling. *Int J Sports Med* 14:38-42, 1993
18. Arkinstall MJ, Bruce CR, Nikolopoulos V, et al: Effect of carbohydrate ingestion on metabolism during running and cycling. *J Appl Physiol* 91:2125-2134, 2001
19. Koyal SN, Whipp BJ, Huntsman D, et al: Ventilatory responses to metabolic acidosis of treadmill and cycle ergometry. *J Appl Physiol* 40:864-867, 1976
20. Hermansen L, Saltin B: Oxygen uptake during maximal bicycle and treadmill exercise. *J Appl Physiol* 26:31-37, 1969
21. Pascoe DD, Costill DL, Roberts RA, et al: Effects of exercise mode on muscle glycogen restorage during repeated days of exercise. *Med Sci Sport Exerc* 22:593-598, 1990
22. Davies CT, Few J, Foster C, et al: Plasma catecholamine concentration during dynamic exercise involving different muscle groups. *Eur J Appl Physiol* 32:195-206, 1974
23. Deschenes MR, Kraemer WJ, McCoy RW, et al: Muscle recruitment patterns regulate physiological responses during exercise of the same intensity. *Am J Physiol* 279:R2229-R2236, 2000
24. Achten J, Jeukendrup AE: Maximal fat oxidation during exercise in trained men. *Int J Sports Med* (in press)