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Research article

Maximal Fat Oxidation: Comparison between Treadmill, Elliptical and Rowing Exercises

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Abstract
Fat oxidation during exercise is associated with cardio-metabolic benefits, but the extent of which whole-body exercise modality elicits the greatest fat oxidation remains unclear. We investigated the effects of treadmill, elliptical and rowing exercise on fat oxidation in healthy individuals. Nine healthy males participated in three, peak oxygen consumption tests, on a treadmill, elliptical and rowing ergometer. Indirect calorimetry was used to assess maximal oxygen consumption ($\dot{V}O_{2peak}$), maximal fat oxidation (MFO) rates, and the exercise intensity MFO occurred (Fat_{max}). Mixed venous blood was collected to assess lactate and blood gases concentrations. While $\dot{V}O_{2peak}$ was similar between exercise modalities, MFO rates were higher on the treadmill (mean ± SD; 0.61 ± 0.06 g·min^{-1}) compared to both the elliptical (0.41 ± 0.08 g·min^{-1}, $p = 0.022$) and the rower (0.40 ± 0.08 g·min^{-1}, $p = 0.017$). Fat_{max} values were also significantly higher on the treadmill (56.0 ± 6.2 %$\dot{V}O_{2peak}$) compared to both the elliptical (36.8 ± 5.4 %$\dot{V}O_{2peak}$, $p = 0.049$) and rower (31.6 ± 5.0 %$\dot{V}O_{2peak}$, $p = 0.021$). Post-exercise blood lactate concentrations were also significantly lower following treadmill exercise ($p = 0.021$). Exercising on a treadmill maximizes fat oxidation to a greater extent than elliptical and rowing exercises, and remains an important exercise modality to improve fat oxidation, and consequently, cardio-metabolic health.

Key words: Substrate oxidation, indirect calorimetry, exercise modality, metabolism.

Introduction

During aerobic exercise, oxidation of carbohydrates and fat, in exercising muscle, is influenced by fitness level (Holloszy and Coyle, 1984), diet (Flatt, 1987), sex (Venables et al., 2005), and intrinsic biochemical factors (e.g. pH, temperature, substrate availability, etc.) (Gevers, 1979; Robergs et al., 2004; Tarnopolsky et al., 1995). The oxidation of substrates is also known to be further altered extrinsically, via exercise duration (Phillips et al., 1996), and exercise modality (Achten et al., 2003; Capostagno and Bosch, 2010; Egan et al., 2016). Substrate metabolism shifts towards greater fat oxidation and reaches higher rates of maximal fat oxidation (MFO) during walking and running compared to cycling (Achten et al., 2003; Capostagno and Bosch, 2010; Chenevière et al., 2010; Knechtle et al., 2004). These results are believed to stem from differences in muscle recruitment patterns and Type II muscle fiber recruitment in cycling from lower muscle mass contribution to total energy production (Achten et al., 2003; Chenevière et al., 2010). Additionally, Chenevière et al. (2010) found that the exercise intensity where MFO occurs, known as Fat_{max} (Jeukendrup and Achten, 2001), occurs at higher intensities on the treadmill compared to a cycle ergometer, while Achten et al. (2003) found no significant difference in Fat_{max} values between these modalities.

Intrinsically, as exercise intensity increases, greater glycolytic activity results in an increased accumulation of lactate and hydrogen ions, decreasing muscle pH. Reductions in fatty acid oxidation are strongly correlated with the accumulation of plasma lactate (Achten and Jeukendrup, 2004). Achten and Jeukendrup (2004) also found that the initial rise in plasma lactate occurred at the same intensity that elicited MFO. It is suggested that decreased muscle pH, due to the accumulation of glycolytic by-products, inhibits the transport of long-chain fatty acid into the mitochondria, reducing fatty acid oxidation (Achten and Jeukendrup, 2004; Sidossis et al., 1997; Starritt et al., 2000).

The elliptical and rower are two modalities increasing in popularity for their ability to offer meaningful aerobic benefits (Brown et al., 2015; Hagerman, 1984; Mercer et al., 2001), as they incorporate whole-body movements. They further provide alternatives to those with limited range of motions and physical disabilities, such as cerebral palsy, multiple sclerosis, and others. Importantly, it has been reported that heart rate and oxygen uptake during elliptical exercise is similar to treadmill when both exercises are performed at self-selected intensities (Porcari et al., 1998). Carey et al. (1974) also demonstrated that maximal oxygen uptake values were not significantly different between treadmill and rowing exercise. Despite some aerobic similarities, MFO and Fat_{max} was reported higher during rowing compared to cycling (Egan et al., 2016). The crossover point, where energy contribution from CHO and fat to total energy expenditure is equal (Brooks and Mercier, 1994), was also reported to occur at a higher relative exercise intensity during rowing than cycling (Egan et al., 2016). Although the elliptical and rower involve a large level of muscle mass (Egan et al., 2016), they involve more regular activation of muscles in the upper limbs compared to treadmill exercise (Bazzucchi et al., 2013; Hagerman, 1984; Sozen, 2010). The muscles

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of the upper limbs have a relatively smaller surface area than those of the lower body (Young et al. 1986), and the metabolic demand across these muscle fibers may be larger during elliptical and rowing exercise, leading to a greater reliance on Type II muscle fibers. This could possibly result in not only a greater production of lactate, but also an earlier reliance on carbohydrate oxidation.

Fat oxidation during exercise has been associated to increases in oxidative enzymatic activity and mitochondrial biogenesis in skeletal muscle (Little et al., 2010). Training designed to improve fat oxidation could help to gain or maintain a healthy metabolic profile via an appropriate selection of exercise modality. We consequently investigated the effects of treadmill, elliptical and rowing exercise on MFO, Fat_{max}, the crossover point, and rates of fat oxidation. It was hypothesized that MFO, Fat_{max}, the crossover point, and absolute fat oxidation would be greater during the treadmill exercise compared to the elliptical or rowing exercises.

Methods

Participants

Nine healthy males (age: 22 ± 1.1 years, height: 1.78 ± 0.03 m, weight: 78.0 ± 3.7 kg, body fat: 8.70 ± 1.15%) participated in the study. Informed written consent was provided prior to testing. Participants were screened with a Get Active Questionnaire and a health screening form for health conditions or diseases that could be aggravated by exercise. None of the participants were on prescribed medications. All procedures were in accordance with the latest revision of the Declaration of Helsinki and approved by the university's Research Ethics Board.

Experimental design

Participants reported to the laboratory, following a 12-hour fasted state, for one familiarization session, followed by three experimental exercise sessions, in a balanced design, consisting of an adapted incremental $\dot{V}O_{2peak}$ protocol to exhaustion during either: 1) treadmill exercise (TM), 2) elliptical exercise (EL), or 3) rowing exercise (ROW). Participants performed each exercise session at the same time of day, between 07:00 h and 11:00 h, five to seven days apart, to minimize the influence of circadian variance. Participants were also requested to avoid alcohol consumption, strenuous exercise, caffeine and tobacco 24 hours prior to each experimental exercise session. To control for dietary influences on metabolism during exercise, participants maintained the same diet each day prior to their exercise sessions, with the built-in assumption that this energy standardization method yields significant variability in food intake between participants (Jeacocke and Burke, 2010).

Experimental protocol

Familiarization session. Participants completed one familiarization session to become accustomed to the exercise protocols, instrumentation, and each of the exercise modalities. Additionally, anthropometric measures were collected, and percent body fat was estimated (Jackson and Pollock, 1978).

Treadmill Exercise (TM). An adapted incremental $\dot{V}O_{2peak}$ exercise protocol was used to ensure that there was a sufficient number of stages to build substrate oxidation curves (Achten et al., 2002; Gagnon et al., 2019). Participants began walking at 3.5 $km \cdot h^{-1}$ with a 1% gradient for the first three-minute stage on the treadmill (BodyGuard 312C Treadmill, BodyGuard Fitness Technology Inc., Saint-Georges, Quebec, CAN). Following the first stage, the speed was increased every three minutes to 4.3 $km \cdot h^{-1}$, 5.5 $km \cdot h^{-1}$, 6.4 $km \cdot h^{-1}$, and finally 7.6 $km \cdot h^{-1}$ for the next four stages. Following the first five stages, the gradient was increased by 2% at every subsequent stage. The gradient of the treadmill was increased until the participants' RER values reached 1.0, indicating that only carbohydrates were being used for energy production, at which point the speed was immediately increased to 9.7 $km \cdot h^{-1}$ with a gradient of 10%. The gradient was then increased by 2% every minute until $\dot{V}O_{2peak}$ was reached.

Elliptical Exercise (EL). An adapted incremental $\dot{V}O_{2peak}$ exercise protocol was used to ensure that there was a sufficient number of stages to build substrate oxidation curves (Dalleck et al., 2004). Participants began exercising at 30 W for the first three-minute stage on the elliptical (S70 Ascent Trainer, Vision Fitness, Cottage Grove, Wisconsin, USA). The placement of hands and feet on the elliptical were standardized for all participants. The gradient was maintained at a midpoint between the low to high ranges, pre-determined on the elliptical, and was maintained throughout the entire test (Dalleck et al., 2004). Every three minutes, the power output was increased by 20 W until participants reached an RER of 1.0. Power output was then increased by 20 W every minute until $\dot{V}O_{2peak}$ was reached. Participants were required to maintain the appropriate exercise intensity by keeping the average power output at the target value.

Rowing Exercise (ROW). An adapted incremental $\dot{V}O_{2peak}$ exercise protocol was used to ensure that there was a sufficient number of stages to build substrate oxidation curves (Egan et al., 2016). Participants began rowing at 30 W for the first three-minute stage on the rower (Model D Rowing Ergometer, Concept2 Inc., Morrisville, Vermont, USA). To standardize the level of drag for all participants, the coefficient of drag was maintained at 130 during all subsequent stages (Egan et al., 2016). The power output was increased by 30 W every three minutes until participants reached an RER of 1.0. Power output was then increased by 30 W every minute until $\dot{V}O_{2peak}$ was reached. Participants were required to maintain the appropriate exercise intensity by keeping the average power output at the target value.

For exercise on all three modalities, $\dot{V}O_2$ was considered to be peak when at least two of the three following conditions occurred, 1) if heart rate did not significantly increase with increasing workload (defined as an increase of no more than 5 bpm), 2) if RER was greater than 1.05, or 3) if $\dot{V}O_2$ did not significantly increase with increasing workload (defined as an increase of no more than 2 $ml \cdot kg^{-1} \cdot min^{-1}$).

Instrumentation and measures

Heart rate (HR) was recorded continuously using a Polar Heart Rate Monitor (H10). Fingertip blood samples were collected using a contact-activated lancet (BD Microtainer, BD, USA) prior to, and immediately following, each exercise session to assess blood lactate (Lactate Pro Test Strip, Arkray, Kyoto, Japan) and glucose (FreeStyle Precision Neo, Abbott Point of Care, Illinois, USA) concentrations. Venous blood samples, from an antecubital vein, were also collected prior to, and immediately following each exercise session to assess concentrations of pH levels, base excess of extracellular fluid (BEecf), bicarbonate levels (HCO_3^-), partial pressure of oxygen (pO_2), partial pressure of carbon dioxide (pCO_2), total carbon dioxide levels (TCO_2), and oxygen saturation (SO_2) (i-STAT Handheld, Abbott Point of Care, Illinois, USA).

Breath-by-breath cardiorespiratory data were collected continuously during exercise using an open circuit ergospirometer in breath-by-breath mode (CPX, MGC Diagnostics, Saint Paul, MN) to obtain measures of oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$), respiratory exchange ratio (RER), and ventilation rate ($\dot{V}E$). Gas analyzers were calibrated with air tanks containing 12% O_2 and 5% CO_2 and the gas flow sensor was calibrated using a 3L calibration syringe before each exercise session. Gas flow was measured through a bidirectional pitot tube flow sensor attached to the face-fitting mask worn by all participants during the exercise sessions.

Calculations and Analyses

For each three-minute stage of the $\dot{V}O_{2peak}$ protocols, the last thirty seconds was averaged for the following measures: HR, $\dot{V}O_2$, $\dot{V}CO_2$, and $\dot{V}E$. The highest mean value over the entire exercise protocol for both HR and $\dot{V}E$ was used to determine peak heart rate (HR_{peak}), and peak ventilation rate ($\dot{V}E_{peak}$) values for each participant.

Calculations of fat and carbohydrate oxidation were completed for each stage using the following stoichiometric equations (Jeukendrup and Wallis, 2005):

(<50% $\dot{V}O_{2peak}$)

$$\text{CHO } (g \cdot min^{-1}) = 4.344 \cdot \dot{V}CO2 - 3.061 \cdot \dot{V}O2 - 0.40 \cdot n \quad \textbf{(1)}$$

(>50% $\dot{V}O_{2peak}$)

$$\text{CHO } (g \cdot min^{-1}) = 4.210 \cdot \dot{V}CO2 - 2.962 \cdot \dot{V}O2 - 0.40 \cdot n \quad \textbf{(2)}$$

$$\text{Fat } (g \cdot min^{-1}) = 1.695 \cdot \dot{V}O2 - 1.701 \cdot \dot{V}CO2 - 1.77 \cdot n \quad \textbf{(3)}$$

where values of $\dot{V}O_2$ and $\dot{V}CO_2$ ($L \cdot min^{-1}$) were collected during exercise and "n" represents nitrogen excretion from the oxidation of proteins (135 $\mu g \cdot kg^{-1} \cdot min^{-1}$) (Jeukendrup and Wallis, 2005). Protein oxidation was not directly calculated as short-term exercise does not alter its contribution (Vallerand and Jacobs, 1989).

Normal distribution of the data was verified via skewness and kurtosis tests, Kolmogorov-Smirnov and Shapiro-Wilk tests, and visual inspection of histograms. Sphericity of the data was verified through Mauchly's test. One-way analyses of variance with repeated measures were used to identify differences between exercise modalities for the following variables: MFO, Fat_{max}, $\dot{V}O_{2peak}$, HR_{peak}, $\dot{V}E_{peak}$, $\dot{V}O_2$/HR, and the crossover point. Two-way analyses of variance with repeated measures (factors: exercise modality and time) were performed to identify differences in blood variables from pre and post exercise between exercise conditions, and for $\dot{V}E/\dot{V}O_2$, $\dot{V}E/\dot{V}CO_2$ throughout each condition. When a significant *F* ratio was observed, pairwise comparisons with Bonferroni correction was conducted. To assess whether differences were present among substrate oxidation curves between exercise modalities, multiple linear mixed-effects regression analyses were performed to examine differences among relative and absolute oxidation curves with %$\dot{V}O_{2peak}$, and exercise modality as variables. To respond to the quadratic (fat oxidation) and exponential (CHO oxidation) natures of the curves, %$\dot{V}O_{2peak}$ squared was added within the model. Statistical significance was set at $p < 0.05$. It was estimated that a sample of nine participants would be sufficient for detection of large effect sizes ($\eta^2 = 0.20$, f = 0.5), assuming standard deviations similar to those previously observed (Capostagno and Bosch, 2010) with a statistical power (1-β err. prob.) of 80% (G*power, Düsseldorf, Germany). Statistical analyses were completed using SPSS statistical package (Version 24, IBM, Armonk, NY, 2016).

Results

Cardiorespiratory Variables

There was no significant difference in $\dot{V}O_{2peak}$ values across the three exercise conditions ($p \geq 0.054$, TM: 60.1 ± 7.0 $mL \cdot kg^{-1} \cdot min^{-1}$, EL: 57.9 ± 7.9 $mL \cdot kg^{-1} \cdot min^{-1}$, ROW: 57.6 ± 7.9 $mL \cdot kg^{-1} \cdot min^{-1}$). However, there was a significant difference in mean HR_{peak} between modalities ($p = 0.004$), where HR_{peak} was higher on the TM (195 ± 5 bpm) *vs.* ROW ($p = 0.005$, 189 ± 7 bpm) but not EL (194 ± 6 bpm). Mean $\dot{V}E_{peak}$ was also not different between the exercise modalities ($p = 0.465$, TM: 139.2 ± 15.8 $L \cdot min^{-1}$, EL: 143.4 ± 10.6 $L \cdot min^{-1}$, ROW: 144.6 ± 13.3 $L \cdot min^{-1}$). Mean $\dot{V}O_2$/HR was not significantly different between modalities ($p = 0.295$). $\dot{V}E/\dot{V}O_2$ and $\dot{V}E/\dot{V}CO_2$ were not different between exercise modalities over the duration of exercise ($p \geq 0.070$).

Metabolism

Mean MFO was higher in TM *vs.* EL ($p = 0.022$) and ROW ($p = 0.017$), but there was no significant difference between EL and ROW ($p = 1.000$, TM: 0.61 ± 0.17 $g \cdot min^{-1}$, EL: 0.41 ± 0.23 $g \cdot min^{-1}$, ROW: 0.40 ± 0.23 $g \cdot min^{-1}$) (Figure 1A). Similarly, Fat_{max} was higher in TM *vs.* EL ($p = 0.049$) and ROW ($p = 0.021$). However, mean Fat_{max} was not different between EL and ROW ($p = 0.765$, TM: 55.9 ± 18.5 %$\dot{V}O_{2peak}$, EL: 36.8 ± 16.2 %$\dot{V}O_{2peak}$, ROW: 31.6 ± 14.9 %$\dot{V}O_{2peak}$) (Figure 1B). There was no difference observed in the mean crossover point between the exercise modalities ($p = 0.388$, TM: 42.2 ± 13.9 %$\dot{V}O_{2peak}$, EL: 34.0 ± 16.9 %$\dot{V}O_{2peak}$, ROW: 35.4 ± 15.9 %$\dot{V}O_{2peak}$).

Figure 2 presents absolute rates of fat and CHO oxidation across the exercise intensity spectrum during treadmill, elliptical and rower exercise. Regression analyses revealed a strong influence of modality on both fat and CHO oxidation curve during exercise ($p < 0.001$). Examination of the fat oxidation curves revealed that curves became linear, and the distribution of the data was greater in the elliptical and rower exercises. The CHO oxidation curves were similar in shape between exercise modalities, but a greater distribution of the data was found in the elliptical condition. Results of the regression model for the relative fat and CHO oxidation are presented in Table 1.

Blood Variables

Mean pH was significantly lower post-exercise compared to pre-exercise for all three exercise modalities ($p<0.001$) (Fig. 3A). However, there was no difference in pH between exercise modalities ($p = 0.061$). Blood lactate concentrations increased across time ($p < 0.001$) (Figure 3B), and were also higher post-exercise in ROW compared to TM ($p = 0.021$). Blood glucose concentrations were not significantly different between exercise modalities ($p = 0.801$). However, glucose was significantly higher post-exercise compared to pre-exercise ($p = 0.004$, Pre-Exercise: 4.36 ± 0.16 mmol·L^{-1}, Post-Exercise: 4.83 ± 0.17 mmol·L^{-1}), regardless of exercise modality.

Mean pO_2 (Figure 3C) and pCO_2 (Figure 3D) were both significantly higher post-exercise compared to pre-exercise across exercise modalities (pO_2: $p = 0.004$; pCO_2: $p = 0.006$). Additionally, pO_2 was higher post-exercise in TM *vs.* ROW ($p = 0.021$). There was also no significant difference in pCO_2 between exercise modalities ($p = 0.158$).

Mean BEecf was significantly lower post-exercise compared to pre-exercise ($p \leq 0.001$) (Figure 3E). BEecf was also significantly lower post-exercise during ROW exercise compared *vs.* TM ($p = 0.045$) and EL ($p = 0.037$). Mean HCO_3^- was significantly lower post-exercise compared to pre-exercise ($p \leq 0.001$) (Figure 3F). There was no significant difference in HCO_3^- between exercise modalities ($p = 0.304$).

There was no significant difference in mean sO_2% between exercise modalities ($p = 0.767$, TM: 47.4 ± 24.27 %, EL: 48.4 ± 28.24 %, ROW: 43.5 ± 19.60 %) or between time points ($p = 0.067$, Pre-Exercise: 40.1 ± 17.75 %, Post-Exercise: 52.81 ± 27.72 %). Mean TCO_2 was significantly lower post-exercise (20.9 ± 2.79 mmHg) compared to pre-exercise ($p \leq 0.001$, 30.5 ± 2.06 mmHg). There was no significant difference in TCO_2 between exercise modalities ($p = 0.482$, TM: 25.8 ± 5.82 mmHg, EL: 26.0 ± 4.86 mmHg, ROW: 25.28 ± 5.81 mmHg).

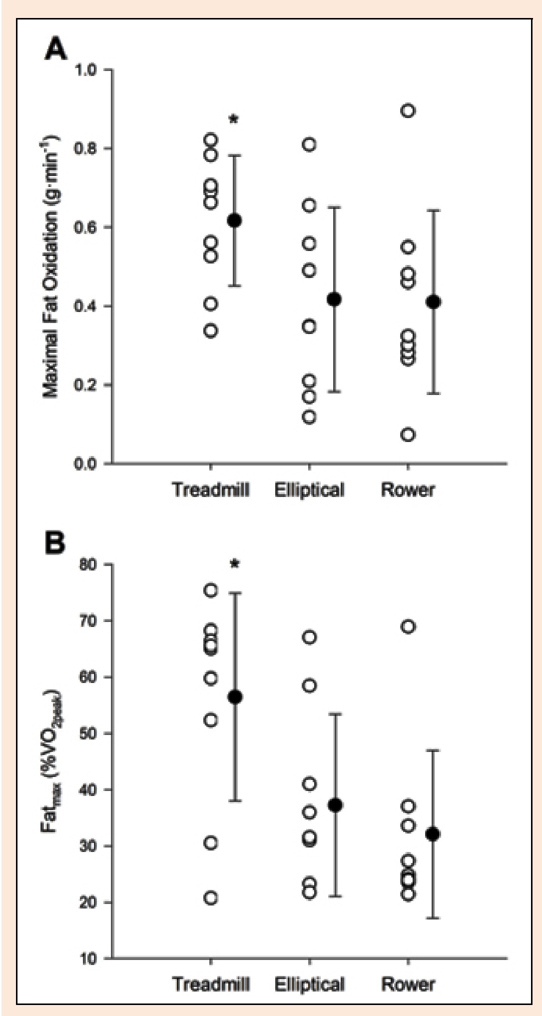

Figure 1. (A) Mean MFO rates between treadmill, elliptical and rowing exercise, (B) Mean Fat$_{max}$ between treadmill, elliptical and rowing exercise. * significantly different from elliptical and rower ($p < 0.05$).

Table 1. Multiple linear mixed-effect regression analyses for treadmill, elliptical and rowing exercise for relative energy contribution of fat and carbohydrates to total energy expenditure, as plotted in Figure 2.

		Coefficient (β)	Std. Err.	Z	P value	95% confidence interval	
FAT	%$\dot{V}O_{2peak}$	0.0323	0.0038	8.56	0.000	0.0249	0.397
	%$\dot{V}O_{2peak}^2$	-0.0004	0.0000	-10.79	0.000	-0.0004	-0.0003
	Modality	-0.1768	0.0340	-5.20	0.000	-0.2435	-0.1101
	Constant	-0.1992	0.1185	-1.68	0.093	-0.4314	0.0330
CHO	%$\dot{V}O_{2peak}$	-0.0244	0.0094	-2.60	0.009	-0.0428	-0.0060
	%$\dot{V}O_{2peak}^2$	0.0009	0.0000	10.63	0.000	0.0007	0.0011
	Modality	0.3696	0.0848	4.36	0.000	0.2034	0.5358
	Constant	0.5210	0.2742	1.90	0.057	-0.0164	1.0585

CHO – carbohydrate; %$\dot{V}O_{2peak}$ – percent peak of oxygen consumption; %$\dot{V}O_{2peak}^2$ – percent peak of oxygen consumption squared

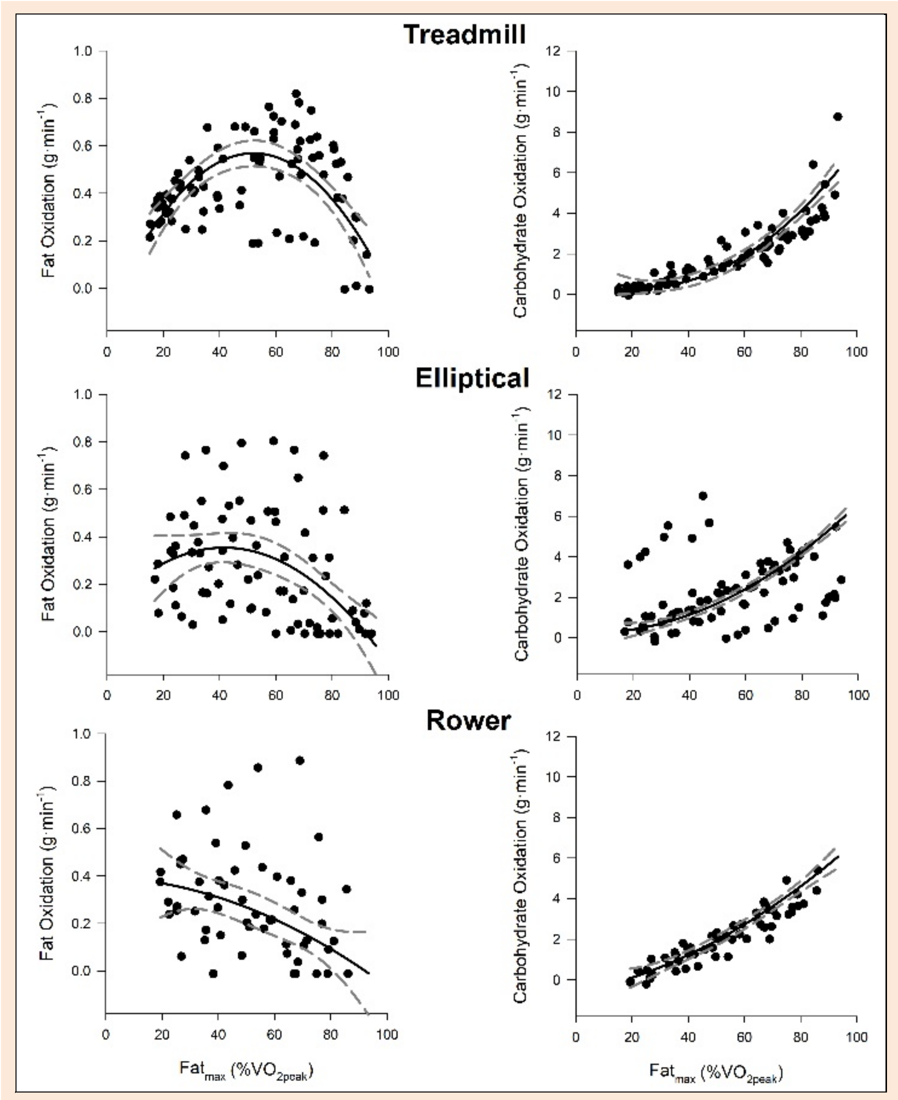

Figure 2. Scatter plot of fat and CHO oxidation over %$\dot{V}O_{2max}$ during treadmill, elliptical and rowing exercise. Trend line represents the nonlinear 2nd order polynomial regression and dotted lines represents the 95% confidence intervals. Regression values are presented in Table 1.

Discussion

The present study investigated the influence of whole-body exercises, including treadmill, elliptical, and rower exercise, on fat oxidation parameters in healthy individuals. The main findings of this study were: *i*) MFO and Fat_{max} were higher during the treadmill condition compared to both the elliptical and rower conditions, *ii*) there was no difference in crossover points between the three conditions, and *iii*) exercise modality influenced absolute rates of CHO and fat oxidation, and thereby modulated their respective curves across the exercise intensity spectrum. The present study supports previous work demonstrating that treadmill exercise results in higher MFO rates than other exercise modalities, and greater metabolic benefits may stem from walking and running exercise (Achten et al., 2003; Chenevière et al., 2010). This work provides critical metabolic insights that may promote further research focused on those suffering from metabolic conditions and physical disabilities.

$\dot{V}O_{2peak}$ values were similar between all three exercise modalities. Maximal $\dot{V}O_2$ values reflect the quantity of active muscle mass during exercise, indicating that all three modalities elicited similar levels of muscle activation. Previous research has identified level of active muscle mass as a mechanism for differences in fat oxidation, particularly between cycling and other whole-body modalities. Achten et al. (2003) and Chenevière et al. (2010) observed higher Fat_{max} values during treadmill exercise compared to cycling in moderately trained and trained individuals. Walking and running on a treadmill utilizes different muscle contraction regimes and elicits greater mechanical efficiency compared to cycling, which may be extended to include elliptical and rowing exercise. The eccentric component of the landing phase during treadmill exercise allows for muscle ‘preloading’, where mechanical energy is absorbed by the muscle and may improve the efficiency of the next contraction (Cavagna 1977; Chenevière et al. 2010). Additionally, the return of elastic energy may reduce recruitment of larger motor units consisting of greater Type II muscle fibres, influencing CHO metabolism, lactate production, and onset of peripheral fatigue (Carter et al. 2000; Chenevière et al. 2010).

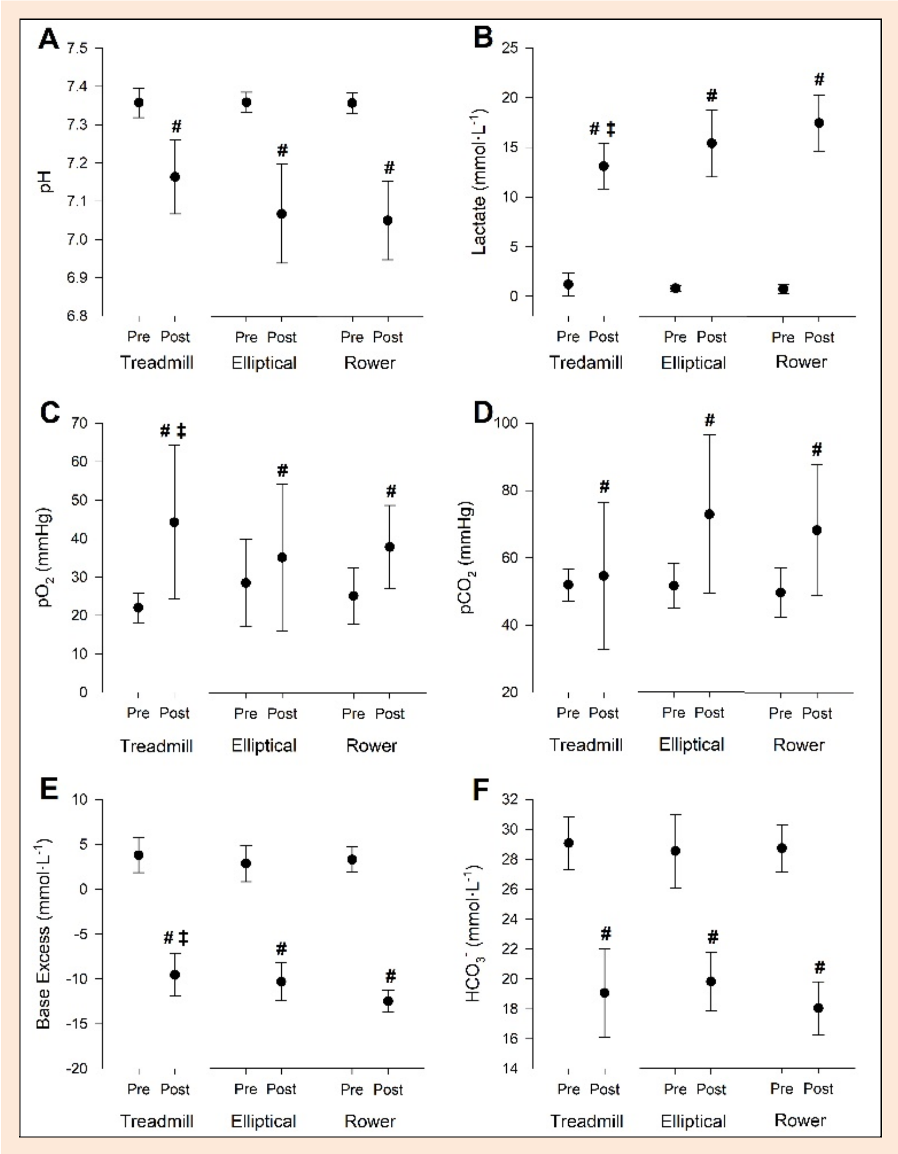

Figure 3. (A) Mean venous blood pH, (B) mean venous blood lactate concentrations, (C) mean partial pressure of oxygen, (D) mean partial pressure of carbon dioxide, (E) mean base excess of extracellular fluid, and (F) mean bicarbonate levels, pre- and post-exercise, between exercise modality. # significantly ($p < 0.05$) different from pre-exercise values, ‡ significantly ($p < 0.05$) different from rower post-exercise.

Egan et al. (2016) and Hagerman et al. (1988) both found that MFO was higher on the rower than the cycle ergometer, again attributable to greater muscle mass activation during rowing. However, the mean MFO rates and Fat_{max} values in the present study were lower on the rowing ergometer than Egan et al. (2016) reported (MFO: 0.71 ± 0.05 g·min^{-1}, Fat_{max}: 42 ± 1 %$\dot{V}O_{2peak}$). Modality-specific training status is highly correlated with MFO and metabolic efficiency, promoting greater fat oxidation (Hagerman, 1984). The present study used healthy males with no explicit training in rowing, while Egan et al. (2016) used club standard rowers. However, this study was designed to provide information for, and reflect how recreational individuals respond to different exercise modalities. Despite this, the lack of familiarization and training with alternative whole-body exercises, particularly during rowing, may have led to decreased efficiency and greater reliance on the muscles of the upper body compared to those who utilize these modalities more often. While untrained rowers display similar muscle synergies (spatiotemporal pattern of muscle activation) as trained rowers (Shaharudin and Agrawal, 2016), body posture and stroke technique can vary greatly between trained and untrained rowers (Cerne et al., 2013). Secher (1993) also detailed that untrained individuals will utilize less upper body movement and focus on the drive of the legs during rowing strokes with increased training. Therefore, even though similar levels in activation of muscle mass occurred between exercise modalities, as indicated by similar $\dot{V}O_{2peak}$ values, the specific muscles utilized for each modality may explain differences in fat oxidation.

Moreover, the lower MFO and Fat_{max} in elliptical and rower *vs.* treadmill could be associated with an increased recruitment of Type II muscle fibers (Achten et al., 2003; Chenevière et al., 2010). The present study demonstrated higher blood lactate concentrations post-exercise in both the elliptical and rowing conditions. Type II muscle fibres are less efficient than Type I muscle fibers since they rely primarily on carbohydrates as their energy source and produce lactate as a by-product (Knechtle et al., 2004). Treadmill exercise primarily uses muscles of the lower extremities, such as the gastrocnemius (Sozen, 2010), composed of a high percentage of Type I fibres (Costill et al., 1976). The elliptical and rower involve greater activation of many muscles of the upper body compared to the treadmill (Bazzucchi et al., 2013; Hagerman, 1984; Sozen, 2010). Although not all of the muscles of the upper body are mainly composed of Type II muscle fibres, the muscles of the upper limbs (i.e. Biceps Brachii, Triceps Brachii) have been known to have a greater percentage of these fibres (Klein et al., 2003; Miller et al., 1993). Finally, these muscles also generally have a smaller surface area than those of the lower body (Young et al., 1986) and the metabolic stress per muscle fibre is expected to be greater (Achten et al., 2003; Chenevière et al., 2010), thus increasing the production of lactate and CHO oxidation.

The increased reliance on muscles of the upper body, and subsequently Tyle II muscle fibres, may have influenced the overall fat oxidation curves for elliptical and rowing exercises (Figure 2). The regression analysis (Table 1) revealed that both fat and CHO oxidation curves were influenced by changes in $\%VO_2$, as well as exercise modality. Visually, curve fitting demonstrated a loss of curvilinearity of the fat oxidation curves in the elliptical and rowing exercise, as the apex of the curve (i.e. the point of maximal fat oxidation) occurred at low exercise intensities. Fat_{max} values for elliptical and rowing exercises were similar to those observed in overweight (Bogdanis et al., 2008) and inactive obese individuals during treadmill walking (Perez-Martin et al., 2001). The reduced ability of muscles to oxidize fat observed in obesity is suggested to result from increased intracellular lipid accumulation, leading to production of reactive oxygen species and disruption of mitochondiral oxidative enzymes (Wells et al., 2008). Therefore, factors such as exercise modalitiy and body weight, can heavily influence intrinsic cellular processes in skeletal muscle, altering substrate metabolism in these tissues.

The accumulation of lactate, and subsequent decrease in pH, lowers fatty acid oxidation with increasing exercise intensities (Achten and Jeukendrup, 2004) as they are known to inhibit long-chain fatty acid entry into the mitochondria (Sidossis et al., 1997). Lower muscle pH decreases the activity of carnitine palmitoyl transferase 1 (CPT-1), responsible for transporting long-chain fatty acids into the mitochondria (Starritt et al., 2000). Even though we did not observe a difference in plasma pH at the end of exercise between modalities, lactate concentrations were different between treadmill and rower, and it has been suggested that plasma lactate concentrations reflect changes in muscle pH (MacLean et al., 1999; Street et al., 2001). Our results further substantiate this response with higher base excess of extracellular fluid in the treadmill and elliptical compared to the rower condition. Previous research has shown that the lactate threshold occurs at a lower $\dot{V}O_2$ during incremental rowing exercise compared to treadmill, even when the same $\dot{V}O_{2max}$ is attained (Weltman et al., 1994). Blood lactate increases in a curvilinear fashion with increasing exercise intensity, resulting in an exponential increase during work above the lactate threshold (Goodwin et al., 2007). The onset of blood lactate accumulation is also highly correlation with the onset of muscle deoxygenation (Grassi et al., 1999). The potential for increased lactate accumulation at an earlier stage (lower $\dot{V}O_2$) during rowing exercise may have resulted in a prompter shift in metabolism, and therefore a higher concentrations of lactate at the end of exercise compared to the treadmill.

Interestingly, a higher venous partial pressure of O_2 was observed in the treadmill condition compared to the rower at the end of exercise. Increases in pO_2 are generally indicative of impaired diffusive O_2 capacity from the circulatory system to active muscles, as observed in mitochondrial myopathic patients (Taivassalo et al., 2002). Additionally, minute ventilation and oxygen pulse remained unchanged across conditions, thereby eliminating the possibility of a higher O_2 uptake at the pulmonary level. While a direct relationship would conclude that higher O_2 availability in venous blood would be the by-product of lower O_2 extraction in the rower condition, $\dot{V}O_{2peak}$ was similar across conditions. However, without blood flow or arterial blood gases we cannot conclusively state that lower O_2 extraction was at play in the present results.

Considerations

Limited use of an elliptical and/or rowing ergometer vs. treadmill in normal exercise routines may have impacted our results, as familiarity and technique with the elliptical and rowing ergometer varied between participants. Even though proper technical instructions and a familiarization session were provided, we cannot ignore possible influence of technique and lower mechanical efficiency, especially during rowing, on substrate oxidation. Therefore, these results may not be generalizable to individuals who use an elliptical or rowing ergometer frequently. Additionally, blood samples were only obtained from the antecubital vein for all three exercise modalities. Blood samples for the rowing and elliptical exercises may have been influenced by the metabolic activity of the arm due to greater upper extremity muscle activation during these exercises. Moreover, the sample used in the present study was composed of young and healthy individuals. Whether clinical or pathological populations would present similar metabolic responses to a variety of exercise modalities remains unknown.

Conclusion

While treadmill, elliptical and rower exercise modalities yield similar $\dot{V}O_{2peak}$ values, the research findings of the present study demonstrated that treadmill exercise elicited higher MFO, Fat_{max}, and absolute rates of fat oxidation compared to elliptical and rower exercise, and that substrate oxidation curves were clearly influenced by exercise modality. The treadmill remains the most efficient modality to increase fat oxidation during exercise and should be considered in training design for those looking to maintain a healthy metabolic profile.

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Key points

- The ability to oxidize fat has been associated with improved oxidative enzymes activity and mitochondrial biogenesis.
- The present study examined the effects of treadmill, elliptical, and rower exercises on maximal fat oxidation rates (MFO), the intensity were MFO was observed (Fat_{max}) and on fat oxidation curves in healthy and young participants.
- Both MFO and Fat_{max} were higher during treadmill exercise. Multiple linear mixed-effects regression analyses further revealed an effect of exercise modality on fat oxidation curves.
- Adequate selection of exercise modality during training may have a meaningful impact on substrate oxidation. Treadmill exercise should be considered in training design for those looking to maintain or improve metabolic profiling.

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