Research Paper

Exercise modality effect on oxygen uptake off-transient kinetics at maximal oxygen uptake intensity

Ana Sousa[1], Ferran A. Rodríguez[2], Leandro Machado[1], J. Paulo Vilas-Boas[1,3] and Ricardo J. Fernandes[1,3]

[1] *Centre of Research, Education, Innovation and Intervention in Sport, Faculty of Sport, University of Porto, Porto, Portugal*
[2] *INEFC-Barcelona Sport Sciences Research Group, University of Barcelona, Barcelona, Spain*
[3] *Porto Biomechanics Laboratory, LABIOMEP, University of Porto, Porto, Portugal*

New Findings

- **What is the central question of this study?**
  Do the mechanical differences between swimming, rowing, running and cycling have a potential effect on the oxygen uptake ($\dot{V}_{O_2}$) off-kinetics after an exercise sustained until exhaustion at 100% of maximal oxygen uptake ($\dot{V}_{O_2\,max}$) intensity?
- **What is the main finding and its importance?**
  The mechanical differences between exercise modes had a potential effect and contributed to distinct amplitude of the fast component (higher in running compared with cycling) and time constant (higher in swimming compared with rowing and cycling) in the $\dot{V}_{O_2}$ off-kinetic patterns at 100% of $\dot{V}_{O_2\,max}$ intensity. This suggests that swimmers, unlike rowers and cyclists, would benefit more from a longer duration of training intervals after each set of exercise performed at $\dot{V}_{O_2\,max}$ intensity.

The kinetics of oxygen uptake ($\dot{V}_{O_2}$) during recovery (off-transient kinetics) for different exercise modes is largely unexplored, hampering the prescription of training and recovery to enhance performance. The purpose of this study was to compare the $\dot{V}_{O_2}$ off-transient kinetics response between swimmers, rowers, runners and cyclists during their specific mode of exercise at 100% of maximal oxygen uptake ($\dot{V}_{O_2\,max}$) intensity and to examine the on–off symmetry. Groups of swimmers, rowers, runners and cyclists ($n = 8$ per group) performed (i) an incremental exercise protocol to assess the velocity or power associated with $\dot{V}_{O_2\,max}$ ($v\dot{V}_{O_2\,max}$ or $w\dot{V}_{O_2\,max}$, respectively) and (ii) a square-wave exercise transition from rest to $v\dot{V}_{O_2\,max}/w\dot{V}_{O_2\,max}$ until volitional exhaustion. Pulmonary exchange parameters were measured using a telemetric portable gas analyser (K4b^2; Cosmed, Rome, Italy), and the on- and off-transient kinetics were analysed through a double-exponential approach. For all exercise modes, both transient periods were symmetrical in shape once they had both been adequately fitted by a double-exponential model. However, differences were found in the off-kinetic parameters between exercise modes; the amplitude of the fast component of the $\dot{V}_{O_2}$ off-response was higher in running compared with cycling (48 ± 5 and 36 ± 7 ml kg^{-1} min^{-1}, respectively; $P < 0.001$), and the time constant of the same phase was higher in swimming compared with rowing and cycling (63 ± 5, 56 ± 5 and 55 ± 3 s, respectively; $P < 0.001$). Although both phases were well described by a double-exponential model, the differences between exercise modes had a potential effect and contributed to distinct $\dot{V}_{O_2}$ off-transient kinetic patterns at 100% of $\dot{V}_{O_2\,max}$ intensity.

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Corresponding author A. Sousa: Rua Dr. Plácido Costa, 91 – 4200.450 Porto, Portugal. Email: sousa.acm@gmail.com

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Experimental Physiology

Introduction

Oxygen uptake ($\dot{V}_{O_2}$) kinetics has been analysed through mathematical modelling of constant work-rate exercise, in both on- and off-transient $\dot{V}_{O_2}$ responses (Whipp & Rossiter, 2005). The exponential nature of the response could indicate first- or second-order kinetics profiles (DiMenna & Jones, 2009), but first-order kinetics mandates on–off symmetry, which means that the change in $\dot{V}_{O_2}$ that occurs when the contractile activity ceases must be a mirror image of that which occurred when it commenced (Rossiter *et al.* 2005). In fact, this analysis has shown symmetry during moderate-intensity exercise (under the lactate threshold; LT) because $\dot{V}_{O_2}$ increases exponentially at the onset of exercise (on-fast component) towards a steady state, decreasing rapidly at the offset of exercise (off-fast component; Paterson & Whipp, 1991; Özyener *et al.* 2001; Scheuermann *et al.* 2001; Kilding *et al.* 2005). For heavy exercise (above the LT), the $\dot{V}_{O_2}$ on-dynamics are more complex and require a second-order model, because $\dot{V}_{O_2}$ is additionally increased (on-slow component) after the on-fast component (Burnley & Jones, 2007; Jones & Burnley, 2009). However, $\dot{V}_{O_2}$ at the offset of exercise shows only an off-fast component (Paterson & Whipp, 1991; Özyener *et al.* 2001; Scheuermann *et al.* 2001), allowing the conclusion that $\dot{V}_{O_2}$ at this exercise intensity evidences an asymmetry between on- and off-kinetics phases. Although in the severe intensity domain (substantially above the LT) the $\dot{V}_{O_2}$ on- and off-kinetics both retain a two-component form (Özyener *et al.* 2001), evidencing a symmetry in second-order kinetic profiles, the $\dot{V}_{O_2}$ kinetics has been less studied.

In recent years, research on $\dot{V}_{O_2}$ off-kinetics has focused mainly on the relationship with training and at lower intensities than $\dot{V}_{O_2\,max}$. Aiming to determine the influence of aerobic fitness level in excess postexercise $\dot{V}_{O_2}$, it was reported that trained subjects had a faster relative decline during the fast-recovery phase compared with untrained subjects after heavy cycling exercise (Short & Sedlock, 1997). Studying the influence of the duration of heavy cycling exercise in $\dot{V}_{O_2}$ off-kinetics, it was concluded that the off-transient kinetics was not related to the exercise time and, therefore, was independent of the magnitude of the contribution of the slow component of the on-transient kinetics (Cunningham *et al.* 2000). Conducted at the severe intensity (still at lower intensities than maximal oxygen uptake; $\dot{V}_{O_2\,max}$), the effect of 4 weeks of intense interval-training running $\dot{V}_{O_2}$ off-transient kinetics was also examined, and it was concluded that this was accelerated with this type of intervention (Billat *et al.* 2002). The performance in repeated sprint tests was also related to the $\dot{V}_{O_2}$ off-kinetics for severe running exercise (120% of $\dot{V}_{O_2\,max}$ intensity), thus strengthening the link found between $\dot{V}_{O_2}$ off-transient kinetics and the ability to maintain the performance during repeated sprints (Dupont *et al.* 2010).

The $\dot{V}_{O_2\,max}$ intensity has never been studied in $\dot{V}_{O_2}$ off-kinetics in any exercise mode may have compromised the recovery in these, because it is considered to be one of the primary areas of interest in training and performance diagnosis. Moreover, studies of the $\dot{V}_{O_2}$ off-kinetics across different exercises modes are scarce and have compared only upper body (arm cranking) and leg cycling exercise (McNarry *et al.* 2012), and it is still unknown whether different exercise modes could have distinct $\dot{V}_{O_2}$ off-kinetic profiles, as stated for the $\dot{V}_{O_2}$ on-kinetics (Sousa *et al.* 2015). In fact, it is known that cycling and running differ greatly in terms of the muscle contraction regimen. The concentric work of cycling may account for a lower mechanical efficiency than running, which relies on a stretch–shortening cycle (Bosco *et al.* 1987), resulting in a shorter on-fast component time constant (τ_{1on}). The muscle contraction regimen used during exercise, including possible differences in motor unit recruitment, has been described as an important influencing factor in the manifestation of a higher on-slow component amplitude in cycling compared with running (Billat *et al.* 1998; Carter *et al.* 2000; Hill *et al.* 2003). Also, it has been suggested that when engaging a larger fraction of muscle mass, muscle perfusion could potentially be compromised (Saltin *et al.* 1998). However, no differences were found in the $\dot{V}_{O_2}$ on-kinetics response between rowing and cycling (Roberts *et al.* 2005), although a greater muscle mass is recruited in the former. Swimming, in contrast, has a key postural difference compared with the other exercise modes, because a horizontal position is adopted, which could result in a lower muscle perfusion pressure (Koga *et al.* 1999), although no studies have been reported considering this exercise mode.

Whether these differences between exercise modes have a potential effect on the $\dot{V}_{O_2}$ off-kinetics, as they have in the $\dot{V}_{O_2}$ on-kinetics response, is unknown. This analysis, specifically the measurement of the off-transient time constant time, could be useful to characterize further and contribute to an athlete's physiological profile, enhancing the performance in each specific mode of exercise. The purpose of this study was to compare the $\dot{V}_{O_2}$ off-transient kinetics response between swimmers, rowers, runners and cyclists during their specific mode of exercise at 100% of $\dot{V}_{O_2\,max}$ intensity and to examine the on–off symmetry of the $\dot{V}_{O_2}$ response. It was hypothesized that the type of exercise would contribute to distinct $\dot{V}_{O_2}$ off-transient kinetic patterns at 100% of $\dot{V}_{O_2\,max}$ intensity, albeit the on- and off-transient kinetics would be symmetrical in shape.

Table 1. Physical characteristics of highly trained male swimmers, rowers, runners and cyclists

Group	Swimmers	Rowers	Runners	Cyclists
Age (years)	$18.6 \pm 3.4^{Ro,Ru,Cy}$	26.4 ± 3.1	25.1 ± 2.5	24.5 ± 3.3
Height (m)	1.78 ± 0.06	1.79 ± 0.05	1.75 ± 0.07	1.77 ± 0.05
Body mass (kg)	70.8 ± 6.4^{Ru}	74.6 ± 4.1^{Ru}	61.4 ± 7.2	68.9 ± 3.7

Values are means ± SD. Significant differences ($P < 0.05$) between each group are indicated, in comparison to rowing (^{Ro}), running (^{Ru}) and cycling (^{Cy}).

Methods

Subjects and ethical approval

Thirty-two male subjects (eight swimmers, eight rowers, eight runners and eight cyclists), whose main physical characteristics (means ± SD) are presented in Table 1, participated in this study. All participants (or parents/guardians when subjects were <18 years old) provided informed written consent before data collection. To be included in this study, subjects had to be highly trained (at least six training sessions per week, 2 h duration each session) and had to be regularly involved in competitive events at national level for at least 3 years.

All participants avoided strenuous exercise in the 24 h before each testing session, and were well hydrated and abstained from food, caffeine and alcohol in the 3 h before testing. The protocols were conducted at the same time of the day for each subject and were separated by at least 24 h. The Institutional Review Board of the University of Porto, Faculty of Sport, approved the study design, and it has therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Experimental design

Subjects were tested on two occasions within a 1 week period. In the first session, $\dot{V}_{O_2\,max}$ and the minimal velocity that elicits $\dot{V}_{O_2\,max}$ ($v\dot{V}_{O_2\,max}$) or the minimal power eliciting $\dot{V}_{O_2\,max}$ ($w\dot{V}_{O_2\,max}$) were determined through a maximal incremental exercise protocol. At the subsequent visit, all subjects completed a single square-wave transition exercise from rest to 100% of $\dot{V}_{O_2\,max}$ intensity to volitional exhaustion. Encouragement was given to motivate the subjects to perform their best effort in the incremental protocols and to perform for as long as possible during the square-wave transition exercise.

Incremental exercise test

The incremental tests were specific according to the exercise mode. Swimmers performed an intermittent protocol for front crawl $v\dot{V}_{O_2\,max}$ assessment, with increments of 0.05 m s^{-1} and 30 s passive intervals between each 200 m stage. The initial velocity was established according to the individual level of fitness and was set at the swimmer's individual performance on the 400 m front crawl minus seven increments of velocity (Fernandes *et al.* 2008). The velocity was controlled at each stage by a visual pacer with flashing lights in the bottom of the pool (TAR.1.1; GBK-electronics, Aveiro, Portugal). Runners performed on an outdoor track field an intermittent protocol of 800 m step duration, with increments of 1 km h^{-1} and 30 s passive intervals between each step. The initial velocity was defined according to the individual runner's individual performance on the 800 m minus seven increments of velocity, which was controlled by an audio feedback (whistle) so that the subjects adjusted their running speed to cones placed at 100 m intervals. Cyclists performed in a Power Tap trainer (CycleOps, Madison, WI, USA) a continuous protocol of 2 min step durations each, with increments of 40 W between steps and an average cadence between 70 and 90 r.p.m. Saddle and handlebar positions were individually adjusted by the athletes according to their own bicycle adjustments. Rowers performed in a rowing ergometer (Concept II, Model D; CTS, Inc., Morrisville, VT) an intermittent protocol of 2 min steps, with increments of 40 W and 30 s passive intervals between steps, with cadence ranging between 30 and 40 r.p.m. For both cyclists and rowers, the initial power was set according to the subject's fitness level, and during the tests the power was controlled by visual feedback. The $\dot{V}_{O_2\,max}$ was considered to be reached according to primary and secondary criteria {$\dot{V}_{O_2}$ plateau despite an increase in velocity/power, [lactate$^-$] ≥ 8 mmol l^{-1}, respiratory exchange ratio (R) ≥ 1.0, heart rate > 90% of [220 – age (in years)] and volitional exhaustion; Howley *et al.* 1995} and as a mean value measured over the last 60 s of exercise. If a plateau less than 2.1 ml min^{-1} kg^{-1} could not be observed, $v\dot{V}_{O_2\,max}$ was calculated as previously described (Kuipers *et al.* 1985).

Square-wave transition exercise

Between 24 and 48 h later, all subjects performed a square-wave transition exercise from rest to 100% of $\dot{V}_{O_2\,max}$ at their previously determined $v\dot{V}_{O_2\,max}$ or $w\dot{V}_{O_2\,max}$. This test consisted in a 10 min warm-up exercise at 50% of the $\dot{V}_{O_2\,max}$ followed by a 5 min rest period, and finally, the maintenance of this specific intensity until exhaustion. In all exercise modes, the velocity/power was controlled by the same feedbacks as for the incremental protocols. All tests ended when the subjects could no longer maintain the required velocity/power dictated by the feedback for three consecutive occasions, followed by a passive recovery until $\dot{V}_{O_2}$ at rest was reached (see Fig. 1) Although direct measurements were made throughout the exercise, the peak oxygen uptake ($\dot{V}_{O_2 peak}$, i.e. the maximal value reached during the square-wave transition exercise) and the mean values of all ventilatory parameters were measured over the last 60 s of exercise.

Experimental measurements

Pulmonary gas-exchange variables were measured directly at the mouth using a telemetric portable gas analyser (K4b^2; Cosmed, Rome, Italy). In swimming, this apparatus was suspended over the water (at a height of 2 m) by a steel cable, following the swimmer along the pool and minimizing disturbances of the normal swimming movements. This equipment was connected to the swimmer by a low hydrodynamic resistance respiratory snorkel and valve system (Aquatrainer; Cosmed; Baldari *et al.* 2012). In-water starts and open turns, without underwater gliding, were used. In rowing, running and cycling exercises, subjects breathed through a low-dead-space facemask (Cosmed), and the gas-analysis device was placed near the body's centre of mass, adding 800 g to the total weight of the subject. The gas analysers were calibrated before each test with gases of known concentration (16% O_2 and 5% CO_2), and the turbine volume transducer was calibrated by using a 3 litre syringe according to the manufacturer's instructions.

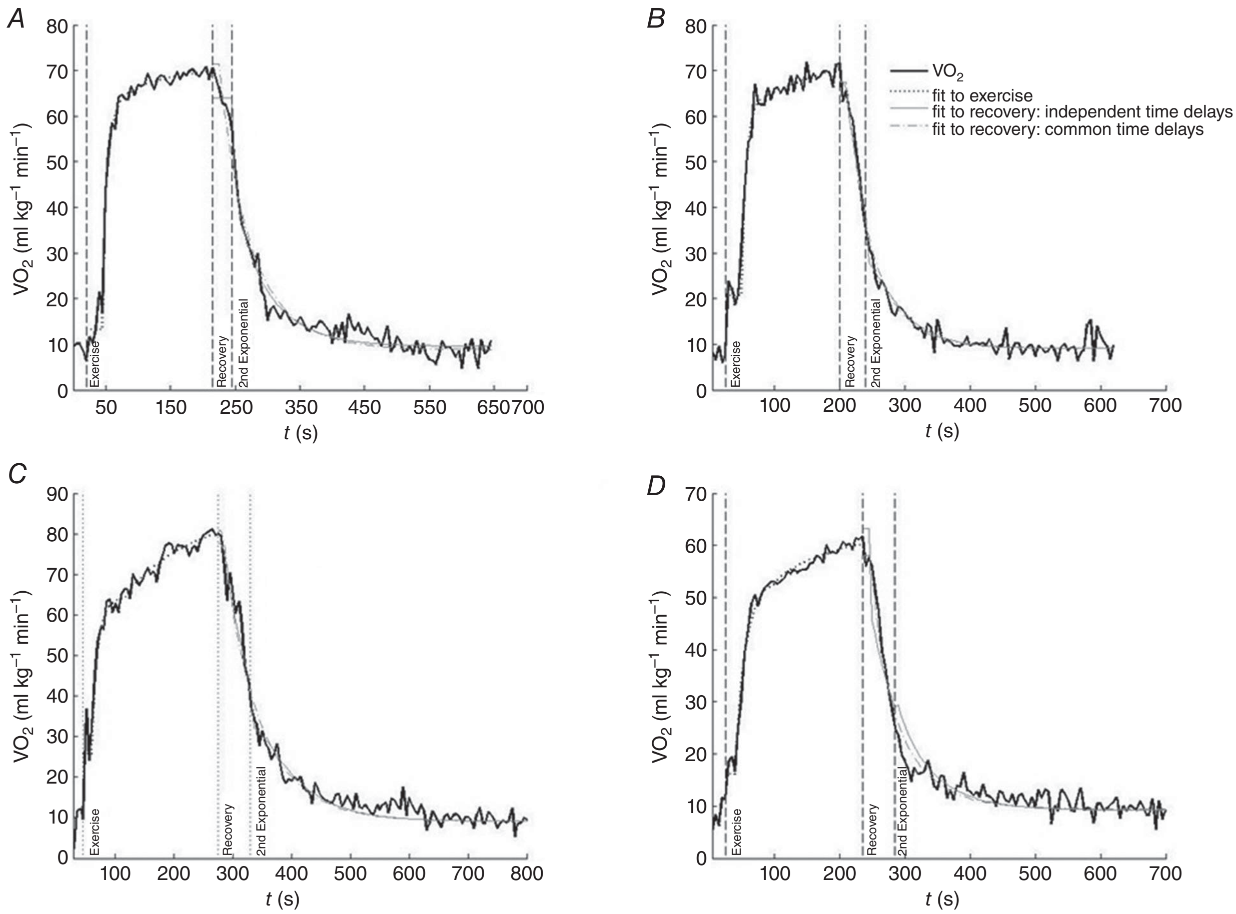

Figure 1. Examples of oxygen uptake ($\dot{V}_{O_2}$)–time curves during and after the square-wave exercises performed at 100% of maximal oxygen uptake ($\dot{V}_{O_2 max}$) in swimming (*A*), rowing (*B*), running (*C*) and cycling (*D*)
Averaged $\dot{V}_{O_2}$ data (thick line) and double-exponential fitted equation during exercise (dotted thin line) and recovery phases with independent time delays (continuous thin line) and with a common time delay (dashed thin line) are identified. Vertical lines indicate the start of the exercise and recovery and the start of the second exponential period.

Data analysis: $\dot{V}_{O_2}$ kinetics

To begin with, errant $\dot{V}_{O_2}$ breath values were omitted from the analysis by including only those in between $\dot{V}_{O_2}$ mean ± 4 SD. Afterwards, individual breath-by-breath $\dot{V}_{O_2}$ values were smoothed by using a three-breath moving average, and 5 s time bin average intervals were used for fitting the corresponding regression equation (Fernandes *et al.* 2012). In both on- and off-analyses, a non-linear least-squares method was implemented in the MatLab Software (Mathworks, Natick, MA, USA) to fit the $\dot{V}_{O_2}$ data with the model. The first 20 s of data after the onset of exercise was not considered for model analyses to exclude the cardiodynamic phase.

To characterize the on-transient $\dot{V}_{O_2}$ kinetics, a double-exponential model eqn (1) was used, as follows:

$$\dot{V}_{O_2}(t) = A_{0on} + A_{1on}\left(1 - e^{-(t-TD_{1on})/\tau_{1on}}\right) + A_{2on}\left(1 - e^{-(t-TD_{2on})/\tau_{2on}}\right) \quad (1)$$

where $\dot{V}_{O_2}(t)$ is the weight-related $\dot{V}_{O_2}$ at time t, A_{0on} is the $\dot{V}_{O_2}$ at rest (in millilitres per kilogram per minute), and A_{1on} and A_{2on} (in millilitres per kilogram per minute), TD_{1on} and TD_{2on} (in seconds), and τ_{1on} and τ_{2on} (in seconds) are the corresponding amplitudes, time delays and time constants of the fast (1) and slow $\dot{V}_{O_2}$ components (2), respectively.

To characterize the off-transient $\dot{V}_{O_2}$ kinetics, two different double-exponential models were used, one with independent time delays for the fast and slow $\dot{V}_{O_2}$ components eqn (2) and the other with a common time delay for both fast and slow components eqn (3), as follows:

$$\dot{V}_{O_2}(t) = A_{0off} + A_{1off}\left(1 - e^{-(t-TD_{1off})/\tau_{1off}}\right) + A_{2off}\left(1 - e^{-(t-TD_{2off})/\tau_{2off}}\right) \quad (2)$$

$$\dot{V}_{O_2}(t) = A_{0off} + A_{1off}\left(1 - e^{-(t-TD_{1off})/\tau_{1off}}\right) + A_{2off}\left(1 - e^{-(t-TD_{1off})/\tau_{2off}}\right) \quad (3)$$

where $\dot{V}_{O_2}(t)$ represents the relative $\dot{V}_{O_2}$ at the time t, A_{0off} is the $\dot{V}_{O_2}$ at rest after the exercise (in millilitres per kilogram per minute) and A_{1off} and A_{2off} (in millilitres per kilogram per minute), TD_{1off} and TD_{2off} (in seconds), and τ_{1off} and τ_{2off} (in seconds) are the corresponding amplitudes, time delays and time constants of the fast (1) and slow $\dot{V}_{O_2}$ components (2) respectively, or the common time delay (TD_1) in eqn (3).

Statistical analysis

For each exercise mode, mean and SD were computed for all variables, and the normality of their distribution was checked with the Shapiro–Wilk test. In the $\dot{V}_{O_2}$ off-transient kinetics analysis, an *F* test was used to decide which double-exponential model (with independent time delays or a common time delay for both components) led to a significant reduction in the sum of squared residuals as the criterion measure for the goodness of fit of the regression model. To test the differences between the on- and off-transient kinetics parameters within each exercise mode, Student's paired *t* test was conducted. The differences between performance variables, off-transient parameters and time sustained between exercise modes were tested using a one-way ANOVA (Bonferroni *post hoc* test). Simple linear regression and Pearson's correlation (r) and determination (r^2) coefficients were also used to test the relationship between the studied variables. All analyses were performed using SPSS (version 10.05; SPSS, Chicago, IL, USA). The confidence level for significance was set at $P < 0.05$.

Results

An example of the $\dot{V}_{O_2}$ on- and off-transient kinetics curves for each mode of square-wave exercise is shown in Fig. 1. For all exercise modes, the off-transient response was better described by a double-exponential equation with a common time delay for both the fast and the slow components, as indicated by the lowest sum of squared residuals. Once they were all fitted by the model, the on- and off-transient periods were symmetrical in shape (mirror image).

The mean ± SD values for $\dot{V}_{O_2peak}$, $v\dot{V}_{O_2\,max}$, $w\dot{V}_{O_2\,max}$, time sustained and the exercise and recovery (on- and off-transient) $\dot{V}_{O_2}$ kinetics estimated parameters of the square-wave exercises performed at 100% of $\dot{V}_{O_2\,max}$ in swimming, rowing, running and cycling are presented in Table 2.

The $\dot{V}_{O_2peak}$ was higher in running compared with cycling ($P = 0.001$) and lower in swimming compared with running ($P = 0.001$). However, no differences were found between $\dot{V}_{O_2\,max}$ (58.9 ± 3.5, 65.9 ± 4.2, 70.8 ± 2.5 and 61.7 ± 3.7 ml kg^{-1} min^{-1}, for swimming, rowing, running and cycling, respectively) reached during the incremental exercise tests and $\dot{V}_{O_2peak}$ values (reached during the square-wave transition exercises) within exercise modes, and time sustained across exercise modes. Regarding the estimated parameters for the off-transient phase, no differences were found between exercise modes, with the exception of A_{1off}, which was larger in running compared with cycling ($P = 0.004$), and τ_{1off}, which was longer in swimming compared with rowing ($P = 0.008$) and cycling ($P = 0.001$).

Table 2. Mean (±SD) values for performance and on- and off-transient oxyen uptake ($\dot{V}_{O_2}$) kinetics parameters in the square-wave exercises performed at 100% of maximal oxyen uptake ($\dot{V}_{O_2\,max}$) in swimmers, rowers, runners and cyclists

Parameters	Swimming (n = 8)	Rowing (n = 8)	Running (n = 8)	Cycling (n = 8)
$\dot{V}_{O_2peak}$ (ml kg^{-1} min^{-1})	59.0 ± 6.6^{Ru}	64.5 ± 5.9	71.9 ± 4.8^{Cy}	60.2 ± 6.0
$v\dot{V}_{O_2\,max}/w\dot{V}_{O_2\,max}$ (m s^{-1} W^{-1})	1.41 ± 0.05	394 ± 30	5.93 ± 0.26	388 ± 33
Time sustained (s)	195 ± 23	191 ± 26	227 ± 27	200 ± 24
Exercise (on-transient kinetics)				
A_{0on} (ml kg^{-1} min^{-1})	17.7 ± 2.4*	17.7 ± 5.0*	16.5 ± 5.0*	14.6 ± 5.6*
A_{1on} (ml kg^{-1} min^{-1})	35.6 ± 8.9	44.3 ± 5.7	48.4 ± 7.0	42.4 ± 14.0
TD_{1on} (s)	13.7 ± 4.8	15.8 ± 5.9	14.3 ± 4.0	18.5 ± 4.4*
τ_{1on}(s)	20.0 ± 3.1*	13.6 ± 4.7*	10.4 ± 4.5*	16.6 ± 8.8*
95% Confidence interval (s)	17.1 – 22.9	9.7 – 17.5	6.2 – 14.5	9.3 – 22.9
A_{2on} (ml kg^{-1} min^{-1})	6.5 ± 1.9	5.5 ± 2.8*	7.1 ± 1.7*	6.8 ± 2.0*
A_{2off} (l min^{-1})	0.5 ± 0.1	0.41 ± 0.2	0.45 ± 0.1	0.5 ± 0.1
TD_{2on} (s)	52.3 ± 25.6	72.8 ± 10.3	65.6 ± 12.5	81.4 ± 11.7
τ_{2on} (s)	110.9 ± 32.9*	48.4 ± 26.4*	96.5 ± 37.3*	20.3 ± 12.2
Recovery (off-transient kinetics)				
A_{0off} (ml kg^{-1} min^{-1})	7.5 ± 3.3	10.7 ± 2.3	10.0 ± 2.9	9.4 ± 1.2
A_{0off} (l min^{-1})	0.5 ± 0.2	0.8 ± 0.2	0.6 ± 0.2	0.7 ± 0.1
A_{1off} (ml kg^{-1} min^{-1})	38.1 ± 7.8	40.4 ± 5.5	47.6 ± 5.4^{Cy}	36.1 ± 7.2
A_{1off} (l min^{-1})	2.7 ± 0.7	3.0 ± 0.3	3.0 ± 0.5	2.5 ± 0.5
TD_{1off} (s)	10.9 ± 6.4	10.5 ± 4.5	10.3 ± 2.6	10.5 ± 5.6
τ_{1off} (s)	63.4 ± 4.6^{Ro,Cy}	55.8 ± 4.6	60.2 ± 6.9	55.4 ± 2.6
95% Confidence interval (s)	59.1 – 67.6	51.9 – 59.6	53.8 – 66.6	53.2 – 57.5
A_{2off} (ml kg^{-1} min^{-1})	11.2 ± 6.0	12.5 ± 2.4	11.3 ± 4.4	11.5 ± 5.2
A_{2off} (l min^{-1})	0.8 ± 0.4	0.9 ± 0.2	0.7 ± 0.3	0.8 ± 0.3
τ_{2off} (s)	20.1 ± 3.3	19.7 ± 1.5	20.7 ± 2.3	18.9 ± 1.7

Abbreviations: $\dot{V}_{O_2peak}$: peak oxygen consumption; $v\dot{V}_{O_2\,max}$: velocity associated with $\dot{V}_{O_2\,max}$; $w\dot{V}_{O_2\,max}$: power associated with $\dot{V}_{O_2\,max}$; A_{0on}: $\dot{V}_{O_2}$ at rest; A_{1on}: amplitude of the fast component - exercise phase; A_{2on}: amplitude of the slow component - exercise phase; TD_{1on}: time delay of the fast component - exercise phase; TD_{2on}: time delay of the slow component - exercise phase; τ_{1on}: time constant of the fast component - exercise phase; τ_{2on}: time constant of the slow component - exercise phase; All the other $\dot{V}_{O_2}$ kinetics parameters have the same definition, but are regarding the recovery phase. Significant differences (P < 0.05) in $\dot{V}_{O_2peak}$ and in the off-transient kinetics between each group are indicated, in comparison to rowing (Ro), running (Ru) and cycling (Cy).
*Significant differences (P < 0.05) between on- and off-transient periods.

When comparing the exercise and recovery estimated parameters across exercise modes, A_{0on} was 43% larger than A_{0off}, but τ_{1off} was 74% longer than τ_{1on}. Likewise, with the exception of swimming, A_{2off} was 45% larger than A_{2on}. In contrast to the fast phase, the off-slow component phase stabilized 76% faster (shorter τ_{2off}) compared with the on-slow component, but only in swimming, rowing and running ($P < 0.05$).

Significant correlations between on- and off-transient $\dot{V}_{O_2}$ kinetic parameters in the square-wave transition in three modes of exercise are shown in Fig. 2. In swimming (Fig. 2*A*), inverse relationships were found between the on- and off-transient fast component amplitudes (A_{1on} and A_{1off}). In rowing (Fig. 2*B*), the subjects who stabilized the fast component earlier during exercise (shorter τ_{1on}) were the ones reaching higher amplitudes of the fast component during recovery (A_{1off}). Runners (Fig. 2*C*) presented a direct relationship between the on- and off-slow component amplitudes (A_{2on} and A_{2off}). No significant correlations were found for the cycling exercise.

Discussion

This study compared the off-transient $\dot{V}_{O_2}$ kinetics responses after a rest to square-wave transition exercise in the severe-intensity exercise domain (i.e. 100% of $\dot{V}_{O_2\,max}$) in four groups of athletes (swimmers, rowers, runners and cyclists) and examined the on–off symmetry of the modelled responses. Although the overall off-kinetics response was very similar in all four exercises, some differences were found; A_{1off} was larger in running compared with cycling (associated with larger $\dot{V}_{O_2peak}$ average values), and τ_{1off} was longer in swimming comparing with rowing and cycling. These findings corroborate the hypothesis that the sport-discipline-related differences would contribute to distinct off-transient $\dot{V}_{O_2}$ kinetic patterns in the severe-intensity exercise domain. Supporting the secondary hypothesis, the on- and off-transient periods were symmetrical in shape (mirror image) for all exercise modes, highlighting that they were both adequately fitted by a double-exponential model.

The absence of differences between $\dot{V}_{O_2\,max}$ and $\dot{V}_{O_2peak}$ values across exercise modes increases the likelihood that a true $\dot{V}_{O_2\,max}$ was measured and that a similar velocity/power were reproduced within the two protocols. The $\dot{V}_{O_2peak}$ values reached at the end of each square-wave transition exercise are in accordance with the specialized literature for each studied sport: rowing (Sousa *et al.* 2014), running (Billat *et al.* 1994; Renoux *et al.* 1999), cycling (Coyle *et al.* 1992; Chavarren & Calbet, 1999) and swimming (Rodríguez *et al.* 2007). The $\dot{V}_{O_2peak}$ values were higher in the group of runners compared with cyclists and swimmers, and similar values were found between the other exercise modes. It is possible that during running, the involvement of movement of the upper limbs and trunk demands a significant oxygen requirement compared with cycling, where the arms and trunk make a smaller contribution to the total exercise $\dot{V}_{O_2}$ (Hill *et al.* 2003). Moreover, although specific muscle activation patterns between running and cycling are developed, diaphragm fatigue has been shown to be similar and therefore independent of postural demand (Wüthrich *et al.* 2014). The lower $\dot{V}_{O_2peak}$ values found for swimmers compared with runners could be explained by the substantially lower body mass of the runners, although no differences were found between runners and cyclists regarding body mass.

In the present study, both on- and off-transient kinetic phases were well described by a double-exponential model (Özyener *et al.* 2001). In the specialized literature, some studies modelled the off-response by using a double-exponential model with independent time delays for the fast and slow components (Dupont *et al.* 2010), whereas others used a common time delay for both (Özyener *et al.* 2001). Only one study compared both double-exponential models in the off-transient kinetics response, though at the heavy-intensity domain, concluding that a significant reduction in residual variance was obtained with the double-exponential model with two independent time delays (Cleuziou *et al.* 2004).

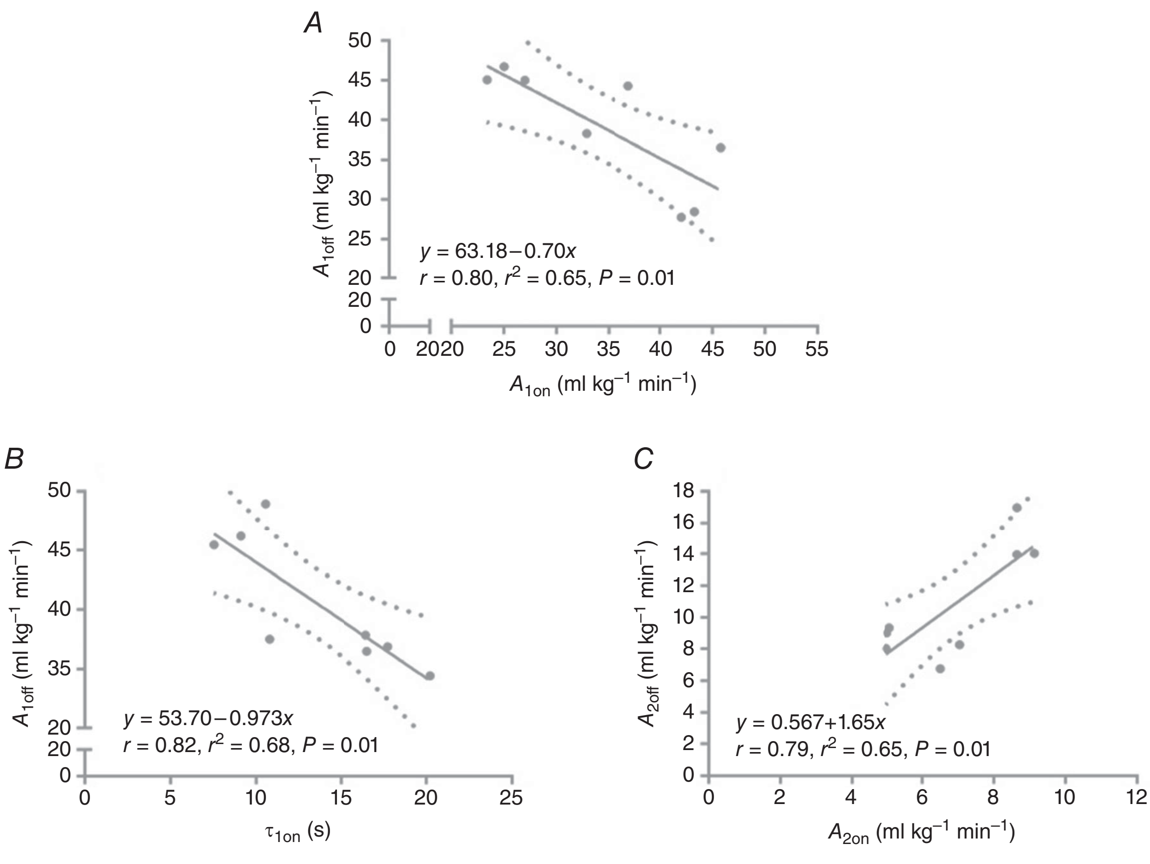

Figure 2. Significant relationships between on- and off-transient fast-component amplitude (A_{1on} and A_{1off}) in swimming (*A*), between off-transient fast-component amplitude (A_{1off}) and on-transient fast-component time constant (τ_{1on}) in rowing (*B*) and between on- and off-transient slow-component amplitude (A_{2on} and A_{2off}) in running (*C*)
All parameters refer to the square-wave transition exercises performed at 100% of $\dot{V}_{O_2\,max}$. The regression equations (continuous lines), Pearson's linear correlation (*r*) and determination (r^2) coefficients, *P* value and ±95% confidence limits (dotted lines) are shown.

In contrast, in the present study and for all exercise modes, the off-transient phases were better described by a double-exponential model with a common fast and slow component time delay, with which a significant decrease in the sum of squared residuals occurred. In fact, the two exponential processes observed during the off-transient kinetics responses were both present at the end of exercise and would decay simultaneously during early recovery, but at different rates. Even if most studies are in agreement with the fact that two phases can be differentiated, there is no consensus in the literature regarding which mathematical model should be used, because a variety of additional factors have been shown to exert an influence on this phenomenon (Cleuziou *et al.* 2004). In this sense, more studies are needed to clarify the physiological explanation for the presence of a second time delay, as well as for the presence of a common time delay in the recovery period.

In the present study, although the overall response profile was similar, differences were found in two of the off-transient kinetic parameters between exercise modes. First, $A_{1\mathrm{off}}$ was larger in running compared with cycling (~24% on average), perhaps simply reflecting the ~16% higher $\dot{V}_{O_2\mathrm{peak}}$ values of the group of runners. It was reported that lower body (cycle) heavy ergometer exercise would result in a higher $A_{1\mathrm{off}}$ compared with upper body (arm cranking) exercise in trained and untrained pubertal girls, although a mono-exponential approach was used (McNarry *et al.* 2012). The difference found in the present study could be explained by the 'gross' O_2 debt, which has been interpreted as the energy necessary to rebuild the high-energy phosphate compounds split at the beginning of exercise (Margaria *et al.* 1933). Although the present study did not focus on this phenomenon, we could hypothesize that the running exercise could induce a greater accumulation of high-energy phosphate, thus explaining higher $A_{1\mathrm{off}}$ values. Notwithstanding, $A_{1\mathrm{off}}$ in running was higher than those reported for the same exercise intensity (Billat *et al.* 2002; Dupont *et al.* 2010), which can be explained by the different training levels of the subjects studied. In cycling exercise, the $A_{1\mathrm{off}}$ value found is similar to previous reports (Cunningham *et al.* 2000; Cleuziou *et al.* 2004; Dupont *et al.* 2010).

Second, $\tau_{1\mathrm{off}}$ was longer in swimming compared with rowing (~16% on average) and cycling (~13%). Given that $\tau_{1\mathrm{off}}$ reflects the rate at which the $\dot{V}_{O_2}$ response achieves the $\dot{V}_{O_2}$ steady state, swimmers evidenced a slower rate of response towards reaching that balance. Knowing that changes in body position (i.e. from supine to orthostatic) may lead to lower systolic volume and muscle perfusion pressure due to central redistribution of blood volume (Sheldahl *et al.* 1987), resulting in a longer $\tau_{1\mathrm{on}}$ (Koga *et al.* 1999), the present findings seem to support the concept that the off-transient kinetics may also be influenced by the different body position adopted during the exercise period, in spite of the upright position adopted during the recovery period. In fact, pulmonary $\dot{V}_{O_2}$ off-kinetics has been reported as a reflexion of muscular phosphocreatine kinetics (Rossiter *et al.* 2002), which in turn is considered to reflect the rate of mitochondrial respiration, and consequently, skeletal muscle oxidative capacity. Thus, the longer $\tau_{1\mathrm{off}}$ values found for swimming may be attributable to a lower muscle oxidative capacity (due to the body position). Collectively, these suggests that swimmers, compared with rowers and cyclists, would benefit more from a longer duration of training intervals after each set of exercise whenever $\dot{V}_{O_2\,\mathrm{max}}$ training intensity is to be enhanced. In fact, by presenting a longer $\tau_{1\mathrm{off}}$, the findings of the present study seem to support the idea that the $\dot{V}_{O_2}$ off-kinetics is modality specific, at least for swimming. Notwithstanding, the $\tau_{1\mathrm{off}}$ mean value found for swimming was similar to previous reports (Sousa *et al.* 2011), because this kinetic parameter seems to remain constant when comparisons between different intensities are made (Cleuziou *et al.* 2004).

All exercise modes evidenced a $\dot{V}_{O_2}$ slow component during the recovery period, as previously shown for heavy- (Cleuziou *et al.* 2004) and severe-intensity exercises (Özyener *et al.* 2001). However, and with the exception of swimming, all exercise modes evidenced larger $A_{2\mathrm{off}}$ values compared with the correspondening on-transient parameter, and no differences were found between exercise modes. These findings support the concept that in the severe-intensity range (i.e. 100% of $\dot{V}_{O_2\,\mathrm{max}}$), while the slow component cannot be discerned or cannot be expressed because of insufficient duration of the exercise, there is a clearly distinguishable slow phase in the recovery from exercise (Özyener *et al.* 2001). Moreover, as the magnitude of the $\dot{V}_{O_2}$ slow component is dependent on the intensity and duration of exercise (Jones & Poole, 2005), considering that the square-wave transition exercises were mainly designed to assess the time for which they could be sustained, the on-slow component development could have been compromised by temporal issues at this particular intensity. We suspect, but cannot prove, that a longer exercise time would induce a greater $\dot{V}_{O_2}$ on-slow component, thus minimizing the differences between the corresponding off-kinetic parameters. Thus, we suggest that the physiological process involved in both on- and off-slow component phases was similar, especially for running, as shown in the relationship found in Fig. 2*C*.

Despite the on–off symmetry observed in the present study, differences between both phases of the response were found. First, A_0 was larger in the on-transient compared with the off-transient in all exercise modes. The 10 min warm-up exercise at 50% of $\dot{V}_{O_2\,\mathrm{max}}$ that preceded the square-wave exercise to exhaustion could explain this difference, although it was reported that the warm-up intensity and duration of exercise had no influence on $\dot{V}_{O_2}$ on-transient kinetics (Bailey *et al.* 2009). Nevertheless, the lack of differences in all exercise modes between A_{1on} and A_{1off} is in accordance with previous results reported for heavy-intensity cycling exercise (Cleuziou *et al.* 2004), although an inverse relationship was observed between these parameters in swimming (Fig. 2*A*). Second, longer τ_{1off} values compared with τ_{1on} were found for all exercise modes. This parameter is a major focus of interest in the $\dot{V}_{O_2}$ kinetics-related literature. A longer τ_{1off} value corroborates previous data obtained in heavy-intensity cycling exercise (Cleuziou *et al.* 2004; Yano *et al.* 2007), extreme-intensity swimming exercise (Sousa *et al.* 2011) and very heavy cycle exercise in adolescents (Lai *et al.* 2008), suggesting that the time needed for $\dot{V}_{O_2}$ steady-state achievement is longer after severe-intensity exercise, independent of the exercise mode performed. Collectively, both the amplitude and the time constant of the fast component (i.e. A_1 and τ_1) suggest that both O_2 deficit and debt during exercise at 100% of $\dot{V}_{O_2\,max}$ intensity do not match, contrary to what was reported for exercise performed at an intensity below the LT (Paterson & Whipp, 1991; Özyener *et al.* 2001), a fact that is evident in the relationship observed for rowing exercise (Fig. 2*B*).

We need to acknowledge some limitations in the present study. First, and most important, the different exercise modes studied were performed by different groups of athletes. Although this seems a good approach in terms of task, testing and training specificity, differences in somatic or physiological characteristics among groups could have influenced the results. Second, the muscle mass and muscle type involved in each exercise modality, as well as differences in muscle flood flow and body position, could also have influenced the outcomes of the kinetic analysis performed. Future studies on this topic should involve groups of athletes capable of performing well in the different exercise modes, thus reducing interindividual variability across exercise modalities and allowing for better statistical models to be used (e.g. multiple repeated-measures ANOVA). The interpretation and application of the present findings are confined only to the severe-intensity exercise domain. Although the measurement of pulmonary $\dot{V}_{O_2}$ at the mouth is accepted to reflect muscle $\dot{V}_{O_2}$ during exercise, the literature is presently non-existent on their relationship in the off-transient kinetics response. Finally, and although no guidelines are presently available regarding the off-transient kinetics (in contrast to the on-transient period), using a single transition may have influenced the confidence intervals found for the kinetic parameters assessed.

In conclusion, this study shows that the on- and off-transient $\dot{V}_{O_2}$ kinetics responses from rest to a square-wave transition exercise in the severe-intensity exercise domain (i.e. 100% of $\dot{V}_{O_2\,max}$) in four groups of athletes (swimmers, runners, rowers and cyclists) of comparable level are well described by a double-exponential model and are symmetrical in shape (mirror image). However, a larger off-transient amplitude in running compared with cycling, associated with a larger $\dot{V}_{O_2peak}$, and a slower rate of $\dot{V}_{O_2}$ decrease during the fast phase of recovery in swimming comparing with rowing and cycling appear to corroborate the hypothesis that sport discipline- or exercise-related differences would contribute to a distinct off-transient $\dot{V}_{O_2}$ kinetics pattern at this particular exercise domain. Further research is needed to establish the influence of somatic, physiological and training subjects' characteristics, as well as of other variables, such as muscle mass involved and body position during exercise and recovery.

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Additional information

Competing interests

None declared.

Author contributions

Conception and design of the experiments: A.S., J.P.V.-B. and R.J.F. Collection, analysis and interpretation of data: A.S. and L.M. Drafting the article or revising it critically for important intellectual content: A.S., F.A.R., L.M., J.P.V.-B. and R.J.F. All authors approved the final version of the manuscript, all persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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