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To cite this version:

Joffrey Bardin, Hugo Maciejewski, Allison Diry, Claire Thomas, Sébastien Ratel. Sex-related differences in oxygen consumption recovery after high-intensity rowing exercise during childhood and adolescence. Pediatric Exercise Science, 2022, 34 (4), pp.210-218. 10.1123/pes.2021-0173 . hal-03906024

HAL Id: hal-03906024
https://hal-insep.archives-ouvertes.fr/hal-03906024

Submitted on 19 Dec 2022

Original article

Sex-related differences in oxygen consumption recovery after high-intensity rowing exercise during childhood and adolescence

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Running title: O_2 uptake recovery in young people

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DECLARATIONS

Author contribution statement

HM, CT and SR designed the research. JB, AD, HM, CT and SR collected the data and performed the research. JB, AD and SR analysed the data and supervised the research. JB and SR wrote the manuscript. JB, HM, AD, CT and SR provided critical revisions important for intellectual content of the finished manuscript, approved the final version of the manuscript, and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

Ethics approval

The present study was approved by an institutional ethics review board (Comité d'Éthique pour la Recherche en Sciences et Techniques des Activités Physiques et Sportives – CERSTAPS, n°2019-18-09-36) and conformed to the standards of use of human participants in research as outlined in the *Sixth Declaration of Helsinki*.

Consent to participate

Written informed consent was obtained from all individual included in the study and from their parents or legal guardians.

Consent for publication

Participants (and their parents or legal guardians) signed informed consent regarding publishing their data.

Acknowledgements

The authors thank Matthieu Chapron, Adrien Druenne, Camille Leclerc, Benjamin Leroux, Nathalie Capelle, all rowers for their participation, the Club of Aviron Marne Joinville, Quentin De Larochelambert and Alexis Baquet for their welcome, technical assistance and availability during this study.

Funding

The authors have no funding sources to declare.

Conflict of interest

The authors declare no competing interests. The results of the study are presented clearly, honestly and without fabrication, falsification or inappropriate data manipulation.

ABSTRACT

Purpose: The aim of this study was to determine sex-related differences in oxygen consumption recovery after high-intensity exercise during childhood and adolescence.

Methods: Forty-two boys and 35 girls (10–17 years) performed a 60-s all-out test on a rowing ergometer. Post-exercise oxygen consumption recovery was analysed from (i) the $\dot{V}O_2$ recovery time constant obtained from a bi-exponential model ($\tau_1\dot{V}O_2$), and (ii) excess post-exercise oxygen consumption calculated over a period of 8 minutes ($EPOC_8$) and until $\tau_1\dot{V}O_2$ was reached ($EPOC\tau_1$). Multiplicative allometric modelling was used to assess the concurrent effects of body mass (BM) or lean body mass (LBM), and age on $EPOC_8$ and $EPOC\tau_1$.

Results: $EPOC_8$ increased significantly more in boys from the age of 14 years. However, the sex difference was no longer significant when $EPOC_8$ was analysed using an allometric model including BM + age or LBM + age. In addition, despite a greater increase in $EPOC\tau_1$ in boys from the age of 14 years, $\tau_1\dot{V}O_2$ was not significantly different between sexes whatever age.

Conclusion: While age and LBM accounted for the sex-related differences of EPOC during childhood and adolescence, no significant effect of age and sex was observed on the $\dot{V}O_2$ recovery time constant after high-intensity exercise.

KEY WORDS: excess post-exercise oxygen consumption; $\dot{V}O_2$ recovery time constant; girls; multiplicative allometric modelling; age.

ABBREVIATIONS

ANOVA	Analysis of variance
AOD	Accumulated oxygen deficit
BM	Body mass
EPOC	Excess post-exercise oxygen consumption
EPOC_8	Excess post-exercise oxygen consumption calculated for 8 minutes after an all-out 60-s rowing exercise
$\text{EPOC}\tau_1$	Excess post-exercise oxygen consumption obtained until $\tau_1\dot{V}O_2$ was reached
LBM	Lean body mass
PCr	Phosphocreatine
$\tau_1\dot{V}O_2$	$\dot{V}O_2$ recovery time constant
$\dot{V}O_2$	Oxygen uptake
$\dot{V}O_{2\text{peak}}$	Peak oxygen uptake

INTRODUCTION

During the recovery from exercise, numerous physiological processes take place, aimed at restoring homeostasis, functional capacity and/or performance. These processes are not linear and their kinetics are widely different (27). The kinetics of these processes have mostly been studied in adults, although some comparative paediatric data do exist (18). From a cardio-respiratory perspective, some studies have reported a faster recovery of oxygen consumption ($\dot{V}O_2$) in prepubertal boys compared with men after high-intensity exercise (8, 15, 21, 40). For instance, using bi-exponential modelling, Zanconato et al. (40) reported a lower $\dot{V}O_2$ recovery time constant ($\tau_1\dot{V}O_2$) in 7-11-year-old children compared with 26-42-year-old adults after a one-minute cycle exercise performed at 125% of maximal oxygen uptake. However, given the small number of studies of children and the lack of data from adolescents, this finding remains to be confirmed. In addition, no study has analysed $\dot{V}O_2$ recovery kinetics in girls during high-intensity exercise and the concurrent effect of age and sex on $\tau_1\dot{V}O_2$ following high-intensity exercise during childhood and adolescence remains to be documented.

In the male population, several mechanisms have been proposed to explain the child-adult difference in the initial phase of $\dot{V}O_2$ recovery kinetics. Suggestions include the smaller body size of prepubertal boys which reduces circulation time into the blood compartment (12). Moreover, due to their different body composition (*e.g.*, less lean body mass (LBM)) prepubertal children are likely to have lower nonoxidative metabolism at the onset of high-intensity exercise (6, 13), allowing a faster post-exercise $\dot{V}O_2$ recovery. If these mechanisms hold true, one might suggest that $\tau_1\dot{V}O_2$ could be shorter in girls compared to boys from the age of 14 years. Indeed, it has recently been shown that non-oxidative energy production measured from accumulated O_2 deficit (AOD) increases more extensively in boys than girls from the age of 14 years (6), *i.e.* about the time of significant sex-related changes in LBM and fat mass (7, 36). However, this assumption remains to be proven.

Beyond the $\dot{V}O_2$ recovery kinetics, post-exercise O_2 consumption is also characterised by the amount of O_2 to be refunded after high-intensity exercise, *i.e.* excess post-exercise oxygen consumption (EPOC). The amount of post-exercise O_2 represents the additional amount of O_2 used by the body to re-establish metabolic homeostasis related to increased body temperature, hormone production, and energy substrate depletion during exercise (5, 19). EPOC could be associated with AOD and its determinants, *i.e.* exercise intensity and duration (5, 25), and individual body dimensions (35). Indeed, Tahara and colleagues (35) showed significant positive correlations between EPOC, body mass (BM) and LBM in 16- to 21-year-old male athletes. This result has also been reported by Campos et al. (9) in 28-year-old professional cyclists for whom EPOC was positively associated with total and lower limb lean mass. A higher muscle power production associated with greater lower limb lean mass could more favourably increase AOD, and thereby EPOC and $\tau_1\dot{V}O_2$ (the two parameters being positively correlated in the study by Campos et al. (9)). To our knowledge, changes in EPOC during childhood and adolescence have not been studied. However, as for $\tau_1\dot{V}O_2$, EPOC may increase more extensively in boys than girls from the age of 14 years due to a greater gain in BM, particularly LBM and greater concomitant metabolic disturbances during high intensity exercise in boys at the time of puberty (6). In addition, while the concept of EPOC has been used in adults, it has been mostly expressed ratio-scaled with BM to compare populations of different body size and composition (*e.g.*, males vs females or sprinters vs long distance runners) (26, 31). However, ratio scaling with BM has been demonstrated to be inappropriate for comparing children and adolescents of both sexes (37, 38), as ratio scaling with BM does not create BM-free physiological variables during childhood and adolescence (38). Numerous studies have demonstrated the fallacy of ratio scaling physiological variables and it has been compellingly argued that with cross-sectional data, allometric scaling based on log-linear regression with multiple covariates is the method of choice when investigating the development of physiological variables during growth (30, 37, 38).

Furthermore, as sex-related differences in EPOC between girls and boys from age 14 onwards could be influenced not only by changes in BM but also by concurrent changes in age, growth and maturation. Thus, concurrently controlling for both BM + age is preferred to just controlling for BM (2, 3, 37). However, as fat mass is metabolically inert (20), LBM as a surrogate of muscle mass is likely to be a more appropriate covariate of physiological variables during exercise than BM (2, 3). LBM varies with age and sex (7), therefore, allometric analyses including both LBM + age as covariates are likely to provide more insights into EPOC than when EPOC is allometrically scaled with BM + age. In addition, previous studies of both paediatric aerobic and anaerobic fitness have consistently demonstrated that with LBM + age controlled for, maturation is a non-significant covariate (2, 3).

Therefore, the aim of the present study was to examine sex-related differences in $\dot{V}O_2$ recovery kinetics (*i.e.*, $\tau_1\dot{V}O_2$) and EPOC after high-intensity exercise during childhood and adolescence. We hypothesised that (i) boys would have higher absolute EPOC values than girls from the age of 14 years, (ii) the sex difference would persist when EPOC is allometrically scaled with BM + age, (iii) the sex difference would not be significant when EPOC is allometrically scaled with LBM + age, and (iv) girls would have faster $\dot{V}O_2$ recovery kinetics than boys from the age of 14 years (*i.e.*, lower $\tau_1\dot{V}O_2$).

MATERIALS AND METHODS

Subjects

Forty-two male and thirty-five female rowers aged from 10 to 17 years volunteered to participate in the present study. All participants trained on average “on water” two to three times per week with similar training volumes between girls and boys. Training sessions lasted from 60 to 90 min and included various exercises aimed at improving rowing performance through movement technique, coordination in the boat between rowers, pacing strategies, etc. The training programme was specifically designed to improve rowing mechanical efficiency rather than components of physical fitness, notably anaerobic capacity or muscle strength. None of the participants had a family history of cardiovascular disease or was under medication. The present study was approved by an institutional ethics review board (Comité d'Éthique pour la Recherche en Sciences et Techniques des Activités Physiques et Sportives – CERSTAPS, n°2019-18-09-36) and conformed to the standards of use of human participants in research as outlined in the *Sixth Declaration of Helsinki*. The participants were informed of the experimental procedures and gave their written assent before any testing was conducted. In addition, written informed consent was obtained from the parents or legal guardians of the participants.

Experimental design

Volunteers were tested in two experimental sessions separated by at least 48 hours. Participants were instructed not to undertake any strenuous activity during the 24 hours preceding each session. The first session was dedicated to gathering participants' physical characteristics (anthropometric measurements and body composition) and peak oxygen uptake ($\dot{V}O_{2peak}$) assessment. During the second session, the volunteers performed a 60-s all-out test. The two exercise sessions were carried out on a rowing ergometer (Model D, Concept2, Morrisville, VT, USA). The participants were fully familiarised with the equipment. The computer of the ergometer continuously delivered the power output. The resistance factor was set by the investigators between 100 and 130 according to age, sex, and the expertise level of young rowers. The same resistance factor was kept for both tests. Verbal encouragement was systematically provided by the investigators during each exercise session.

Experimental measurements

Session 1: anthropometric characteristics and body composition

Body mass (BM in kg) was measured using a digital weight scale with a precision of ± 0.01 kg (Seca 899, Seca, Germany). Standing height (in m) was assessed using a stadiometer with a precision of ± 1 mm (Seca 213, Seca, Germany). Skinfold thicknesses were measured at the triceps and subscapular sites using a Harpenden calliper (British Indicators Ltd, St Albans, UK) and the mean value from three reproducible measurements was calculated. The measurements were taken by the same experienced investigator on the right side of the body to reduce variability in the results for girls and boys. Body fat percentage and LBM (in kg) were determined using the equations developed by Slaughter et al. (34). These equations are specific to sex, ethnicity and age, and are recommended for assessing body fat and LBM in children and adolescents (8-18 years of age).

Session 1: maximal oxygen uptake test

Each participant performed a progressive test to exhaustion to determine $\dot{V}O_{2peak}$ (in $L \cdot min^{-1}$). The initial power was set between 40 and 80 W during the first five minutes and the power was incremented by 10-30 W every 3 minutes according to age, sex and the expertise level of participants.

Oxygen uptake, carbon dioxide output and ventilation were continuously monitored using a breath-by-breath analyser (Quark CPET, Cosmed, Italy). The gas analysers were calibrated before each test using a gas mixture of known concentration (16.0% O_2 and 5% CO_2). Calibration of the flowmeter was performed with a 3-L air syringe. Heart rate was continuously recorded with a heart rate monitor (HRM-Dual, Garmin, Kansas, USA). $\dot{V}O_{2peak}$ was considered to be reached during the last step when at least two of the following criteria were met: (i) $\dot{V}O_2$ levelling-off, (ii) maximal respiratory exchange ratio ≥1.1 and (iii) maximal heart rate ≥ 95% of the age-predicted maximal heart rate (208.609 – 0.716 · age) (33). Forty-eight (62%) participants out of 77 showed a $\dot{V}O_2$ plateau at completion of the maximal test. The criterion for a $\dot{V}O_2$ plateau was the $\dot{V}O_2$ levelling-off despite an increase in minute ventilation at maximal effort (16).

Session 2: 60-s all-out test

After a standardised 15-min warm-up at about 130-140 beats·min^{-1} and two short sprints (10-s) in the last 5 minutes, all participants performed a 60-s rowing all-out test followed by an 8-min sitting recovery. Before starting the test, each participant was requested to ensure that their technique is as close as possible to what they would do on the water. The starting position was standardized so as the participants have the arms straight, the knees against the trunk, the shoulders in front of the hips and the shins vertical. The feet were strapped during the test. The 60-s all-out test was performed 10-min after the end of the warm-up. They were asked to participants to provide their maximal effort at each stroke throughout the test. No feedback was given on split time, stroke rate or covered distance. The investigators strongly encouraged the volunteers during each test. Cardio-respiratory parameters were continuously measured using a breath-by-breath analyser (Quark CPET, Cosmed, Italy). Individual accumulated oxygen deficit (AOD in L O_2 Eq.) was determined as previously described (6, 13). In addition, the recovery kinetics of oxygen consumption were modelled and the excess post-exercise oxygen consumption (EPOC) calculated (see below for further details).

Measurements and calculations

Oxygen uptake recovery kinetic modelling

The post-exercise $\dot{V}O_2$ recovery kinetics were determined by considering the net changes of each value, *i.e.* minus baseline (net $\dot{V}O_2$, in L·min^{-1}), which was obtained during 3-min before the warm-up. The breath-by-breath $\dot{V}O_2$ were interpolated second-by-second between 0 and 8 minutes and the recovery kinetics were then modelled using a biexponential function (Origin 2020b, Massachusetts, USA), as previously proposed after high-intensity exercise (40):

$$\dot{V}O_2(t) = A \times e^{\frac{t}{\tau_1}} + B \times e^{\frac{t}{\tau_2}} + C \qquad \text{(Eq. 1)}$$

where $\dot{V}O_2(t)$ is the oxygen uptake at the time t, A and B the amplitudes of the fast and slow components, respectively, τ_1 and τ_2 the corresponding time constants and C the $\dot{V}O_2$ at rest. The determination coefficients (r^2) ranged between 0.82 and 0.98 (mean ± SD: 0.93±0.03; IC95%: 0.92-0.94).

Excess Post-exercise Oxygen Consumption (EPOC) calculation

Excess post-exercise oxygen consumption was calculated by subtracting the integrated area under resting $\dot{V}O_2$ from the integrated area under the $\dot{V}O_2$ recovery curve over the first 8 minutes of recovery ($EPOC_8$) and until τ_1 was reached ($EPOC\tau_1$). $EPOC\tau_1$ was calculated to quantify the rapid replenishment of phosphocreatine as well as reoxygenation of myoglobin (19). Those two parameters were expressed in absolute value (L), and with allometric exponents (*i.e.*, BM + age; LBM + age) (see below for further details). The $EPOC_8$/AOD ratio was also calculated to know whether the changes in AOD and $EPOC_8$ evolved in the same proportions during childhood and adolescence with respect to sex.

Allometric modelling procedure

As BM, LBM and age may have influenced EPOC during recovery, we further investigated the influence of these factors on $EPOC_8$ and $EPOC\tau_1$ through a multiplicative allometric model proposed by Nevill and Holder (29). This procedure considers the influence of the size descriptor (*i.e.*, BM or LBM) and age on EPOC variables (*i.e.*, $EPOC_8$ or $EPOC\tau_1$) as follows:

$$\text{EPOC variable} = \text{size descriptor}^{\,b} \cdot \exp(a + c \cdot \text{age}) \cdot \varepsilon \qquad \text{(Eq. 2)}$$

where *a* is the proportionality coefficient, *b* the scaling factor associated with the size descriptor (*i.e.*, BM or LBM), *c* the scaling factor associated with age, and *ε* the normally distributed error. The statistical approach to allometry is to use a multiple logarithmic transformation, as previously done by Carvalho et al. (10), as follows:

$$\log(\text{EPOC variable}) = b \cdot \log(\text{size descriptor}) + a + c \cdot \text{age} + \log \varepsilon \qquad \text{(Eq. 3)}$$

where *a* is the intercept, *b* and *c* are the slopes of the multiple linear regression. These slopes are calculated by ordinary multiple regression analysis (Rstudio, Massachusetts, USA) where *b* and *c* are equal to the scaling factors.

Statistical analysis

Statistical procedures were performed using Statistica 8.0 software (Statsoft, Inc., USA). Descriptive statistics were expressed as mean ± standard deviation (SD) by age group (group 1: 10-11.9 yr, group 2: 12-13.9 yr, group 3: 14-15.9 yr, group 4: 16-17.9 yr) and sex, as proposed by Doré et al. (14) and Bardin et al. (6). Data were screened for normality of distribution and homogeneity of variances using a Shapiro-Wilk test and the Levene's test, respectively. Two-way ANOVA was used to examine the effects of sex and age group on the participants' physical and fitness characteristics, EPOC_8 and $\text{EPOC}\tau_1$ (in absolute values and scaled with allometric exponents), AOD, EPOC_8/AOD ratio and $\tau_1\dot{V}O_2$. When ANOVA revealed a main or interaction significant effect, an HSD Tukey's *post-hoc* test was applied to test the discrimination between means. The effect size and statistical power have also been reported. The effect size was assessed using the partial eta-squared (η^2) and ranked as follows: ~ 0.01 = small effect, ~ 0.06 = moderate effect, ≥ 0.14 = large effect (11). Linear regression models between age, BM, LBM, EPOC_8, $\text{EPOC}\tau_1$ and AOD were fitted by the least-squares method by considering boys and girls separately, and the squared Bravais-Pearson determination coefficients (r^2) of these linear regression models were calculated. The linear regressions between age, BM, LBM, EPOC_8 and $\text{EPOC}\tau_1$ were established to check the effects of age, BM and LBM on EPOC_8 and $\text{EPOC}\tau_1$ and then justify the use of BM + age or LBM + age as scaling factors through the multiplicative allometric models. The statistical significance level was set at 5% ($p < 0.05$).

RESULTS

Participants' physical and fitness characteristics

Participants' characteristics are described by age group and sex in Table 1. Statistical analysis revealed significant sex × age group interaction effects for height ($F_{(3, 69)} = 5.69$, $p < 0.001$, $\eta^2 = 0.20$, power = 0.93), BM ($F_{(3, 69)} = 7.98$, $p < 0.001$, $\eta^2 = 0.26$, power = 0.99), body fat ($F_{(3, 69)} = 3.40$, $p < 0.05$, $\eta^2 = 0.13$, power = 0.74), LBM ($F_{(3, 69)} = 11.85$, $p < 0.001$, $\eta^2 = 0.34$, power = 0.99) and $\dot{V}O_{2peak}$ in absolute values ($F_{(3, 68)} = 11.00$, $p < 0.001$, $\eta^2 = 0.33$, power = 0.99) but not for $\dot{V}O_{2peak}$ allometrically scaled with LBM + age ($F_{(3, 68)} = 0.64$, $p = 0.593$, $\eta^2 = 0.03$, power = 0.18). No sex-related significant difference was observed for height, LBM and $\dot{V}O_{2peak}$ before the age of 14 years, and for BM before the age of 16 years. However, between

14.0 and 17.9 years, boys exhibited significantly higher values than girls for height, LBM and $\dot{V}O_{2peak}$ ($p < 0.001$). Boys also showed significantly higher values than girls for BM ($p < 0.01$) between 16.0 and 17.9 years. Finally, girls had significantly higher values for body fat than boys whatever age group ($p < 0.05$ at least).

- Please insert Table 1 near here –

Determination coefficients and allometric exponents

In boys, age was positively correlated with BM ($r^2 = 0.67$, $p < 0.001$) and LBM ($r^2 = 0.68$, $p < 0.001$). In girls, age was positively correlated with LBM ($r^2 = 0.11$, $p < 0.05$) but not with BM ($p = 0.143$). $EPOC_8$ was positively associated with age (boys: $r^2 = 0.75$, $p < 0.001$; girls: $r^2 = 0.37$, $p < 0.001$), BM (boys: $r^2 = 0.79$, $p < 0.001$; girls: $r^2 = 0.27$, $p < 0.001$), LBM (boys: $r^2 = 0.83$, $p < 0.001$; girls: $r^2 = 0.38$, $p < 0.001$) and AOD (boys: $r^2 = 0.85$, $p < 0.001$; girls: $r^2 = 0.19$, $p < 0.01$). $EPOC\tau_1$ was positively correlated with age (boys: $r^2 = 0.61$, $p < 0.001$; girls: $r^2 = 0.19$, $p < 0.01$), BM (boys: $r^2 = 0.70$, $p < 0.001$; girls: $r^2 = 0.28$, $p < 0.001$) and LBM (boys: $r^2 = 0.76$, $p < 0.001$; girls: $r^2 = 0.35$, $p < 0.001$). Allometric scaling exponents are displayed by sex in Table 2.

- Please insert Table 2 near here –

Accumulated oxygen deficit

AOD values are displayed by age group and sex in Table 3. Two-way ANOVA showed a sex × age group interaction effect for AOD ($F_{(3, 64)} = 10.84$, $p < 0.001$, $\eta^2 = 0.33$, power = 0.99). *Post-hoc* tests showed significantly higher values for AOD in boys than girls between 14.0 and 17.9 years ($p < 0.001$).

- Please insert Table 3 near here -

Excess post-exercise oxygen consumption

EPOC$_8$, EPOC$_8$/AOD ratio and EPOCτ_1 are displayed by age group and sex in Table 3. Two-way ANOVA revealed a significant sex × age group interaction effect for absolute EPOC$_8$ ($F_{(3, 69)} = 13.05$, $p < 0.001$, $\eta^2 = 0.36$, power = 0.99). *Post-hoc* tests showed significantly higher EPOC$_8$ with increasing age ($p < 0.01$ at least) in both sexes. *Post-hoc* tests also showed significantly higher values for absolute EPOC$_8$ in boys than girls between 14.0 and 17.9 years ($p < 0.001$). However, there was neither a significant age effect ($F_{(3, 69)} = 0.97$, $p = 0.413$, $\eta^2 = 0.04$, power = 0.25) nor a sex × age group interaction effect ($F_{(3, 69)} = 1.25$, $p = 0.298$, $\eta^2 = 0.05$, power = 0.32) for EPOC$_8$ allometrically scaled with BM + age. In the same way, there was neither a significant age effect ($F_{(3, 69)} = 1.01$, $p = 0.394$, $\eta^2 = 0.04$, power = 0.26) nor a sex × age group interaction effect ($F_{(3, 69)} = 1.24$, $p = 0.303$, $\eta^2 = 0.05$, power = 0.32) for EPOC$_8$ allometrically scaled with LBM + age. Two-way ANOVA also showed no sex × age group interaction effect for EPOC$_8$/AOD ratio ($F_{(3, 64)} = 0.30$, $p = 0.827$, $\eta^2 = 0.01$, power = 0.10).

Two-way ANOVA revealed a significant sex × age group interaction effect for absolute EPOCτ_1 ($F_{(3, 69)} = 9.99$, $p < 0.001$, $\eta^2 = 0.30$, power = 0.99). *Post-hoc* tests showed significantly higher EPOCτ_1 with increasing age for boys but not for girls ($p < 0.001$). *Post-hoc* tests also showed significantly higher values for absolute EPOCτ_1 in boys than girls between 14.0 and 17.9 years ($p < 0.001$). However, there was neither a significant age effect ($F_{(3, 69)} = 0.41$, $p = 0.745$, $\eta^2 = 0.02$, power = 0.13) nor a sex × age group interaction effect ($F_{(3, 69)} = 2.36$, $p = 0.078$, $\eta^2 = 0.09$, power = 0.57) for EPOCτ_1 allometrically scaled with BM + age. In the same way, there was neither a significant age effect ($F_{(3, 69)} = 0.61$, $p = 0.611$, $\eta^2 = 0.03$, power = 0.17) nor a sex

× age group interaction effect ($F_{(3, 69)} = 1.56$, $p = 0.206$, $\eta^2 = 0.06$, power = 0.39) for EPOCτ_1 allometrically scaled with LBM + age.

Recovery time constant

Oxygen uptake during and after the all-out 60-s rowing test in boys and girls is shown in Figure 1. Oxygen uptake recovery time constant ($\tau_1\dot{V}O_2$) is displayed in Table 3. Two-way ANOVA revealed a significant main effect for sex ($F_{(3, 69)} = 8.47$, $p < 0.01$, $\eta^2 = 0.11$, power = 0.82) but not for age ($F_{(3, 69)} = 0.52$, $p = 0.671$, $\eta^2 = 0.02$, power = 0.15). No significant sex × age group interaction effect was observed for $\tau_1\dot{V}O_2$ ($F_{(3, 69)} = 2.57$, $p = 0.061$, $\eta^2 = 0.10$, power = 0.61).

- Please insert Figure 1 near here –

DISCUSSION

The purpose of the present study was to determine during childhood and adolescence the effects of age and sex on oxygen uptake recovery after high-intensity exercise. The main results confirm our first hypothesis since the absolute amount of O_2 consumed during recovery (EPOC$_8$ and EPOCτ_1) increased more extensively in boys than girls from the age of 14 years, and EPOC$_8$ and EPOCτ_1 were no longer significantly different with respect to age and sex when the effects of LBM + age were considered in allometric modelling. However, the results of the present study do not confirm our last hypothesis since we do not show a difference between girls and boys in the $\dot{V}O_2$ recovery time constant ($\tau_1\dot{V}O_2$) from 10 to 17 years old. Therefore, despite the more significant increase in EPOC in boys compared to girls from 14 years of age due to their greater LBM gain, the $\dot{V}O_2$ recovery kinetics after high-intensity exercise were not different between sexes during childhood and adolescence.

The results of the present study show, for the first-time, a significant age × sex interaction effect on $EPOC_8$, indicating an increase in excess post-exercise oxygen consumption after high-intensity exercise from childhood into adolescence, with higher absolute values in boys from the age of 14 years. This result is likely explained by the sex-related changes in body size and composition between girls and boys with advancing age since a sex difference was no longer significant when $EPOC_8$ was analysed using a multiplicative allometric modelling including either BM + age or LBM + age. The absence of difference in results between BM + age and LBM + age as scaling factors is noteworthy because of the normally marked sex-related differences in LBM and fat mass from the age of about 14 years (7). This finding could be explained by the nature of rowing that is a BM-supported activity and where body composition (LBM vs fat mass) could have less effect on physiological responses during exercise than non-BM-supported activities such as running. Also, in the present study, girls exhibited no significant difference in fat mass between age groups probably due to their training activity (Table 1), thereby attenuating the effect of sex-related differences in body composition on EPOC. Another point of consideration in the present study is that, once age was controlled for, $EPOC_8$ increased proportionally more than BM and LBM in boys (b: 1.11 and 1.10, respectively). However, this was not the case in girls (b: 0.61 and 0.67, respectively). This is likely explained by the closer relationships obtained between age, BM, LBM and $EPOC_8$ in boys. Taken together, these results show that both age and body mass and composition play a major role in explaining sex-related differences in EPOC after high-intensity exercise from the age of 14 years. However, the greater $EPOC_8$ in boys from the age of 14 years could be also attributed to greater non-oxidative energy production (*i.e.*, AOD) incurred at the onset of high-intensity exercise via a greater mobilisation of LBM. Indeed, the results of our study show significant relationships between $EPOC_8$, AOD and LBM, but with greater determination coefficients in boys than girls. From a physiological perspective, sex-related changes in $EPOC_8$ from the age of 14 years could be attributed to factors accounting for the concomitant increase in AOD. These could include a higher production of androgen hormones (*e.g.*, testosterone) at the time of puberty in boys (17, 23), increasing more favourably muscle mass and the specific area of type II fibres and thereby the activity of non-oxidative metabolism during exercise and possibly $EPOC_8$ during recovery. However, these factors could act on $EPOC_8$ in the same proportions during childhood and adolescence since no significant sex × age group interaction effect for $EPOC_8$/AOD ratio was found in the present study.

The results of the present study also show in boys a significant increase with age in the amount of O_2 required to replenish muscle phosphagens and reoxygenate myoglobin (*i.e.*, $EPOC\tau_1$). This finding was not found in girls, which led to a sex difference in $EPOC\tau_1$ from the age of 14 years (Table 3). Multiplicative allometric modelling, however, highlighted that when age was considered concurrently with BM or LBM, the difference in $EPOC\tau_1$ between girls and boys was no longer significant ($p = 0.079$ for BM + age; $p = 0.206$ for LBM + age). Moreover, when age was considered in the allometric procedure, $EPOC\tau_1$ increased proportionally more than BM or LBM in boys (b: 1.03 and 1.13, respectively) but not in girls (b: 0.71 and 0.80, respectively). Accordingly, the amount of O_2 required for phosphagen replenishment and myoglobin reoxygenation would be influenced by the changes in LBM with age, but with less evidence in girls as indicated by their lower determination coefficients between LBM and $EPOC\tau_1$ (0.35 *vs* 0.76 in girls and boys, respectively). However, while $EPOC\tau_1$ increased with age and differed between both sexes from 14 years onwards, the $\dot{V}O_2$ recovery time constant (*i.e.*, $\tau_1\dot{V}O_2$) did not significantly increase during childhood and adolescence in either boys or girls. This result does not seem to be in accordance with some previously published studies reporting faster $\dot{V}O_2$ recovery kinetics in prepubertal children than adults (21, 40). However, in the present study, data were collected among a population aged 10 to 17 years, thus not including adults. In girls, our data are consistent with those reported by McNarry et al. (28) showing no difference in the $\dot{V}O_2$ recovery time constant obtained from a monoexponential model between 11-12- and 14–15-year-olds following both cycle and upper body submaximal exercise. Therefore, $\tau_1\dot{V}O_2$ could remain stable from childhood into adolescence for both girls and boys, and then increase in the transition to adulthood, but this still remains to be confirmed.

Due to the close inverse relationship between the initial phase of the $\dot{V}O_2$ recovery kinetics and the phosphocreatine (PCr) resynthesis kinetics obtained from ^{31}P-magnetic resonance spectroscopy (^{31}P-MRS) following exercise (24, 32), $\tau_1\dot{V}O_2$ may be considered as a surrogate of PCr recovery rate, and thereby muscle oxidative capacity. In relation to this, Kappenstein et al. (22) showed following ten sets of 30-s high-intensity dynamic plantar flexion that the PCr recovery time constant obtained from a monoexponential function did not differ significantly between 9.4-year-old boys and girls and 26.1-year-old men and women. Likewise, Willcocks et al. (39) reported no significant effect of age, sex, and age × sex interaction on the PCr recovery kinetics following fatiguing isometric quadriceps exercise in thirteen 13-year-old adolescents (6 males and 7 females) and fourteen 29-year-old adults (6 males and 8 females). Therefore, although this has yet to be confirmed due to the high interindividual variability in the PCr recovery kinetics, ^{31}P-MRS data appear to show no significant age × sex interaction on the PCr recovery time constant after exercise during childhood and adolescence, which supports our data obtained from $\tau_1\dot{V}O_2$ from 10 to 17 years in both sexes.

Strengths and limitations

This study presents cross-sectional data and would have been enhanced with measures of maturity status. However, it has been demonstrated in longitudinal studies that once age and LBM have been controlled for in multiplicative allometric analyses, maturity status does not make an additional, significant contribution to explaining the development of aerobic fitness, anaerobic fitness or ventilatory variables of 11–18-year-olds (1, 3, 4). In addition, even if the length of exercise training exposure was not determined and considered in the present study, peak oxygen uptake allometrically scaled with LBM + age was found to be comparable between age groups and sex, thereby indicating a similar level of aerobic fitness between boys and girls during childhood and adolescence.

A unique strength of the present study lies in the adoption for the first-time of allometric modelling to analyse oxygen consumption recovery, notably EPOC. This approach has provided new insights into the influence of age and sex and their interaction on EPOC and $\tau_1\dot{V}O_2$ during childhood and adolescence.

CONCLUSION

The results of the present study show, for the first-time, that oxygen consumption recovery after high-intensity exercise (quantified by EPOC) increased with age, with boys differing from girls from the age of about 14 years, likely an outcome of a greater gain in BM and LBM. Multiplicative allometric modelling showed that when age is considered concurrently with BM or LBM, the sex difference in EPOC is reduced during childhood and adolescence. In addition, despite a sex-related difference in the amount of O_2 required for phosphagen resynthesis and myoglobin reoxygenation (*i.e.*, EPOCτ_1) in boys from 14 years of age onwards, the $\dot{V}O_2$ recovery kinetics (*i.e.*, $\tau_1\dot{V}O_2$) is not altered during childhood and adolescence irrespective of sex.

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Table 1: Participants' physical and fitness characteristics (n = 77).

	Group 1 (*n* = 13) 10 – 11.9 yr		**Group 2 (*n* = 17) 12 – 13.9 yr**		**Group 3 (*n* = 27) 14 – 15.9 yr**		**Group 4 (*n* = 19) 16 – 17.9 yr**	
	Girls (n = 6)	*Boys (n = 7)*	*Girls (n = 6)*	*Boys (n = 11)*	*Girls (n = 14)*	*Boys (n = 13)*	*Girls (n = 8)*	*Boys (n = 11)*
Age (yr)	11.4±0.7	11.5±0.4	12.7±0.7	13.2±0.4	15.0±0.6	15.0±0.7	16.8±0.9	16.7±0.5
Height (m)	1.55±0.05	1.53±0.11	1.63±0.09	1.63±0.08	1.66±0.04	1.79±0.07 ***	1.66±0.05	1.78±0.07 **
BM (kg)	48.7±4.6	41.9±7.5	58.8±11.8	51.6±8.9	58.7±6.4	66.7±9.7	56.6±4.3	70.0±5.8 **
Body fat (%)	24.9±6.1	17.6±4.1 *	25.2±5.0	13.7±6.1 ***	22.3±3.3	6.7±2.0 ***	23.2±2.1	10.4±2.0 ***
LBM (kg)	36.4±2.7	34.4±5.7	43.7±7.1	44.6±9.1	45.6±4.7	62.2±8.9 ***	43.4±3.6	62.7±4.9 ***
$\dot{\mathbf{V}}\mathbf{O}_{\mathbf{2peak}}$ ($L \cdot min^{-1}$)	2.0±0.2	2.2±0.4	2.3±0.2	2.8±0.8	2.7±0.3	4.2±0.6 ***	2.8±0.4	4.5±0.3 ***
$\dot{\mathbf{V}}\mathbf{O}_{\mathbf{2peak}}$ [$L/(kg\ LBM^{b} \cdot \exp(a + c \cdot age)$]	1.00±0.09	1.05±0.12	1.01±0.07	0.96±0.11	1.01±0.09	1.01±0.09	0.98±0.17	1.01±0.09

Values are presented as mean ± SD. BM: body mass; LBM: lean body mass; $\dot{V}O_{2peak}$: peak oxygen uptake; $\dot{V}O_{2peak}$ [$L/(kg\ LBM^{b} \cdot \exp(a + c \cdot age)$]: peak oxygen uptake allometrically scaled with LBM + age as follows: $\log(\dot{V}O_{2peak}) = b \cdot \log(LBM) + a + c \cdot \log(age)$ (see section "Allometric modelling procedure" for further explanations). *, **, and ***: significantly different from girls within each age group at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

Table 2: Allometric exponents obtained from multiplicative modelling of $EPOC_8$ and $EPOC\tau_1$ for body size variables and age.

	Allometric coefficients	
	Girls	Boys
$EPOC_8$:		
Proportionality coefficient	-1.83	-3.86
BM	0.61	1.11
Age	0.05	0.07
$EPOC_8$:		
Proportionality coefficient	-1.80	-3.42
LBM	0.67	1.10
Age	0.05	0.05
$EPOC\tau_1$:		
Proportionality coefficient	-3.45	-5.10
BM	0.71	1.03
Age	0.03	0.07
$EPOC\tau_1$:		
Proportionality coefficient	-3.49	-4.91
LBM	0.80	1.13
Age	0.02	0.04

$EPOC_8$: excess post-exercise oxygen consumption calculated for 8 minutes after a 60-s all-out rowing exercise; $EPOC\tau_1$: excess post-exercise oxygen consumption calculated until $\tau_1\dot{V}O_2$ was reached; BM: body mass; LBM: lean body mass.

Table 3: Parameters describing the oxygen uptake recovery kinetics and excess post-exercise oxygen consumption following an all-out 60-s rowing exercise test in seventy-seven children and adolescents 10-17 years of age in both sexes.

	Group 1 (*n*=13) **10 – 11.9 yr**		**Group 2 (*n*=17)** **12 – 13.9 yr**		**Group 3 (*n*=27)** **14 – 15.9 yr**		**Group 4 (*n*=20)** **16 – 17.9 yr**	
	Girls (n=6)	*Boys (n=7)*	*Girls (n=6)*	*Boys (n=11)*	*Girls (n=14)*	*Boys (n=13)*	*Girls (n=9)*	*Boys (n=11)*
EPOC$_8$ (L)	3.1±0.3	3.1±0.6	3.8±0.2	3.9±1.2 †	4.4±1.0	6.7±1.0 $^{\dagger\dagger\dagger,\ ***}$	4.7±0.5 ††	7.6±0.8$^{\dagger\dagger\dagger,\ ***}$
EPOC$_8$ [L/(kg BM^b· exp(a + c · age)]	0.98±0.12	1.06±0.08	1.01±0.12	0.92±0.17	1.01±0.17	1.07±0.15	1.03±0.12	1.01±0.11
EPOC$_8$ [L/(kg LBM^b· exp(a + c · age)]	0.99±0.13	1.08±0.10	1.02±0.12	0.92±0.14	1.00±0.17	1.02±0.13	1.03±0.11	1.04±0.11
AOD (L O_2 Eq.)	1.9±0.4	1.9±0.6	2.4±0.4	2.7±0.7	2.8±0.6	4.6±0.9 $^{\dagger\dagger\dagger,\ ***}$	2.9±0.6	5.2+0.7 $^{\dagger\dagger\dagger,\ ***}$
EPOC$_8$/AOD ratio	1.66±0.35	1.60±0.21	1.61±0.32	1.50±0.18	1.61±0.52	1.47±0.20	1.74±0.33	1.47±0.18
$\tau_1\dot{V}O_2$ (s)	50±6	41±7	50±7	42±11	48±12	48±7	51±7	46±8
EPOCτ_1 (L)	0.7±0.1	0.7±0.1	0.9±0.2	0.8±0.3	0.9±0.2	1.5±0.3 $^{\dagger\dagger\dagger,\ ***}$	1.0±0.2	1.5±0.2 $^{\dagger\dagger\dagger,\ ***}$
EPOCτ_1 [L/(kg BM^b· exp(a + c · age)]	1.02±0.12	1.07±0.20	1.03±0.2	0.94±0.27	0.97±0.15	1.12±0.18 $^{\dagger\dagger,\ ***}$	1.06±0.17	0.97±0.14 †

EPOCτ_1 [L/(kg LBM$^{b'}$· exp(a' + c' · age)]	1.03±0.10	1.09±0.16	1.03±0.19	0.94±0.26	0.95±0.15	1.06±0.16	1.08±0.15	1.01±0.15

EPOC$_8$: excess post-exercise oxygen consumption calculated for 8 minutes after a 60-s all-out rowing exercise; AOD: accumulated oxygen deficit; BM: body mass; LBM: lean body mass; $\tau_1\dot{V}O_2$: $\dot{V}O_2$ recovery time constant obtained from a bi-exponential model; EPOCτ_1: excess post-exercise oxygen consumption calculated until $\tau_1\dot{V}O_2$ was reached. Values are presented as mean ± SD. †, ††, †††: significantly different from the group 1 within each sex category at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. ***: significantly different from girls within each age group at $p < 0.001$. AOD was calculated on one girl and four boys less for technical reasons.

FIGURE LEGEND

Figure 1: Oxygen uptake ($\dot{V}O_2$) during and following an all-out 60-s rowing test in boys and girls 10-17 years of age. $\dot{V}O_2$ recovery kinetics were modelled using a bi-exponential function. $\dot{V}O_2$ values are presented as net values, *i.e.* minus baseline. Grey zone corresponds to the 60-s all-out rowing exercise.