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Exercise intensity and oxygen uptake kinetics in African-American and Caucasian women

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Abstract

The effect of exercise intensity on the on- and off-transient kinetics of oxygen uptake (VO_2) was investigated in African American (AA) and Caucasian (C) women. African American (n=7) and Caucasian (n=6) women of similar age, body mass index and weight, performed an incremental test and bouts of square-wave exercise at moderate, heavy and very heavy intensities on a cycle ergometer. Gas exchange threshold (LT_{GE}) was lower in AA ($13.6 \pm 2.3 mL \cdot kg^{-1} min^{-1}$) than C ($18.6 \pm 5.6 mL \cdot kg^{-1} min^{-1}$). The dynamic exercise and recovery VO_2 responses were characterized by mathematical models. There were no significant differences in 1) peak oxygen uptake (VO_{2peak}) between AA ($28.5 \pm 5 mL\ kg^{-1} min^{-1}$) and C ($31.1 \pm 6.6 mL\ kg^{-1} min^{-1}$) and 2) VO_2 kinetics at any exercise intensity. At moderate exercise, the on- and off- VO_2 kinetics was described by a mono-exponential function with similar time constants $\tau_{1,on}$ (39.4±12.5s;38.8±15s) and $\tau_{1,off}$ (52.7±10.1s;40.7±4.4s) for AA and C, respectively. At heavy and very heavy exercise, the VO_2 kinetics was described by a double-exponential function. The parameter values for heavy and very heavy exercise in the AA group were respectively: $\tau_{1,on}$ (47.0±10.8;44.3±10s), $\tau_{2,on}$ (289±63;219±90s), $\tau_{1,off}$ (45.9±6.2;50.7±10s), $\tau_{2,off}$ (259±120;243±93s) while in the C group were respectively: $\tau_{1,on}$ (41±12;43.2±15s); $\tau_{2,on}$(277±81;215±36s), $\tau_{1,off}$ (40.2±3.4;42.3±7.2s), $\tau_{2,off}$ (215±133;228±64s). The on- and off-transients were symmetrical with respect to model order and dependent on exercise intensity regardless of race. Despite similar VO_2 kinetics, LT_{GE} and gain of the VO_2 on-kinetics at moderate intensity were lower in AA than C. However, generalization to the African American and Caucasian populations is constrained by the small subject numbers.

Keywords

Pulmonary O_2 dynamics; slow component; modeling; young women; race; cycle ergometer

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Introduction

The systematic characterization of the VO_2 kinetic response to a step increase in work rate is important in clinical instances in which the VO_2 kinetic response is markedly slowed in patients with heart, lung and skeletal muscle diseases. Analyses of the VO_2 kinetic responses to exercise have been found to be useful to detect impairment of oxygen delivery and utilization in patients with peripheral arterial disease (Bauer et al. 2004), metabolic myopathies (Grassi et al. 2009), and diabetes (Regensteiner et al. 1998).

The time course of the pulmonary oxygen uptake (VO_2) response in the transition from rest to constant-work-rate exercise (VO_2 on-kinetics), describes the rate at which the cardiorespiratory system is able to adjust delivery of oxygen to skeletal muscle and the rate at which oxygen is consumed by skeletal muscle (Barstow and Mole 1991; Grassi et al. 1996; Linnarsson 1974; Whipp and Wasserman 1972; Weissman et al., 1982; Whipp et al. 2005). The characterization of VO_2 kinetics provides indirect information on utilization of oxidative and glycolytic energy sources during skeletal muscle contraction (Jones and Poole, 2005). In particular, a faster VO_2 kinetics is associated with greater oxidative contribution to the ATP demand during exercise.

In most VO_2 kinetics studies, the data have been collected on male subjects. While few studies have investigated VO_2 kinetics in women (Regensteiner et al. 1998; Stathokostas et al. 2009), even less attention has been given to potential VO_2 kinetics differences between African American and Caucasian women. In the African American population, the characterization of on- and off- kinetics was obtained only in male adolescents (Lai et al., 2008) while other studies investigated racial differences in a) muscle oxidative capacity in women (Hickner et al., 2001; Hunter et al. 2001; Roy et al. 2006; Sirikul et al. 2006); and b) cardiovascular response in children of both sexes (Trowbridge et al. 1997) and in adult males (Berry et al. 1993; Vehrs et al. 2006). The maximal oxygen consumption (VO_{2max}) observed in healthy children (Trowbridge et al. 1997) and women (Hunter et al. 2001; Roy et al. 2006; Sirikul et al. 2006) was lower in African Americans than in Caucasians regardless of the level of physical activity. The reduced VO_{2max} has been related to lower muscle oxidative capacity and hemoglobin content in African Americans in comparison to Caucasians. In these studies, the skeletal muscle oxidative capacity was determined from the characterization of the recovery rate of ADP measured by magnetic resonance spectroscopy (MRS) technique after isometric plantar flexion exercise. The recovery rate of ADP was faster in Caucasian than in African American women.

Indication of physiologic and metabolic differences in lean African American and Caucasian women was also reported in studies (Chitwood et al., 1996; Hickner et a., 2003) performed during exercise at the whole body level with respiratory exchange ratio measurement at different workloads and in studies performed *in vitro* (Privette et al., 2003; Cortright et al., 2006) with skeletal muscle fat oxidation rate measurement. These *in vitro* and *in vivo* studies suggest that the skeletal muscle of lean African American women has a lower capacity to oxidize fatty acid than that of Caucasian women.

Neither lactate threshold nor the effect of exercise intensity on VO_2 kinetics was investigated in any of these studies (Berry et al. 1993; Chitwood et al., 1996; Cortright et al., 2006; Hickner et al., 2003; Hunter et al. 2001; Roy et al. 2006; Sirikul et al. 2006; Vehrs et al. 2006; Suminski et al., 2000). Lactate or gas exchange threshold (LT_{GE}) is often used in combination with VO_{2max} measurement to characterize aerobic fitness and endurance performance. These cardiorespiratory exercise performance parameters are also important factors for determining relative exercise intensity and prescribing exercise for subjects (Salvadego et al., 2010). VO_2 kinetics present different characteristics depending on the exercise intensity as determined on the basis of LT_{GE} and VO_{2max}. Higher values of LT, VO_{2max} and exercise economy were positively correlated with higher muscle oxidative capacity as represented by the percentage of type I fibers (Barstow et al., 1996). Therefore, lactate threshold, maximal aerobic power and exercise economy in combination with the characterization of VO_2 kinetics could be used to discriminate potential differences in bioenergetic and physiological function between groups at different exercise intensities. So far, this possibility has not been systematically investigated in a comparison of Caucasian versus African American women at different exercise intensities. Furthermore, it is not presently known whether the dynamic `on-off' O_2 uptake asymmetry with the slow component being evident at the on- but not, or much less prominently at, the off-transient described in males (Cunningham et al. 2000; Linnarsson 1974; Ozyener et al. 2001; Paterson and Whipp 1991) is also evident in women.

Therefore, the aim of the present study was to characterize and compare aerobic energetics parameters such as gas exchange threshold, maximal aerobic power, and pulmonary VO_2 on- and off-kinetics in healthy African American and Caucasian women.

Methods

Subjects

Thirteen healthy women (7 African Americans; 6 Caucasians) participated in the study (Table 1). All subjects gave written informed consent to take part in this study and were not smoking, taking medications, or involved in competitive athletics at the time of the study. All investigational procedures were approved by the University Hospital of Cleveland Institutional Review Board.

Exercise tests

Subjects reported to the laboratory on five occasions within a 2-week period. They were instructed to refrain from eating and exercise for 2 hours prior to each scheduled exercise test. All anthropometric measurements were obtained on day 1, prior to the maximal exercise test. Stature was measured with a standard, calibrated stadiometer (Seca, Vogel and Halke; Hamburg, Germany) and body mass with a balance beam scale (Seca, Vogel and Halke; Hamburg, Germany). All exercise tests were performed on an electronically braked cycle ergometer (Ergometrics 800, SensorMedics; Yorba Linda, CA) at approximately the same time of day and were completed within a period of two weeks.

On the first day the subjects performed a 20 $W \cdot min^{-1}$ incremental ramp test to the limit of tolerance for determination of peak VO_2 (VO_{2peak}) and gas exchange threshold (LT_{GE}) via respiratory measurements (Beaver et al. 1986). This allowed the delta parameter ($\Delta = VO_{2peak} - LT_{GE}$) to be determined for the assignment of the individual work rates for each of the exercise intensity domains investigated. On the four subsequent visits, the subjects performed a series of eight square-wave exercise tests; two per day, at selected work rates, which corresponded to: a) 90% LT_{GE} (moderate, M), b) LT_{GE} + 25% of Δ (heavy, H), and c) LT_{GE} + 75% of Δ (very heavy, VH). Each subject exercised three times at the moderate and heavy intensities and twice at the very heavy intensity. All square-wave tests were preceded by a 3-min baseline period (subjects sat quietly on the cycle ergometer) and a 3-min warm-up period (cycling at 20 W at a cadence of ~70 rpm). At the end of the test, the work rate was abruptly reduced to 20 W for a 10-min active recovery period, which was followed by an additional 5 minutes of passive recovery while the subjects remained seated quietly on the cycle. At all exercise intensities, the pedalling rate was kept constant at ~70 rpm. During moderate exercise, subjects exercised for 5 min at the predetermined work rate. During heavy exercise, subjects were asked to continue pedalling at the specified work rate until they had achieved a steady state, which was defined as 2 min of less than a 5% change in VO_2 as discerned from the computerized metabolic cart display.

Finally, during the very heavy exercise bouts, the subjects were asked to pedal until they could no longer maintain the pedalling frequency above 60 rpm despite vigorous encouragement. Instructions to begin and end testing were given by voice without warning. "Steady-state" values, for the moderate and heavy intensity tests were calculated by averaging data recorded over the last 30 sec of exercise and the end-exercise values for the very heavy exercise were averages over the last 15 sec. All square-wave tests performed on day two to five were assigned in a randomized sequence to avoid ordering effects. A break of 60–90 min was enforced between exercise bouts conducted on a single day.

Measurements of pulmonary gas exchange

Prior to exercise, and before data collection, a facemask (8940 Series, Hans Rudolph, Inc.; Kansas, MO) was carefully fitted and sealed with a gel (Hans Rudolph, Inc.) to obviate any gas leaks. The subjects were given several minutes to familiarize themselves with the breathing apparatus in order to minimize unusual breathing patterns. In order to measure gas exchange, subjects breathed through a mass flow sensor (hot-wire anemometer) connected to a metabolic measurement system (VMax 29, SensorMedics, Yorba Linda, CA). Before each exercise test, the volume sensor was calibrated using a 3-liter syringe while the O_2 and CO_2 analyzers were calibrated with gases of known compositions. Before, during, and after exercise and recovery, ventilatory and metabolic variables (minute ventilation (V_E), pulmonary oxygen uptake (VO_2) and carbon dioxide release (VCO_2)) were continuously monitored. These measurements permitted determination of the ventilatory equivalents for O_2 (V_E/VO_2) and CO_2 (V_E/VCO_2) as well as the respiratory exchange ratio (VCO_2/VO_2). A 3-lead electrocardiogram (SensorMedics, Yorba Linda, CA) was continuously displayed with heart rate determined from the R-R interval. Systemic systolic/diastolic blood pressure was measured every 3 min during the maximal exercise test with an automated cuff system (Tango, SunTech Inc.).

Data Processing, Modeling, and Dynamic Analysis

Prior to estimating parameter values, VO_2 data from individual repetitions of submaximal exercise at a constant predetermined work rate were processed. First, VO_2 data values greater than four standard deviations from their local means were omitted from those used for parameter estimation. Second, breath-by-breath responses for each trial were linearly interpolated to obtain a VO_2 value at each second. Corresponding values on a second-by-second basis were then ensemble-averaged to produce a mean VO_2 dynamic response. Then, averaged VO_2 values every two seconds were calculated and utilized for kinetic analysis. According to the strategy used by other investigators (Ozyener et al., 2001) data obtained during the first 20 sec of the on and off-transients were excluded from the analysis. To characterize the VO_2 kinetics responses to square wave changes in work rate, the nonlinear curve fitting function ("lsqcurvefit") available in Matlab (The Mathworks, Natick, MA) was customized and applied to the mean VO_2 responses and the exponential model listed below. For the on-transient phase, the following models were used:

Model 1:

$$\Delta VO_2(t) = VO_2(t) - VO_{2BL} = A_1 \cdot \left(1 - e^{-(t-\delta_1)/\tau_1}\right) \cdot U(t - \delta_1)$$

Model 2:

$$\Delta VO_2\,(t) = VO_2\,(t) - VO_{2BL} = A_1\cdot\left(1 - e^{-(t-\delta_1)/\tau_1}\right)\cdot U\,(t-\delta_1) + A_2\cdot\left(1 - e^{-(t-\delta_2)/\tau_2}\right)\cdot U\,(t-\delta_2)$$

For the off-transient:

Model 1:

$$\Delta VO_2\,(t) = VO_2\,(t) - VO_{2END} = \left(A_1\cdot e^{-(t-\delta_1)/\tau_1}\right)\cdot U\,(t-\delta_1)$$

Model 2:

$$\Delta VO_2\,(t) = VO_2\,(t) - VO_{2END} = \left(A_1\cdot e^{-(t-\delta_1)/\tau_1}\right)\cdot U\,(t-\delta_1) + \left(A_2\cdot e^{-(t-\delta_2)/\tau_2}\right)\cdot U\,(t-\delta_2)$$

where VO_{2BL} represents the steady-state VO_2 values at baseline (i.e., warm up, BL) and VO_{2END} is the VO_2 value at the end of active recovery; A_1 and A_2 are the amplitudes of the exponential terms; τ_1 and τ_2 are the time constants; and δ_1 and δ_2 are the time delays. The step functions $U(t-\delta_1)$ and $U(t-\delta_2)$ are used to constrain the exponential terms to their corresponding time domains. Accordingly, $U(t-\delta_1)$ takes a value of one when Phase II starts (i.e., at $t=\delta_1$). Subscripts “1” and “2” denote the fast (or fundamental) and slow components of Phase II and III of the pulmonary VO_2 dynamic response, respectively. From the Phase II and III amplitudes A_1', A'_2) and the change in work rate from baseline (ΔWR), the functional gains of the primary response (G_1) and the end-exercise response (G_{TOT}) were calculated: $G_1/\Delta WR$ and $G_{TOT} = A_1' + A'_2/\Delta WR$, where T_{End} is the end-exercise time and amplitudes are given by $A_1{}' = A_1\cdot\left(1 - e^{-(\delta_2-\delta_1)/\tau_1}\right)$ and $A_2{}' = A_2\cdot\left(1 - e^{-(T_{END}-\delta_2)/\tau_2}\right)$. Both models 1 and 2 were used to characterize the VO_2 dynamic responses. For each data set, an F-test was performed to evaluate whether the data were fit significantly better by model 2 than model 1 with a smaller number of parameters than model 2.

Statistical Analyses

All data are expressed as means ± SD. Comparisons of VO_2 and estimated kinetics parameters within a group were performed using a mixed model analysis of variance accounting for repeated measures on each subject. Post hoc analysis with a Tukey test was used to discern differences in the parameters among intensity domains. A $P\text{-value} \le 0.05$ was considered statistically significant. Statistical analyses were performed using Sigma Stat software (Sigma stat 2.03, SPSS, USA).

Results

Baseline physical characteristics and responses to the ramp exercise test are presented in Table 1. Participants from the two racial groups were similar in age, height, weight, and BMI. Also, there was no significant difference in VO_{2peak} and peak WR between groups; however, the two groups differed ($P < 0.05$) in VO_2 and WR at the LT_{GE}. In African Americans as compared to Caucasians, the VO_2 at the LT_{GE} was 0.81±0.19 (47.5±8% VO_{2peak}) versus 1.20±0.27 $l\cdot min^{-1}$ (59.8±18% VO_{2peak}) and occurred at work rates of 65±15 and 91±16 watts, respectively.

The on- and off-transient VO_2 responses of representative African American and Caucasian women during M, H, and VH intensities are shown in Fig. 1 and 2. Overall, an early cardiodynamic period (phase I) was evident for the VO_2 response at all work intensities ($\delta_{1,on}$~16 s) in both groups. The on- and off-transient VO_2 kinetics in both groups were well fitted by the single exponential model (Model 1) for M, while a double exponential model (Model 2) provided a statistically better description of the VO_2 responses to H and VH (Fig. 1 and 2). Thus, the gain of the fundamental component of the on- and off- kinetics (exercise and recovery) across the M, H and VH exercise intensity domains were symmetric with respect to the number of exponential terms (Model 1 vs. Model 2); these characteristics were independent of racial origin. The pulmonary oxygen uptake steady state values and kinetic parameters for the on- and off-transients during cycling exercise in African American and Caucasian women are presented in Tables 2 and 3, respectively.

Both groups presented similar pre-exercise (warm up) baseline VO_2 values (VO_2BL) regardless of exercise intensity (Table 2). Moreover, the mean VO_2 values at the end of active recovery were similar to the corresponding pre-exercise warm-up values at all intensities, i.e., VO_2 returned to baseline values (Table 2). As expected, the mean VO_2 values at the end of the on-transition period (VO_2E) increased ($P < 0.05$) with increasing exercise intensity in both groups. Between groups, however, Caucasians had a 27% higher VO_2E than African Americans at M and H ($P < 0.05$). At VH, VO_2E values were not significantly different between groups (Table 2).

The amplitude of the on-transient fundamental phase ($A_{1,on}$) of VO_2 increased with exercise intensity ($P < 0.05$) in both groups (Table 3). Between groups, $A_{1,on}$ was significantly greater ($P < 0.05$) in Caucasians at each corresponding intensity (M: 48%, H: 30%, and VH: 23%) than in African Americans (Table 3). Similar patterns were also observed during recovery. Specifically, $A_{1,off}$ increased with exercise intensity ($P < 0.05$) in both groups (Table 3). However, $A_{1,off}$ was significantly higher ($P < 0.05$) in Caucasians at M (43%) and H (30%) intensities than in African-Americans, but not at VH intensity. The duration of the time delay of the on-transient ($\delta_{1,on}$) and off-transient ($\delta_{1,off}$) fundamental phase did not differ significantly among the three exercise intensity domains (M, H, VH) nor between racial groups (Table 3). In general, within each racial group, the mean values of the fundamental time constants were independent of exercise intensity ($P>0.25$) during both the on- and the off-transient responses. Also, the values for $\tau_{1,off}$ were similar to those of $\tau_{1,on}$ in both groups at all intensities, except during M in African Americans ($\tau_{1,off}$: 53 s > $\tau_{1,on}$: 39 s; $P < 0.005$).

In both groups, a VO_2 slow component became evident after approximately three minutes of the on- and off-transient (Phase II) exercise responses at H and VH. The mean values of the phase III time constants of the on- and off-transient response ($\tau_{2,on}$, $\tau_{2,off}$) were similar and not different among work intensities or between races ($P > 0.05$), but they were several minutes longer than those corresponding to the fundamental component ($\tau_{1,on}$, ($\tau_{1,off}$)) (Table 3).

The magnitude of the functional gain of the fundamental phase $G_{1,on}$) at moderate intensity in African Americans was significantly lower than that measured in Caucasian women. At H and VH, $G_{1,on}$ was similar ($P > 0.05$) in both groups (Table 3). At H, the total exercise gains of the on-transient response ($G_{TOT},_{on}$) for African Americans and Caucasians were similar, but significantly greater than their respective fundamental gains (Table 3). During recovery, $G_1,_{off}$ was similar ($P>0.05$) for all exercise intensities in both groups while $G_{TOT},_{off}$ displayed a similar trend as during the on-transient ($P>0.05$). At VH, $G_{TOT},_{on}$ and $G_{TOT},_{off}$ showed similar behavior as during H (Table 3).

The end-exercise VO_2 percentage of VO_{2peak} attained during bouts of M, H, and VH corresponded to 45±6%, 67±8%, and 92±20% in African Americans; and 60±11, 80±10%, and 95±10% in Caucasians, respectively. During recovery, steady states for the pulmonary off-response were attained in approximately five minutes for M, seven minutes for H and within ten minutes for VH (Fig. 2).

Discussion

This is the first study to investigate the dynamics of the on- and off-transient pulmonary VO_2 responses to a step change in work rate of moderate, heavy, and very heavy intensity in healthy African American and Caucasian women. The main findings of this study were as follows: a) the LT_{GE} was significantly lower in African American women as compared to Caucasian women with similar aerobic power; b) VO_2 on- and off- kinetics responses in African American women were similar to those measured in Caucasian women while the gain of the fundamental component of the on- VO_2 kinetics at moderate exercise intensity was significantly lower in African American than Caucasian women; and c) on- and off-transients were symmetrical for M, H and VH in both groups.

The underlying mechanism for the apparent LT_{GE} difference between the two groups is challenging to ascertain. Neither group was involved in regular exercise beyond recreational activity nor were age, BMI, or VO_{2peak} significantly different between the two groups. Therefore, activity level and body composition of the two groups of women appeared to be very similar. However, since systematic assessment of the physical activity was not performed, it cannot be excluded that fitness level may contribute to the difference in the lactate threshold between these groups of women. The LT_{GE} difference between the two groups of women is statistically significant. The analysis of the 95 % confidence interval for the difference of the LT_{GE} means between the African American and Caucasian women (-0.64, -0.1 $L{\cdot}min^{-1}$) permits determination of a statistically significant racial effect size on LT_{GE}. The estimated LT_{GE} in Caucasians expressed as a percentage of the VO_{2peak} (60% VO_{2peak}) (Table 1) was similar to values found (57–60%) in the VO_2 kinetics studies of women with body weight and BMI values similar to those of our study (Fawkner et al. 2002; Regensteiner et al. 1998). Lack of data in the literature prevents a direct comparison between the LT_{GE} value (48% VO_{2peak}) of the African American women of our study and other women of the same age and racial group. However, the LT was close to that obtained in our previous study (Lai et al. 2008) on African American male adolescents (50% VO_{2peak}). Thus, our data have confirmed a tendency towards lower LT_{GE} in African Americans as compared to Caucasians. The LT_{GE} in African American women has never been investigated and compared with that in Caucasian women. Thus, this study provides evidence of a racial difference in LT_{GE} and confirms the importance of combined measurements of VO_{2peak} and LT_{GE} in determining cardiorespiratory exercise performance. It should be noted that these parameters are essential in exercise evaluation and prescription at different intensities in healthy and diseased populations (Salvadego et al. 2010). The combination of several factors such as acid-base regulation, ventilation, and oxygen delivery as well as the utilization of oxidative and glycolytic sources contributes to determine the lactate threshold. Higher glycolytic capacity and/or earlier development of metabolic acidosis might impair oxidative metabolism (Conley et al., 2000). An arm crank exercise study using Magnetic Resonance Spectroscopy (MRS) reported a lower intramuscular pH level during exercise in African-American than Caucasian men (Suminski et al., 2000). However, a limitation of our study is that LT was not directly determined by blood lactate measurements, but instead the noninvasive gas exchange LT was measured. This along with the absence of direct measures of muscle fiber type and glycolytic/oxidative properties prevents a conclusive explanation for the potential LT difference between African American and Caucasian women. Thus, further studies should be designed to investigate the factors associated with the lower gas exchange/ventilatory threshold (and perhaps the lactate threshold itself) in African American women.

The functional gain of the primary response of VO_2 ($G_{1,on}$) at heavy and very heavy exercise intensities was not significantly different between African American and Caucasian women and was close to that reported in a study conducted in men (Ozyener et al. 2001) (M: 11.5±0.8, H: 11±0.7, VH: 10.7±0.4). However, at moderate exercise intensity, $G_{1,on}$ was lower in African American than Caucasian females. The 95 % confidence interval for the difference of the $G_{1,on}$ means (−3.295, −0.1268) mL min^{-1} W^{-1} provides sufficient evidence to rule out the possibility that the two samples have the same $G_{1,on}$ means. Previous VO_2 kinetics studies (Barstow et al. 1996; Pringle et al. 2003) indicated that $G_{1,on}$ and ventilatory threshold were linearly correlated with the percentage of type I fibers which have a greater oxidative capacity than type II fibers. Further, other studies (Ama et al. 1986; Duey et al., 1997) of histochemical and biochemical skeletal muscle characteristics conducted in different racial groups suggested that in African Americans, skeletal muscle energy metabolism relies more on glycolytic than oxidative sources as compared to Caucasians.

A lower percentage of type I fibers and a correspondingly greater percentage of type II fibers could result in slower dynamic responses of VO_2 ($\tau_{1,on}$) (Pringle et al. 2003). Therefore, it would be expected that African Americans with a higher percentage of type II fibers than Caucasians should have had greater $\tau_{1,on}$ than Caucasian women. However, the $\tau_{1,on}$ values were similar and independent of race and exercise intensity (~ 44.0 s). Despite the finding that $\tau_{1,on}$ was independent of race, our results are consistent with those reported by Barstow et al. (1996), in which $\tau_{1,on}$ was not significantly correlated with the percentage of type I fibers. However, it is possible that our statistical power was not sufficient to affirmatively conclude that mean values of $\tau_{1,on}$ in African American are not significantly different from those in Caucasian women.

The hypothesis that African American women rely on a different pattern of oxidative and glycolytic energy sources in comparison to Caucasian women with similar physical activity and body composition characteristics would imply a racial difference that is expressed through lower VO_{2max}, lower LT_{GE}, and lower $G_{1,on}$, but similar VO_2 dynamic responses in African American as compared to Caucasian women. These predictions are based on the results of Barstow et al.(1996) and Ama et al. (1986). Barstow et al. (1996) found a positive correlation between LT_{GE} and $G_{1,on}$, on the one hand, and percentage of type I fiber composition on the other, but no relationship was evident for $\tau_{1,on}$. The results of Ama et al. (1986) suggest that African Americans generally have a lower type I percentage and higher type II percentage in terms of muscle fiber composition. Accordingly, on the basis of an assumed fiber type difference, our results (lower LT_{GE} in AA, lower $G_{1,on}$ in AA, and similar VO_2 kinetics between AA and C) coincide with predictions with the exception of no difference in VO_{2max} between the AA and C groups.

The cause of these apparent racial differences could be attributed to a different pattern of oxygen delivery and fiber recruitment within the skeletal muscle engaged during contraction. Although this hypothesis appears speculative in the absence of a characterization of the muscle blood flow dynamics and biochemical properties in these two groups, there is evidence for racial metabolic differences. Previous studies at the whole body level and in cell cultures showed that African Americans have a lower capacity of skeletal muscle to oxidize fatty acids than do Caucasians (Chitwood et al., 1996; Cortright et al., 2006; Hickner et a., 2003; Privette et al., 2003).

During heavy and very heavy intensity exercise, the inclusion of a second exponential term (slow component) in the model provided a statistically better fit (F-test) than using a single exponential in both groups. The time constants (fundamental, τ_1; and slow component, τ_2) of the on-transient response were not different between the two groups of women. At H, a steady state for VO_2 was achieved while at VH, a steady state VO_2 was not achieved in either group. This observation is consistent with previous findings in males demonstrating that in this domain, it was not possible for subjects to perform a constant work rate that provided a sustained VO_2 equivalent to a particular percentage of the VO_{2peak} (Wilkerson et al. 2004). As expected, the amplitude of the on-transient fundamental phase ($A_{1,on}$) of VO_2 increased with exercise intensity in both groups. The $A_{1,on}$ was greater in Caucasians than in African Americans at each corresponding intensity (M: 43%, H: 30%, and VH: 23%) because of a higher absolute work rate in correspondence with the greater LT_{GE} in the Caucasian group. The estimated amplitudes of the slow component ($A_{2,on}$) at H and VH were not significantly different between the races or among exercise intensities (Table 3). However, there was a trend for the VO_2 slow component to increase as exercise intensity increased. The $A_{2,on}$ was ~18% (H) and ~28% (VH) of the fundamental component in both groups. Although, $A_{1,on}$ was increased from moderate to very heavy exercise intensity, the $A_{2,on}$ was not significantly increased from heavy to very heavy intensity in either group. This could be attributed to the fact that neither group exercised for enough time to fully manifest the slow component at very heavy intensity. Indirect evidence in favor of this point is that the VO_2 values at the end of the exercise were not significantly different between groups at very heavy intensity (Table 3). In previous studies, the amplitude of the slow component was dependent on exercise intensity domain in adult males (Ozyener et al. 2001) but independent of exercise intensity in adolescent males (Lai et al. 2008).

During moderate intensity exercise the on- and off-responses were properly characterized using a single exponential model in both groups. These findings are in agreement with other studies which have reported that the VO_2 off-transient response to exercise below the LT follows a similar time course as that seen during the on-transient in male subjects (Linnarsson 1974; Ozyener et al. 2001). During H and VH, the characteristics of the on- and off-transient kinetics did not vary between the two groups of women. The symmetry in African-American as well as in Caucasian women seen before at moderate intensity domains, is also present at heavy and very heavy intensity domains for which both the on- and off- VO_2 responses were described by a double exponential function. These data are also consistent with previous findings in males (Cunningham et al. 2000; Lai et al. 2008) suggesting that the fundamental time course of exercise and recovery are independent of race and sex. However, this on-and-off symmetry observed in both Caucasian and African American women differs from results on males reported by Whipp and colleagues (Ozyener et al. 2001; Paterson et al. 1991), who showed that for heavy exercise the off-transient VO_2 could be adequately fitted by a monoexponential function, even when a double exponential provides a better fit for the on-transient data. Nevertheless, other studies agree with our results and have reported symmetry in the on- and off transient VO_2 kinetics for work rates performed above the LT (Cunningham et al. 2000).

An MRS study showed a faster recovery rate of ADP after plantar flexion exercise in Caucasian than African American women (Hunter et al. 2001; Sirikul et al. 2006). This result was attributed in part to a lower oxidative capacity of the skeletal muscle in African Americans than in Caucasians. Despite the racial difference in the ADP recovery found in these MRS studies, in our study the VO_2 recovery was not significantly different between groups. Therefore, it is possible that central and peripheral factors related to the ability of the cardiovascular and skeletal muscle systems to deliver oxygen to mitochondria may have influenced the dynamics of the VO_2 recovery (Berry et al. 1993; Hunter et al. 2001; Roy et al. 2006; Vehrs et al. 2006). While a reduced VO_{2peak} found in African American women compared to Caucasian women was correlated with a lower hemoglobin content and aerobic capacity in the African Americans (Hunter et al. 2001; Roy et al. 2006), a different study (Berry et al. 1993) found no racial difference in the cardiac output response to exercise while heart rate was lower in African Americans than in Caucasians. However, there is no clear evidence of racial group differences in exercise performance as measured by maximal aerobic power (Boulay et al. 1988; di Prampero and Cerretelli 1969).

In general, within each racial group of this study, the fundamental and slow time constants (τ_1; τ_2) were not significantly affected by work intensity. Similarly, the magnitudes of the functional gains of the fundamental and slow phases (G_1, G_2) of the on-transient were similar in African Americans and Caucasians. Yet, the G_1 and G_2 of the off-transient were similar regardless of work intensity or race. These results are in agreement with previous findings that support the concept of a linear relationship between the fundamental amplitude (Phase II) and work rate and an invariant time constant for all exercise intensities (Barstow et al. 1991 and 1996; Ozyener et al. 2001). However, other studies have reported variation of amplitude and time constant with differing exercise intensity (Hughson et al. 2000; Pringle et al. 2003). In fact, there is still disagreement on the linearity vs. non-linearity of amplitude and time constant to a step change in work rate at different intensities. In this context, the use of empirical models is very helpful for characterizing the dynamic response of VO_2; however, it introduces uncertainties regarding the meaning and value of the estimated parameters according to the model and method used to fit the data (Hughson et al. 2000). Thus, experimental and analytical methods to analyze VO_2 kinetics do not permit quantification of the extent of the factors such as oxygen transport (convection and diffusion) and cellular metabolism which affect VO_2 regulation under different experimental conditions. Alternatively, an integrative systems physiology approach that incorporates experimental data at different whole body levels (cell, fiber, organs) can quantify the main biochemical and biophysical processes responsible for the VO_2 regulation (Hughson et al. 2009; Lai et al. 2009).

In summary, the results of this investigation show a) racial differences in gas exchange/ventilatory threshold between African American and Caucasian women having similar maximal aerobic power; b) a smaller gain relative to work rate in the fundamental VO_2 response in African American women at moderate intensity, c) on-transient VO_2 kinetics in African American and Caucasian women are characterized by a monoexponential model for moderate exercise and a double exponential model for heavy and very heavy exercise intensity domains; and d) on- and off-transients are symmetrical with respect to model order and dependent on the exercise intensity. Despite these suggested differences, a limitation of the current study is the small number of subjects which limits statistical power and prevents definitive conclusions with regard to VO_2 dynamics in African American and Caucasian women. However, the racial difference in the LT_{GE} and fundamental gain at moderate exercise intensity are interesting findings in support of a potential difference in exercise endurance and utilization of oxidative and glycolytic sources in African American as compared to Caucasian women. These racial physiological differences are worthy of further studies in which muscle fiber composition, acid base regulation, and oxygen delivery during exercise are all measured in these groups of women.

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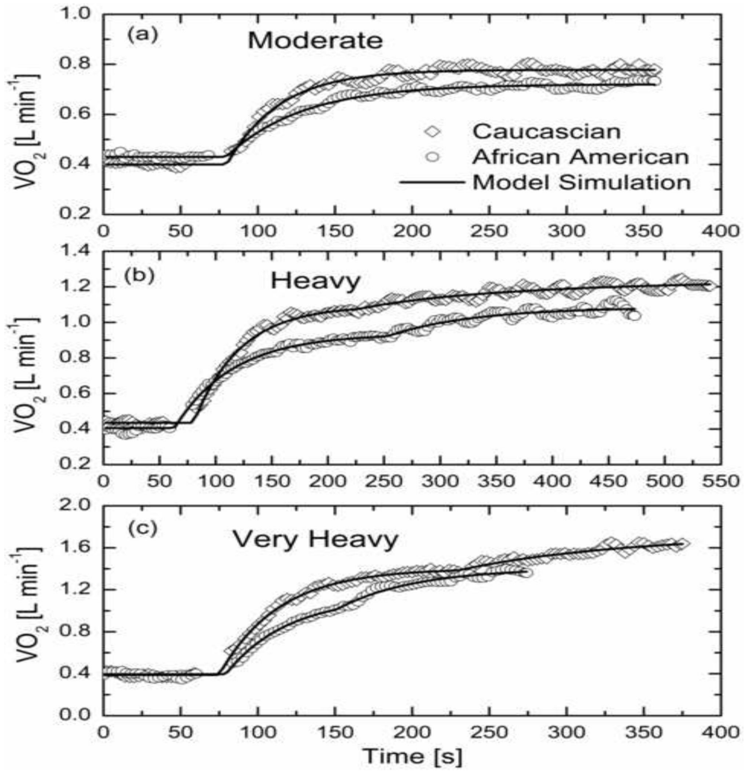

Figure 1.

Comparison of model simulations (line) and experimental data of mean VO_2 on-dynamic response to constant work rate exercise of moderate (M) (a), heavy (H) (b), and very heavy (VH) (c) intensity in a representative African American (circles symbols) and Caucasian (diamond symbols) women. The graphs of the mean responses are showed with 2 seconds intervals of time- and ensemble-averages of interpolated and time-aligned breath-by-breath data from individual transitions from warm up at 20 watts.

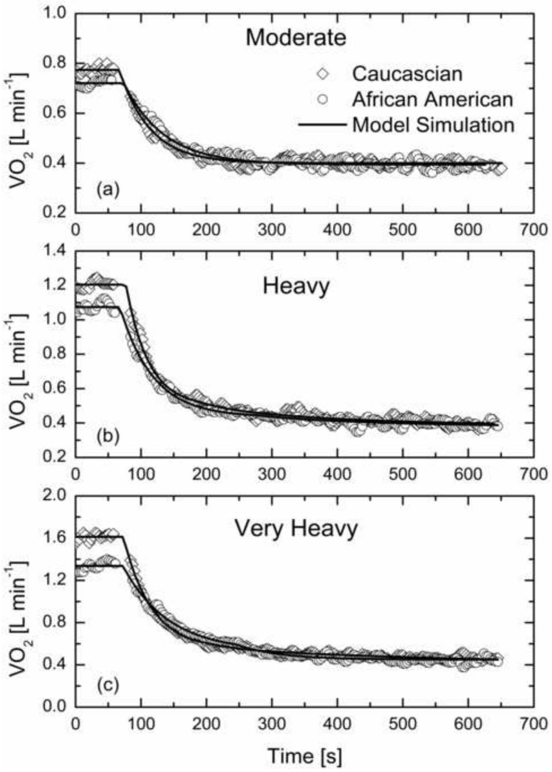

Figure 2.

Comparison of model simulations (line) and experimental data of mean VO_2 off-dynamic responses to constant work rate exercise of moderate (M) (a), heavy (H) (b), and very heavy (VH) (c) intensity in a representative African American (circles symbols) and Caucasian (diamond symbols) women. The graphs of the mean responses are showed with 2 seconds intervals of time- and ensemble-averages of interpolated and time-aligned breath-by-breath data from individual transitions.

Table 1

Subject characteristics by race.

		African Americans	Caucasians
	n	7	6
Age	(yr)	22.9±2.5	20.8±1.9
Height	(m)	1.69±0.05	1.65 ± 0.06
Weight	(kg)	59.3±8	64±12.5
Body Mass Index	($kg \cdot m^{-2}$)	20.7±2.6	23.5±3.8
VO_{2peak}	($L \cdot min^{-1}$)	1.7±0.4	1.9±0.2
VO_{2peak}	($mL \cdot kg^{-1} \cdot min^{-1}$)	28.5±5	31.1±6.6
WR at VO_{2peak}	(W)	143±27	165±17.2
LT_{GE}	($L \cdot min^{-1}$)	0.81±0.19	1.2±0.27[b]
LT_{GE}	($mL \cdot kg^{-1} \cdot min^{-1}$)	13.6±2.3	18.6±5.6[b]
Work Rate at LT_{GE}	(W)	65.0±14.7	91±16[b]

[b] $P < 0.05$, significant influence of race.

Table 2

Pulmonary oxygen uptake steady state values for warm up, moderate (M), heavy (H) and very heavy (VH) exercise by race.

	African Americans			**Caucasians**		
	M	**H**	**VH**	**M**	**H**	**VH**
VO_{2BL} (L·min^{-1})	0.41±0.04	0.40±0.06	0.43±0.04	0.44±0.04	0.46±0.05	0.40±0.05
VO_{2E} (L·min^{-1})	0.77±0.1	1.14±0.13[a]	1.57±0.3[a]	1.15±0.2[b]	1.53±0.19[b]	1.81±0.2[a]

[a] P<0.05, significantly different from other exercise intensities within group.

[b] P<0.05, significant influence of race (considering the specific intensity domain).

Table 3

Effect of exercise intensity on kinetic parameters of the VO_2 on and off-kinetics responses to square-wave exercise of moderate (M), heavy (H) and very heavy (VH) intensity by race.

	African Americans			Caucasians		
On	**M**	**H**	**VH**	**M**	**H**	**VH**
A_1 (L min^{-1})	0.36±0.12	0.67±0.15[a]	1.01±0.17[a]	0.69±0.19[b]	0.97±0.15[a,b]	1.27±0.16[a]
A_2 (L min^{-1})		0.12±0.09	0.29±0.32		0.17±0.08	0.35±0.2
δ_1 (s)	19.1±5.2	16.4±2.5	15.3±1.7	17.2±3.8	15.2±2.2	15.0±3.7
δ_2 (s)		174.6±35.8	107.0± 18.3		148.5±36.8	123.2±25.4
τ_1 (s)	39.4±12.5	47.0±10.8	44.3±10	38.8±15	41.0±12	43.2±15
τ_2 (s)		288.6±63	219.3±90		276.5±81	215.0±36
G_1 (mL min^{-1} W^{-1})	9.3±0.7	10.3±1.9	9.9±1.5	ll±0.9[b]	10.8±0.7	10.1±1.4
G_{TOT} (mL min^{-1} W^{-1})		12.3±1.85[c]	12.4±3.1[c]		12.7±1.1[c]	12.9±1.9[c]
OFF	**M**	**H**	**VH**	**M**	**H**	**VH**
A_1 (L min^{-1})	0.39±0.14	0.70±0.13[a]	1.03±0.26[a]	0.68±0.18[b]	1.00±0.17[a,b]	1.21±0.16[a]
A_2 (L min^{-1})		0.08±0.03	0.16±0.1		0.09±0.05	0.15±0.08
δ_1 (s)	14.0±1.3[d]	13.4±1.8	15.4±2.2	14.1±1.5	15.7±1.2	16.2±2.2
δ_2 (s)		142.7±74	151.6±26		142.7±44.7	149.5±31.6
τ_1 (s)	52.7±10.1[d]	45.9±6.2	50.7±10	40.7±4.4	40.2±3.4	42.3±7.25
τ_2 (s)		258.9±120	242.6±93		214.8±132.8	222.7±64.1
G_1 (mL min^{-1} W^{-1})	10.1±0.9	10.9±1.3	10.0±2.5	10.8±0.7	11.2±1.2	9.6±1
G_1 (mL min^{-1} W^{-1})		12.3±1.5[c]	11.5±3.2[c]		12.2±l[c]	10.8±1.6[c]

[a] $P<0.05$, significantly different from other exercise intensities within group.

[b] $P<0.05$, significant influence of race (considering the specific intensity domain).

[c] $P<0.05$, greater than their respective fundamental gains.

[d] $P<0.05$, significantly different from VO_2 on response (considering the specific intensity domain).