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Higher rate of fat oxidation during rowing compared with cycling ergometer exercise across a range of exercise intensities

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The relative contribution of carbohydrate and fat oxidation to energy expenditure during exercise is dependent on variables including exercise intensity, mode, and recruited muscle mass. This study investigated patterns of substrate utilization during two non-weightbearing exercise modalities, namely cycling and rowing. Thirteen young, moderately trained males performed a continuous incremental (3-min stages) exercise test to exhaustion on separate occasions on an electronically braked cycle (CYC) ergometer and an air-braked rowing (ROW) ergometer, respectively. On two further occasions, participants performed a 20-min steady-state exercise bout at ~50% $\dot{V}O_{2peak}$ on the respective modalities. Despite similar oxygen consumption, rates of fat oxidation

(FAT_{ox}) were ~45% higher during ROW compared with CYC ($P < 0.05$) across a range of power output increments. The crossover point for substrate utilization occurred at a higher relative exercise intensity for ROW than CYC (57.8 ± 2.1 vs $42.1 \pm 3.6\%$ $\dot{V}O_{2peak}$, $P < 0.05$). During steady-state submaximal exercise, the higher FAT_{ox} during ROW compared with CYC was maintained ($P < 0.05$), but absolute FAT_{ox} were 42% (CYC) and 28% (ROW) lower than during incremental exercise. FAT_{ox} is higher during ROW compared with CYC exercise across a range of exercise intensities matched for energy expenditure, and is likely as a consequence of larger muscle mass recruited during ROW.

Rowing combines intense dynamic movement of most of the major muscle groups of the body with a requirement for large force production during each stroke at high intensities of exercise. While rowing as a sport requires skill and considerable time invested to master the technique (Hagerman, 1984; Soper & Hume, 2004), indoor rowing ergometer exercise is safe, relatively easy to learn, and effective for rehabilitation and improving aerobic fitness (Hagerman, 1984). The recruitment of a relatively large proportion of muscle mass compared with activities like cycling can result in higher energy expenditure during exercise (Hagerman et al., 1988; Zeni et al., 1996; Moyna et al., 2001). Several studies have investigated a range of physiological parameters in response to rowing compared with cycling in participants ranging from novice to elite to elderly (Hagerman et al., 1988; Szal & Schoene, 1989; Zeni et al., 1996; Beneke et al., 2001; Moyna et al., 2001), but none have compared the metabolic responses and rates of substrate utilization to these exercise modes.

A myriad of intrinsic biochemical factors influence the relative contributions of fat and carbohydrate to energy expenditure during exercise (Spriet & Watt,

2003; Brooks, 2012), but extrinsic factors such as the intensity and mode of exercise are important regulators of substrate utilization (Romijn et al., 1993; van Loon et al., 2001; Achten et al., 2003; Knechtle et al., 2004). The contribution of fat to energy expenditure is greatest during low- and moderate-intensity exercise but declines thereafter (Romijn et al., 1993; van Loon et al., 2001). The maximal rate of fat oxidation typically occurs between 45% and 65% of peak oxygen consumption ($\dot{V}O_{2peak}$), and this intensity has been termed “ FAT_{max} ” (Achten et al., 2002). FAT_{max} on an individual basis is influenced by training and nutrition status, gender, and the mode of exercise (Achten & Jeukendrup, 2003a, 2004; Achten et al., 2003; Venables et al., 2005). Because of the deleterious effects of ectopic fat deposition on the function of liver and skeletal muscle (Savage et al., 2007), and the causal role of skeletal muscle insulin resistance in numerous lifestyle-related chronic diseases (Wolfe, 2006), there is increasing interest in the prescription of exercise specifically around an intensity that maximizes fat oxidation (Achten & Jeukendrup, 2004; Brun et al., 2012; O'Hagan et al., 2013).

When comparing exercise modes, running elicits a greater rate of fat oxidation (FAT_{ox}) compared with cycling across a wide range of exercise intensities, a finding that has been attributed to the weight-bearing nature and greater quantity of muscle mass recruited while running (Achten et al., 2003; Knechtle et al., 2004; Capostagno & Bosch, 2010). For individuals with obesity and type 2 diabetes, it is important to identify a mode of exercise that can safely and effectively maximize energy expenditure, but because of complications such as peripheral neuropathy or degenerative arthritis, these individuals require alternative modes of exercise that are non-weightbearing (Colberg et al., 2010). Like cycling, rowing is a non-weightbearing mode of exercise, but the recruitment of a markedly greater proportion of the body's muscle mass may positively affect FAT_{ox} during exercise. Therefore, the primary aim of this study was to compare the pattern of substrate utilization and FAT_{ox} over a range of intensities during cycling and rowing ergometer exercise using the FAT_{max} protocol (Achten et al., 2002). We hypothesized that FAT_{ox} would be greater during rowing compared with cycling at the same relative intensities of exercise. Additionally, because the validity of this protocol has been questioned based on the use of incremental 3-min stages (Bordenave et al., 2007), a secondary aim of this study was to compare FAT_{ox} observed during incremental exercise to steady-state submaximal exercise.

Methods

Experimental design

Thirteen healthy male, moderately trained club-standard rowers participated in this study: age, 23.2 ± 1.6 years; height, 1.82 ± 0.02 m; body mass, 77.0 ± 1.6 kg; body mass index, 23.2 ± 0.3 kg/m²; body fat, $9.1 \pm 1.2\%$; lean body mass, 69.9 ± 1.3 kg. All participants had a rowing training history of at least 2 years, and were completing at least 1.5 h per week of cycling as part of their overall training plan. The participants performed an incremental exercise test to exhaustion on two separate occasions in random order; once on a cycle ergometer (CYC; VO_{2peak} , 55.7 ± 1.6 mL/kg/min) and once on a rowing ergometer (ROW; VO_{2peak} , 57.5 ± 1.5 mL/kg/min), in order to measure rates of substrate oxidation over a wide range of exercise intensities (Achten et al., 2002, 2003). Two further exercise tests were subsequently performed in random order, once on each ergometer, at an intensity corresponding to $\sim 50\% VO_{2peak}$ of the respective mode. Because of time commitments external to the study, only 9 of the 13 participants completed this second phase of the study. This study was approved by the Dublin City University Research Ethics Committee, and was performed in accordance with the Declaration of Helsinki. Each participant provided written informed consent after explanation of the experimental procedures.

Pre-test preparation

Participants were familiarized with all equipment and procedures prior to the commencement of testing. All tests were performed between 07:30 and 10:00 h (ambient temperature 19 °C), and participants performed subsequent tests at the same time as their first test. Pre-test preparation was the same for each visit. Participants

were asked to abstain from caffeine and alcohol and refrain from strenuous exercise for 24 h prior to testing, and all testing took place after an overnight (~ 8 to 10 h) fast. Participants were asked to keep a one day portion estimate food diary on the day prior to the first day of testing, which was scanned and emailed to participants 48 h prior to each subsequent visit after which they were asked to repeat this pattern of intake on the day preceding each test. During the first visit, body composition was estimated from skinfold thickness measurements using a Harpenden skinfold caliper at seven sites (Jackson & Pollock, 1978), and body mass (to nearest 0.1 kg) and height (to nearest 0.01 m) were measured using a digital scales and wall-mounted stadiometer, respectively.

Incremental exercise tests

The incremental exercise tests were based on the method of Achten et al. (2002) for determining the intensity (FAT_{max}) eliciting maximal rate of fat oxidation. Briefly, on an electronically braked cycle ergometer (Ergoline 900, SensorMedics, Yorba Linda, California, USA) or air-braked rowing ergometer (Model C Indoor Rower, Concept II, Nottingham, UK), participants began exercise at 95 W and the power output was increased by 35 W every 3 min thereafter until volitional fatigue. A minor modification was required during ROW such that participants maintained the required exercise intensity by keeping the average power output at the target value. At the end of each 3-min stage, the ergometer monitor was reset to clear the average power output of the previous stage. The wind vanes were adjusted to set the coefficient of drag at 130 (as per Irish Amateur Rowing Association protocol). The order of these tests was randomized, and each was separated by 7 or 14 days.

Immediately prior to each test, an indwelling catheter (Insyte-W 20/22G, Becton Dickinson, Franklin Lakes, New Jersey, USA) for serial blood sampling was introduced into an antecubital vein for CYC, or a superficial forearm vein for ROW. During the last 20 s of each stage, a blood sample (~ 3 mL) was collected in a pre-chilled vacutainer (FX Plus, Becton Dickinson) for measurement of plasma lactate (YSI 2300 Stat Plus, Yellow Springs Instruments, Ohio, USA), and heart rate (Vantage, Polar Electro, Kempele, Finland) and rating of perceived exertion (RPE) were recorded at the same time.

Submaximal exercise tests

On two separate days in random order, participants completed a submaximal exercise test at $\sim 50\% VO_{2peak}$ on each ergometer. In each submaximal test, participants exercised for 20 min. During the last 30 s of each 5-min period, HR and RPE were recorded (data not shown). During the last 15 s of the 20-min bout, a blood sample was taken from the indwelling catheter for measurement of plasma lactate. Each of these tests was undertaken at least 7 days after the last incremental exercise test. The power output required to elicit this target oxygen uptake was interpolated based on the linear relationship between oxygen uptake (y-axis) and power output (x-axis). On the day prior to each submaximal test, participants performed a brief exercise bout to verify the power output corresponding to the intensity to be used in the subsequent test. This verification session involved 15 min of exercise at exercise intensities approximating to $50\% VO_{2peak}$.

Calculations of substrate utilization

Expired air was collected continuously throughout each exercise test, and breath-by-breath measurements were performed using a Vmax 29C gas analysis system (SensorMedics, Yorba Linda, California, USA). Average values for VO_2 and VCO_2 were calculated during the last 2 min of each 3-min stage in the incremental tests

as described by the established determination of FAT_{max} protocol (Achten et al., 2002), and during the last 10 min of the 20 min submaximal tests. The rate (g/min) of carbohydrate and fat oxidation (CHO_{ox} and FAT_{ox} , respectively) and energy expenditure during each stage were calculated (Jeukendrup & Wallis, 2005). The percentage contribution of carbohydrate and fat to total energy expenditure during exercise was also calculated (Kuo et al., 2005). A comparison of oxidation rates measured during steady-state submaximal exercise to oxidation rates predicted based on gas exchange data collected during the incremental tests was based on linear regression of the relationship between oxidation rate (y-axis) and oxygen uptake (x-axis) recorded during the incremental exercise tests.

Statistical analysis

Data were evaluated using GraphPad Prism 6 (GraphPad Software, Inc., San Diego, California, USA), and are presented as mean \pm SEM. Two-way (mode \times time) repeated measures analysis of variance were used to determine differences between the two modes of exercise for variables with serial measurements, for example, VO_2 , VCO_2 , $\%W_{max}$, HR, RER, and lactate. On the incremental exercise tests, there were two sub-analyses performed on the data using this approach; the first as a comparison of responses at the same power output (W), and the second as a comparison of responses at the same relative intensity ($\%VO_{2peak}$). The latter was possible by comparing each stage in ROW with the next power output increment in CYC, that is, ROW stage 1 (95 W) vs CYC stage 2 (130 W), ROW stage 2 (130 W) vs CYC stage 3 (165 W), because at these power outputs, VO_2 and $\%VO_{2peak}$ were similar between modes (Table 1). When a main effect of exercise mode, or an interaction effect between exercise mode and time, was indicated, post-hoc tests of pair-wise comparisons were performed using the Student–Newman–Keuls test. A paired *t*-test was used to compare differences between modes for variables with single measurements. The significance level was set at $\alpha = 0.05$ for all statistical tests.

Results

Physiological responses to incremental exercise

VO_2 , VCO_2 , and HR were all higher ($P < 0.05$) during ROW compared with CYC at all power outputs

(Table 1), but VO_{2peak} and HR_{max} were similar for ROW and CYC (4.49 ± 0.20 vs 4.36 ± 0.18 L/min; 188 ± 3 vs 189 ± 3 bpm, respectively). W_{max} , calculated from the power output of last completed stage plus the fraction of time spent in the final non-completed stage multiplied by the power output increment (Jeukendrup et al., 1996), tended to be higher in CYC (331 ± 9 vs 352 ± 15 W, $P = 0.098$) and peak lactate levels tended to be higher in ROW (12.3 ± 0.8 vs 10.6 ± 0.5 mM, $P = 0.057$). VO_2 was ~ 0.35 to 0.65 L/min higher at each stage during ROW, and therefore, expressed as a percentage of VO_{2peak} , the relative exercise intensity was higher at all power outputs during ROW ($P < 0.05$; Table 1). However, when comparing each stage in ROW with the next power output increment in CYC, that is, ROW stage 1 (95 W) vs CYC stage 2 (130 W), ROW stage 2 (130 W) vs CYC stage 3 (165 W), and so on, VO_2 and $\%VO_{2peak}$ were similar between modes (Table 1). Hence, it was possible to compare each dependent variable between CYC and ROW in terms of power output (W) and relative exercise intensity ($\%VO_{2peak}$) and comparisons are referred to such. For instance, RER was similar at the same power output in CYC and ROW but was significantly lower during ROW for all time points when matched for relative exercise intensity ($P < 0.05$; Table 1). The relative power output ($\%W_{max}$) was higher during ROW ($P < 0.05$) each power output increment > 165 W, but when compared as a function of relative exercise intensity, $\%W_{max}$ was higher during CYC ($P < 0.05$; Table 1).

Substrate utilization during incremental CYC and ROW exercise

CHO_{ox} increased and FAT_{ox} decreased progressively with each increment in power output (Fig. 1). The highest FAT_{ox} during exercise was 45% higher in ROW

Table 1. Physiological responses, as a function of power output, during incremental exercise on cycling (CYC) and rowing (ROW) ergometers

		Power output (W)						
		95	130	165	200	235	270	305
$\%VO_{2peak}$	CYC	35 \pm 1	44 \pm 2	53 \pm 2	63 \pm 2	73 \pm 2	82 \pm 2	90 \pm 4
	ROW	42 \pm 1*	53 \pm 1*	63 \pm 2*	75 \pm 2*	84 \pm 2*	92 \pm 2*	98 \pm 1*
$\%W_{max}$	CYC	28 \pm 1	39 \pm 2 [†]	48 \pm 2 [†]	58 \pm 2 [†]	68 \pm 3 [†]	78 \pm 3 [†]	86 \pm 3
	ROW	29 \pm 1	41 \pm 1	51 \pm 2*	61 \pm 2*	72 \pm 2*	83 \pm 3*	90 \pm 2*
VO_2 (L/min)	CYC	1.49 \pm 0.05	1.89 \pm 0.06	2.27 \pm 0.06	2.70 \pm 0.07	3.14 \pm 0.09	3.54 \pm 0.13	3.98 \pm 0.22
	ROW	1.85 \pm 0.08*	2.35 \pm 0.09*	2.82 \pm 0.09*	3.35 \pm 0.11*	3.73 \pm 0.13*	4.08 \pm 0.15*	4.39 \pm 0.16*
VCO_2 (L/min)	CYC	1.22 \pm 0.05	1.65 \pm 0.06	2.06 \pm 0.06	2.51 \pm 0.08	3.04 \pm 0.10	3.59 \pm 0.12	4.01 \pm 0.25
	ROW	1.48 \pm 0.08*	2.03 \pm 0.08*	2.50 \pm 0.10*	3.08 \pm 0.10*	3.61 \pm 0.12*	4.21 \pm 0.13*	4.69 \pm 0.13*
RER	CYC	0.82 \pm 0.01	0.88 \pm 0.01 [†]	0.90 \pm 0.01 [†]	0.93 \pm 0.01 [†]	0.97 \pm 0.01 [†]	1.01 \pm 0.02 [†]	1.04 \pm 0.02
	ROW	0.80 \pm 0.02	0.86 \pm 0.01	0.89 \pm 0.01	0.92 \pm 0.01	0.97 \pm 0.02	1.04 \pm 0.02	1.07 \pm 0.01
HR (bpm)	CYC	102 \pm 3	115 \pm 4	130 \pm 4	144 \pm 4	158 \pm 4	170 \pm 4	179 \pm 4
	ROW	109 \pm 3*	124 \pm 3*	137 \pm 3*	153 \pm 4*	165 \pm 4*	175 \pm 3*	184 \pm 3*

Data presented as mean \pm SEM, $n = 13$.

* $P < 0.05$, CYC vs ROW at same power output (W).

[†] $P < 0.05$, CYC vs ROW at same relative intensity ($\%VO_{2peak}$).

$\%VO_{2peak}$, percentage peak oxygen uptake; $\%W_{max}$, percentage of maximal power output; HR, heart rate; RER, respiratory exchange ratio; VCO_2 , carbon dioxide production; VO_2 , oxygen uptake.

Fat oxidation during rowing vs cycling

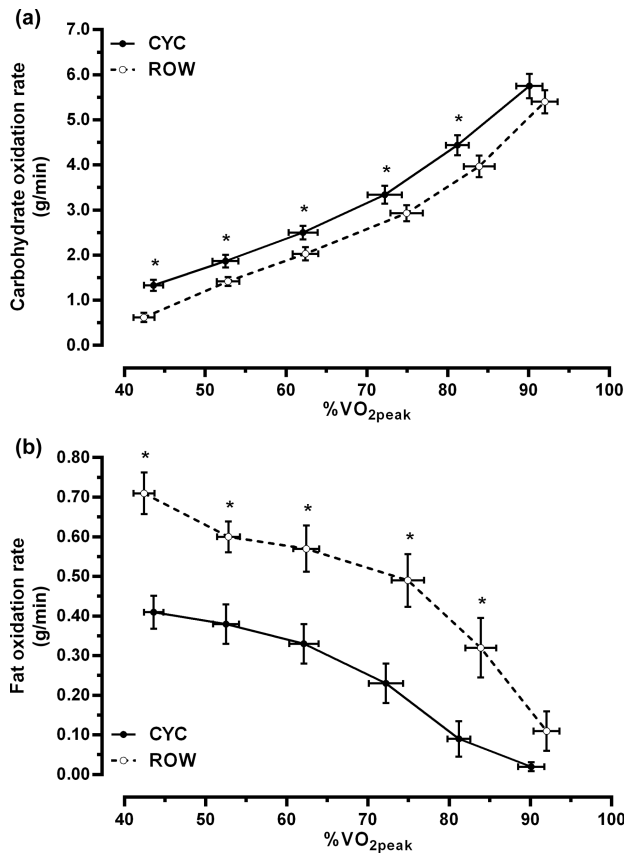


Fig. 1. Rates of carbohydrate (a) and fat (b) oxidation as a function of exercise intensity during incremental cycling (CYC) or rowing (ROW) ergometer exercise. Values are presented as mean \pm SEM. * P < 0.05, CYC vs ROW. %VO_{2peak}, peak oxygen uptake.

compared with CYC (0.71 ± 0.05 vs 0.49 ± 0.04 g/min, P < 0.05) and occurred in the first stage of both the CYC and ROW tests (95 W). With respect to the comparison of oxidation rates at the same relative intensity, that is, as a function of %VO_{2peak}, despite a similar rate of oxygen consumption and whole-body energy expenditure, FAT_{ox} was higher during ROW at the same relative intensity throughout a range of submaximal exercise intensities between ~43% and 84%VO_{2peak} (Fig. 1), commensurate with higher CHO_{ox} during CYC. The relative contribution of fat to energy expenditure was greater across the range of exercise intensities (Fig. 2). Additionally, the crossover point, that is, the exercise intensity after which carbohydrate oxidation predominates for energy provision (Brooks & Mercier, 1994), occurred at lower relative exercise intensity during CYC ($42.1 \pm 3.6\%$ VO_{2peak}) compared with ROW ($57.8 \pm 2.1\%$ VO_{2peak}, P < 0.05). Compared as a function of relative exercise intensity, there was no effect of exercise mode on plasma lactate concentrations (Fig. 3), but concentrations were higher during ROW compared with CYC (P < 0.05) at 270 W (7.45 ± 1.30 vs 5.38 ± 0.86 mM, P < 0.05) and 305 W (8.94 ± 1.22 vs 6.96 ± 0.89 mM, P < 0.05).

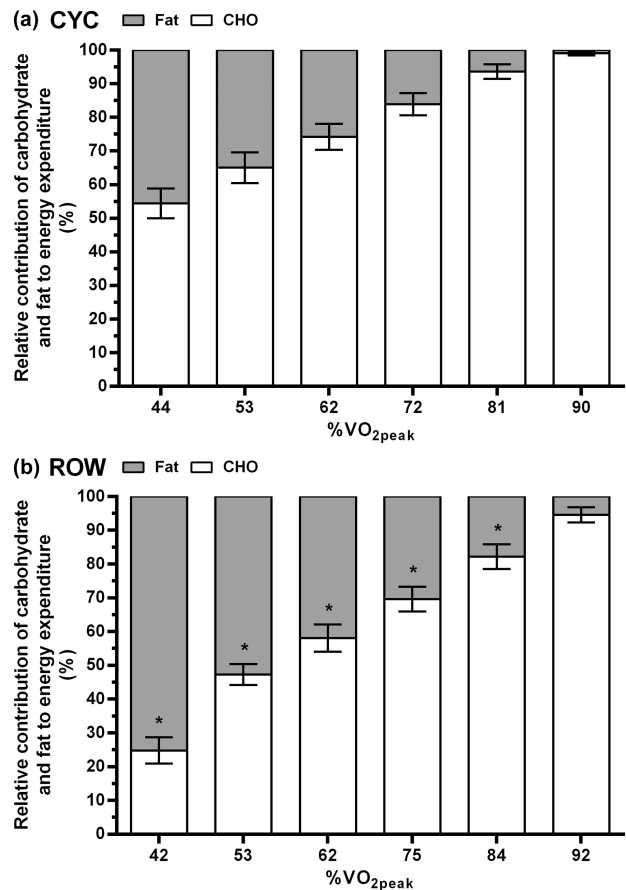


Fig. 2. Relative contribution of carbohydrate and fat to energy expenditure during incremental cycling (CYC) and rowing (ROW). Values are presented as mean \pm SEM. * P < 0.05, CYC vs ROW. %VO_{2peak}, peak oxygen uptake.

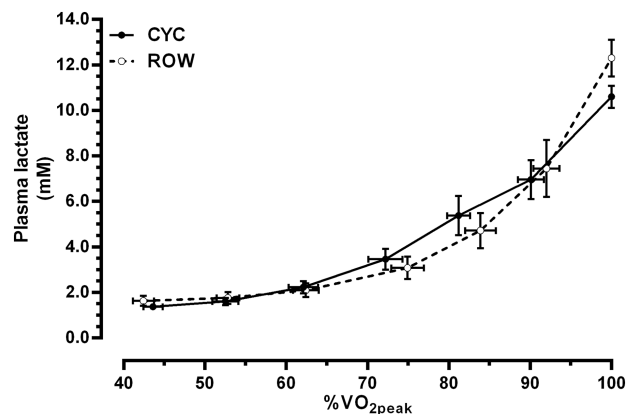


Fig. 3. Plasma lactate concentrations as a function of exercise intensity during incremental cycling (CYC) or rowing (ROW) ergometer exercise. Values are presented as mean \pm SEM. %VO_{2peak}, peak oxygen uptake.

Substrate utilization during submaximal steady-state exercise

During the steady-state submaximal exercise tests, no difference occurred between the exercise modes in terms of relative exercise intensity ($46.1 \pm 1.5\%$ vs

Table 2. Measured steady-state oxidation rates during submaximal (~50%VO_{2peak}) cycling (CYC) and rowing (ROW) exercise compared with rates predicted by an incremental exercise test

		VO ₂ (L/min)	VCO ₂ (L/min)	RER	CHO _{ox} (g/min)	FAT _{ox} (g/min)
CYC	Steady-state	1.98 ± 0.08	1.80 ± 0.08	0.91 ± 0.01	1.75 ± 0.10	0.30 ± 0.02
	Predicted	1.98 ± 0.08	1.68 ± 0.06*	0.85 ± 0.02*	1.29 ± 0.14*	0.51 ± 0.06*
ROW	Steady-state	2.08 ± 0.13	1.82 ± 0.11	0.88 ± 0.01†	1.53 ± 0.10†	0.43 ± 0.05†
	Predicted	2.08 ± 0.13	1.67 ± 0.16*	0.79 ± 0.03*	1.09 ± 0.15*	0.59 ± 0.05*

Data presented as mean ± SEM.

**P* < 0.05 predicted vs steady-state exercise.

†*P* < 0.05 CYC vs ROW.

CHO_{ox}, calculated rates of carbohydrate oxidation; FAT_{ox}, calculated rates of fat oxidation; RER, respiratory exchange ratio; VCO₂, carbon dioxide production; VO₂, oxygen uptake.

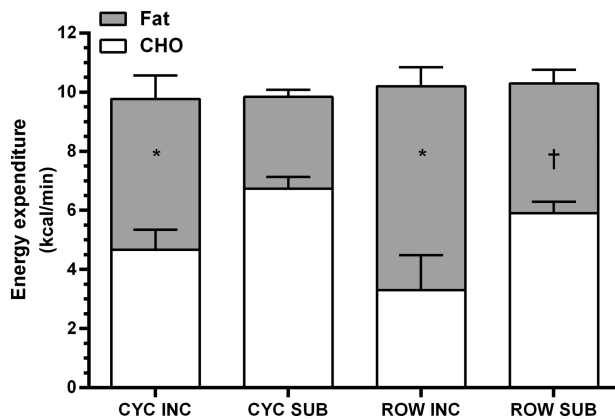


Fig. 4. Contribution of carbohydrate (CHO) and fat to energy expenditure (kcal/min) during steady-state submaximal (SUB) cycling (CYC) and rowing (ROW) exercise compared with incremental (INC) exercise. Values are presented as mean ± SEM. **P* < 0.05, SUB vs INC, †*P* < 0.05 CYC SUB vs ROW SUB.

48.4 ± 1.5%VO_{2peak}), VO₂ (1.98 ± 0.08 vs 2.08 ± 0.13 L/min) or plasma lactate concentration (1.20 ± 0.17 vs 1.03 ± 0.13 mM; all CYC vs ROW, respectively). The pattern for higher FAT_{ox} observed for ROW compared with CYC during incremental exercise was maintained during the submaximal exercise test (Table 2). This was equivalent to ~43% higher FAT_{ox} during ROW (0.43 ± 0.05 vs 0.30 ± 0.02 g/min, *P* < 0.05). This reflected a lower RER value recorded during ROW (0.88 ± 0.01 vs 0.91 ± 0.01, *P* < 0.05). Therefore, the contribution of fat to energy expenditure (Fig. 4) was greater in ROW (42.3 ± 2.8%) compared with CYC (31.6 ± 2.2%, *P* < 0.05). Despite a similar pattern of substrate utilization during the submaximal exercise test, the absolute values for FAT_{ox} were markedly lower compared with incremental exercise (Table 2). Based on values predicted by linear regression of gas analysis data recorded during incremental exercise, FAT_{ox} during steady-state exercise was ~42% lower for CYC and 28% lower for ROW (both *P* < 0.05 for steady-state vs predicted). These data reflect higher VCO₂ and hence higher RER, values during the submaximal exercise bout than predicted based on the incremental data (Table 2).

Discussion

The present study compared patterns of substrate utilization during two non-weightbearing modes of exercise, namely cycling and rowing, over a range of exercise intensities. The principal finding is that FAT_{ox} is higher during rowing compared with cycling exercise eliciting similar rates of oxygen consumption during incremental exercise based on the FAT_{max} protocol (Achten et al., 2002). The higher FAT_{ox} observed during rowing was maintained during submaximal exercise, but in agreement with others (Bordenave et al., 2007), this protocol resulted in an overestimation of the absolute FAT_{ox} value observed during steady-state exercise.

Exercise intensity and duration are the major determinants of substrate utilization during exercise (Romijn et al., 1993; Brooks & Mercier, 1994; van Loon et al., 2001), but the influence of exercise mode is less well-described. Comparisons of different exercise modes can be problematic when there are large inter-mode differences between VO₂ resulting in greater energy expenditure at the same relative exercise intensity. Alternatively, normalizing exercise intensity to an individual's lactate threshold for each exercise mode has been proposed (Baldwin et al., 2000; Arkinstall et al., 2001). Despite no differences in VO_{2peak} between rowing and cycling, VO₂ for each power output increment during rowing was higher than cycling, as reported by others (Hagerman et al., 1988; Zeni et al., 1996; Moyna et al., 2001). However, in the present study, energy expenditure and plasma lactate concentration did not differ as a function of the relative exercise intensity in either the incremental or submaximal exercise tests.

Several studies have compared physiological responses to rowing and cycling (Hagerman et al., 1988; Szal & Schoene, 1989; Zeni et al., 1996; Beneke et al., 2001; Moyna et al., 2001), but none have investigated differences, if any, in substrate utilization. We report that FAT_{ox} is higher during rowing compared with cycling exercise at the same rate of energy expenditure across a range of exercise intensities up to ~85%VO_{2peak}. Similar patterns and higher FAT_{ox} occur during running when compared with cycling (Achten et al., 2003; Knechtle et al., 2004; Capostagno & Bosch, 2010). The highest

FAT_{ox} in the present study is similar to values in moderately trained males during cycling (0.60 ± 0.07 g/min; Achten et al., 2002), and values ranging from ~0.45 to 0.65 g/min reported in subsequent studies (Achten et al., 2002; Achten & Jeukendrup, 2003a; Venables et al., 2005). Moreover, higher FAT_{ox} and lower CHO_{ox} during rowing are reflected by the crossover point (Brooks & Mercier, 1994) occurring at a higher relative exercise intensity in rowing. That the highest FAT_{ox} occurred in the first stage of the incremental protocol has been previously observed (Achten & Jeukendrup, 2003b), whereas the intensity at which the highest FAT_{ox} occurs is variable, ranging from 54% to 65% (Achten et al., 2002, 2003) and from 25% to 77% (Venables et al., 2005). Employing an incremental protocol that differs from the original FAT_{max} protocol, peak FAT_{ox} occurred ~43% and ~50% in untrained and trained subjects, respectively (Nordby et al., 2006). Clearly, the protocol used, the participants recruited, and the habitual diet are the three most important factors determining the relationship between FAT_{ox}, FAT_{max} and exercise intensity (Achten & Jeukendrup, 2004).

Differences in substrate utilization between exercise modes have been attributed to divergence in the quantity of recruited muscle mass. One proposed mechanism involves a reduced activation of lipolysis because of a lower catecholamine response during cycling as a consequence of the recruitment of a smaller proportion of muscle mass (Achten et al., 2003). This is speculative as catecholamines are also potent stimulators of glycogenolysis during exercise (Hargreaves, 2006), and increase only modestly during low intensities of exercise (Galbo, 1983). An alternative explanation is that when a larger proportion of muscle mass is recruited for the same rate of energy expenditure, the metabolic demand per skeletal muscle fiber is lower (Hoffman et al., 1996; Beneke et al., 2001), and the reliance on carbohydrate metabolism is reduced (Costill et al., 1971; Coyle et al., 1988; Richter et al., 1988).

Next, we compared FAT_{ox} measured during the incremental exercise tests to rates elicited during submaximal steady-state exercise at ~50%VO_{2peak}. The current protocol, which uses 3-min stages at each power output increment, may overestimate FAT_{ox} in sedentary individuals (Bordenave et al., 2007). We extend these findings to moderately trained individuals as FAT_{ox} observed during submaximal exercise was 42% and 28% lower in CYC and ROW, respectively, compared with incremental exercise at the same energy expenditure. The explanation for this observation is likely to reside at the level of VCO₂ kinetics. When comparing predicted to measured gas exchange data during steady-state exercise, VCO₂ values were markedly higher during steady-state exercise. These data suggest that the rate of carbon dioxide production at the onset of exercise, or when the exercise intensity increases, lags behind VO₂ and thereby results in an artificially lower RER value during 3-min incre-

ments at a given power output. This is unsurprising given the half-time of VCO₂ on-kinetics is approximately 30% to 60% longer than VO₂ on-kinetics due to higher solubility and tissue storage of CO₂ (Diamond et al., 1977; Zhang et al., 1991; Poole & Jones, 2012). The lower than predicted FAT_{ox} during submaximal exercise reflects this artifact in RER caused by the disparity in VO₂ and VCO₂ kinetics. However, FAT_{ox} remained ~43% higher in rowing compared with cycling during steady-state submaximal exercise matched for energy expenditure. Therefore, predicting substrate utilization rates from 3-min stages during incremental exercise may overestimate the magnitude (g/min) of FAT_{ox} during submaximal exercise, but the pattern of higher FAT_{ox} during rowing persists.

The training status of the participants may have influenced the patterns of substrate utilization, as those with previous rowing experience were recruited in order to minimize the influence of inefficiencies in rowing technique of novices. Therefore, the higher FAT_{ox} observed may reflect the training history of the participants in the present study, so these findings should be explored in other populations. A final explanation for observed differences in FAT_{ox} may be that, secondary to mechanical alterations arising from generating high levels of ventilation in a variable seated position, rowing exercise results in a relative hypocapnia at the same power output compared with cycling (Szal & Schoene, 1989). Thus, the lower VCO₂ could contribute to the aforementioned lower RER value, but this remains to be assessed at low-to-moderate exercise intensity.

Perspectives

Indoor rowing ergometry is an attractive exercise mode because of its non-weightbearing nature. As a form of physical activity, rowing for as little as 1 h per week is associated with 18% risk reduction of developing coronary heart disease (Tanasescu et al., 2002). Moreover, during inter-mode comparisons, energy expenditure is greater for rowing when the intensity of exercise is matched by self-selected RPE (Zeni et al., 1996; Moyna et al., 2001). Therefore, exercises such as rowing that recruit larger muscle mass for the same perceived effort may be most beneficial by optimizing the contribution of FAT_{ox} to energy expenditure (Achten & Jeukendrup, 2004; Brun et al., 2012), while simultaneously presenting a training stimulus that is perceptually preferable (Moyna et al., 2001). Moreover, even when energy expenditure is similar, rowing exercise elicits a greater rate of fat oxidation than cycling across a broad range of intensities.

Despite absolute FAT_{ox} values being overestimated during incremental exercise testing, the greater relative contribution of fat to energy expenditure during rowing persists during submaximal exercise. This phenomenon

may be related to the quantity of muscle mass recruited, the rate of carbon dioxide production and/or the training status of the participants. However, because the present study was performed with physically active young males, and that the protocol was performed in the fasted state, two factors known to result in elevated FAT_{ox} (Achten & Jeukendrup, 2004), the observed results are likely to reflect a “best-case scenario” in relation to FAT_{ox} during rowing exercise. Future work should explore whether these patterns are maintained in sedentary and at-risk populations, potentially in the postprandial state, in order to better inform exercise

prescription of non-weightbearing exercise and intensities individualized for maximal fat oxidation.

Key words: Exercise modality, energy expenditure, fuel utilization, aerobic, non-weightbearing.

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