

Physiological comparison of intensity-controlled, isocaloric intermittent and continuous exercise

Adrien Combes¹, Jeanne Dekerle², Valérie Bougault¹ and Frédéric N. Daussin¹

¹ Univ. Lille, Univ. Artois, Univ. Littoral Côte d'Opale, EA 7369 - URePSSS - Unité de Recherche Pluridisciplinaire Sport Santé Société, F-59000 Lille, France ; ² Centre for Sport, Exercise Science and Medicine (SESAME), University of Brighton, Eastbourne, UK

Correspondance:

Frédéric N Daussin, Eurasport – 413 avenue Eugène Avinée – 59120 LOOS, E-mail: frederic.daussin@univ-lille.fr, Phone: +33 (0)3 20 88 73 69

The research was conducted in the university of Brighton

Intermittent exercise show different physiological responses compared to continuous exercise despite a same exercise intensity

Abstract

VO₂ fluctuations are argued to be an important mechanism underpinning chronic adaptations following interval training. We compared the effect of exercise modality, continuous vs. intermittent realized at a same intensity, on electrical muscular activity, muscular oxygenation and on whole body oxygen uptake. Twelve participants (24±5 years; VO₂peak: 43±6 mL·min⁻¹·kg⁻¹) performed (i) an incremental test to exhaustion to determine peak work rate (WR_{peak}); two randomized isocaloric exercises at 70% WR_{peak}: (ii) 1 bout of 30 min; (iii) 30 bouts of 1 min work intercepted with 1 min passive recovery. For EMG, only the CON exercise showed change for the vastus lateralis root mean square (+6.4±5.1 %, P <0.01, 95%CI 3.2, 8.3) and mean power frequency (-5.2±4.8, P <0.01, 95%CI -8.2, -3.5). Metabolic fluctuations (i.e. Oxygen Fluctuation Index and HHb Fluctuation Index) were higher in the intermittent modality, while post exercise blood lactate concentrations (4.80±1.50 vs. 2.32±1.21 mM, respectively for the CON and INT, P <0.01, 95%CI 1.72, 3.12) and the time spent over 90% of V̇O₂ target (1644±152 vs. 356±301 sec, respectively for the CON and INT, P <0.01, 95%CI 1130, 1446) were higher in the continuous modality. In conclusion, despite a similar energy expenditure and intensity, intermittent and continuous exercises showed two very different physiological responses. The intermittent modality would lead to a larger recruitment of fast twitch fibers that are less mitochondria-equipped and therefore may be more likely respondent to mitochondrial adaptations. In addition, this modality induces greater metabolic variations, a stimulus who could lead to mitochondrial development.

Keywords:

Endurance; Exercise; Rehabilitation; Training;

Introduction

Continuous and intermittent exercise modalities are regularly used in training to improve aerobic capacity (Gorostiaga, Walter, Foster, & Hickson, 1991; MacDougall et al., 1998). Previous studies have shown that interval training (IT) can induce greater improvements in maximal oxygen uptake ($\dot{V}O_{2\max}$) (Daussin et al., 2008; Gorostiaga et al., 1991). Two hypotheses have been put forward to explain these greater improvements: (1) A longer time spent at/or near $\dot{V}O_{2\max}$ alongside (2) greater homeostasis disturbances within the muscle cells (Billat, 2001; Combes et al., 2015; Seiler, Jøranson, Olesen, & Hetlelid, 2013; Swain, 2005). The latter is caused by the metabolic reactions involved with the supply of ATP during the on-transient phases of an IT session. During each of these on-transient phases, the rate of the metabolic reactions will increase substantially in order to maintain the ATP:ADP ratio in the working muscle cells, to then decrease during the following off-transient phase (Kunz, 2001). These metabolic fluctuations have been shown to be effective for an improvement in cardiorespiratory fitness (Daussin et al., 2008; Gorostiaga et al., 1991; Tjønnå et al., 2008). Interestingly, the use of continuous training at a given intensity has never been compared to an intermittent exercise performed at the same relative intensity and for a similar work accumulated.

Exercise induces chronic and acute adaptations within a muscle fibre that are dependent on their type as discussed previously (Godin, Ascah, & Daussin, 2010). So muscle fibres recruitment should be considered when interpreting physiological adaptations to endurance training adaptations (Godin, Ascah, & Daussin, 2010). It has been reported for instance that the motor unit recruitment changes over a 1h ride performed at a given rate of perceived exertion (Cochrane et al., 2015). A deeper understanding of the effect of the modality of exercise (continuous *vs.* intermittent) on the muscular and respiratory function shall provide evidence for informed exercise training prescription.

The aim of the present study was to describe the muscular and respiratory responses following a continuous and an intermittent exercise performed at the same exercise intensity. We hypothesised that the exercise modality will influence the recruitment of muscle fibre and that the intermittent modality will reduce muscle fatigue and maintain the fibre recruitment pattern throughout the exercise. We also measured tissue oxygenation using transmitting and receiving light in the near infrared spectrum to the skin surface in order to quantify muscle

metabolic fluctuations.

Materials and methods

Subjects

Twelve voluntary healthy active (2-3 one-hour training sessions per week) men participated in this study (mean \pm SD: age, 24 ± 5 years; mass, 76 ± 10 kg; height, 1.80 ± 0.06 m; BMI, 23.4 ± 2.2 kg·m⁻²; $\dot{V}O_{2\text{peak}}$, 43 ± 6 mL·min⁻¹·kg⁻¹; WR_{peak} , 282 ± 31 W). The subjects were instructed to pursue their habitual training throughout the study, and to refrain from alcohol and caffeine intake for at least 48 h prior to any of the testing sessions. They provided signed informed consent prior to their participation. The design of this study was approved by the local ethics committee of the University. Our study conforms to the ethical standards in sport and exercise science research (Harriss & Atkinson, 2015).

Exercise protocols

Participants performed (1) an incremental, (2) a continuous and (3) an intermittent exercise. All exercises were separated by a minimum of 48 h rest and the two last exercises were performed in an arbitrary random order. The incremental test to define $\dot{V}O_{2\text{peak}}$ and peak work rate (WR_{peak}) was performed until volitional exhaustion and each subject carried out a maximal effort according to Howley (Howley, Bassett, & Welch, 1995). The test was performed on an electrically braked ergometer (SRM, Germany) and began with a 3-min stage at 75 W followed by increments of 25 W per 2 min. Respiratory variables were measured breath by breath and $\dot{V}O_{2\text{peak}}$ was defined as the highest 30s average. Peak work rate (WR_{peak}) corresponded to the power output of the last increment completed. The continuous and intermittent exercises were performed on a customised cycle ergometer (620 Ergomic; Monark, Varberg, Sweden). After a standardised warm-up, subjects performed 30 min of continuous pedalling at 70% WR_{peak} and 30 bouts of 1 min of cycling at 70% WR_{peak} interspersed with 1 min of passive recovery for the intermittent condition.

Oxygen uptake ($\dot{V}O_2$)

Pulmonary gas exchange was recorded breath-by-breath using an online gas analysis system (MediSoft, Germany). Averaged $\dot{V}O_2$ values over 5 sec periods were used to calculate the following variables: (1) $\dot{V}O_2$ cumulated during the exercise period (L); (2) mean $\dot{V}O_2$ ($L \cdot \text{min}^{-1}$) during the exercise period; (3) time spent above 90% of the $\dot{V}O_2$ corresponding to 70% WR_{peak} as determined from the linear $\dot{V}O_2$ -power output relationship; (4) the sum of amplitude variations (A, in $L \cdot \text{min}^{-1}$) during the exercise period; (5) the average derivative (RR_{moy} , in $\text{mL} \cdot \text{sec}^{-2}$) calculated by dividing the total amplitude by the time during which the signal increased; and (6) the oxygen fluctuation index (OFI) calculated using amplitude and derived average (see Equation 1).

Equation 1: $\text{OFI (in mL}^2 \cdot \text{sec}^{-3}) = A \cdot RR_{\text{moy}}$ where A is the $\dot{V}O_2$ amplitude during the exercise and RR_{moy} is the $\dot{V}O_2$ derived average during exercise.

Capillary blood lactate concentrations

During the incremental exercise test, capillary blood samples were taken at rest, immediately at the end of exercise and 3 min after the end of exercise. For the two other exercises, capillary blood samples were taken at rest, after the warm-up, at 30 min and/or immediately at the end of exercise. Blood lactate concentration ($[\text{La}]_b$) was determined using a Yellow Springs Instrument (YSI 2300 Stat Plus; Analox, Sheffield, UK) from 50 μl of blood collected at the fingertip (D957G-70-35; Clinitubes, Radiometer, Copenhagen, Denmark).

Perception of exertion

The rate of perceived exertion (RPE) was recorded using a Borg's category scale 20 (Borg, 1982), thus at the end of each stage during the incremental exercise and every 10 min of pedalling during continuous and intermittent exercise.

Pedalling power and frequency

Mechanical external power output and cadence were continuously recorded (Power Control V, SRM GmbH, Jülich, Germany). The total work accumulated during each condition was calculated retrospectively, and expressed in kJ.

Electromyography (EMG)

The electrical activity of the quadriceps *vastus lateralis* (VL) and *vastus medialis* (VM) of the left leg was recorded with two pairs of surface electrodes connected to an electromyography (PowerLab 16/30 - ML880 / P; ADInstruments, Bella Vista, NSW, Australia). The electrodes were placed at 80% of the distance of the line connecting the anterior superior iliac spine and the joint space in front of the anterior border of the medial ligament for the VM, and to 2/3 of the distance of the line between the anterior superior iliac spine and the lateral border of the patella for the VL (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000). The reference electrode was positioned on the anterior superior iliac spine. The electrode position was marked with indelible ink to ensure identical placement during subsequent visits.

Electromyographic signals were amplified (gain, 1000), filtered (bandwidth of frequency, 10 Hz to 1 kHz) and recorded (sampling frequency, 4 kHz) with an acquisition device (PowerLab 16/30 ML880; ADInstruments, Bella Vista, NSW, Australia) and its associated software (LabChart 7 ADInstruments, Bella Vista, NSW, Australia). The calculations were performed on four sets of 30 bursts EMG for the first minute and then every 10 and 20 min respectively for the continuous and intermittent exercise. Root mean square (RMS Root-mean-square) was calculated subsequently. Mean power frequency (MPF) was determined from spectral analysis of the signal. Values were expressed as percent of maximal voluntary contraction (MVC) measured before each exercise (3 MVC of 5 sec intercepted with 45 sec of rest), in a sitting position with a knee extended at 90 degrees.

Near Infra-Red Spectroscopy (NIRS)

The emitter-detector pair (PortaMon, Artemis Medical Systems, Netherlands) was placed on the muscle belly of the VL of the right leg, midway between the lateral epicondyle and the greater trochanter of the femur. The variables determined with NIRS were: (1) HbO₂ (arbitrary unit (a.u.)), (2) HHb (a.u.), and (3) the amount of total haemoglobin (Hbtot, $Hbtot = HbO_2 + HHb$).

The signal was averaged over periods of 5 sec. HHb values was used to determine the following variables: 1) Time spent at an intensity greater than 90% of the maximum value observed for

the subject, 2) Sum of amplitude variations (A, a.u.) during the exercise period, 3) Average derivative (RR_{moy} in $UA \cdot sec^{-1}$) calculated by dividing the total amplitude by the time during which the signal increases, and 4) HHb fluctuation index (HFI) calculated using amplitude and derived average (see equation 2).

Equation 2: HFI (in $a.u. \cdot sec^{-1}$) = $A \cdot RR_{moy}$ where A is the amplitude of HHb during the exercise (u.a.) and RR_{moy} is the HHb average derivative during the exercise ($a.u. \cdot sec^{-1}$).

Statistical analysis

Data are presented as means \pm SD, 95% CI. Statistical analyses were performed using Sigma Stat for Windows (version 3.0, SPSS Inc., Chicago, IL). RPE data was analysed using a Friedman's test followed by a Wilcoxon post-hoc analysis. Normality for all remaining variables was tested with the Kolmogorov-Smirnov test. The compound symmetry, or sphericity, was checked using the Mauchly's test. A two-way analysis of variance (ANOVA) with repeated measures and a post-hoc Tukey test were performed to examine the influence of modality (2) and time (3) for RMS and MPF with an additional time point for $[La]_b$. A subsequent one-way ANOVA with repeated measures and a post-hoc Tukey test were performed to examine the influence of time (1h of exercise) on measures of $[La]_b$ for the intermittent exercise. The same approach was used to identify the presence of a drift of the $\dot{V}O_2$ and HHb signals during the two exercises. The Student *t*-test for paired samples was used when only two sets of data were compared (interval vs. continuous). The significance level was set at $P < 0.05$.

Results

Energetic expenditure

No difference was observed between the two exercises for the total amount of work done (in kJ: 342 ± 40 and 345 ± 34 , for the CON and INT, respectively) and total $\dot{V}O_2$ over a 1 h period (O_2 L: 89 ± 12 and 85 ± 15 , for the CON and INT, respectively). The CON exercise, compared to the INT exercise, was characterised by a higher average $\dot{V}O_2$ (in $L \cdot min^{-1}$: 2.61 ± 0.32 vs. 1.46 ± 0.24 , $P < 0.01$) and a higher time spent over 90% of the target $\dot{V}O_2$ (in sec: 1644 ± 152 vs. 356 ± 301 , respectively for the CON and INT, $P < 0.01$). $[La]_b$ and RPE results are presented

in table 1.

$\dot{V}O_2$ fluctuation

The analysis of the $\dot{V}O_2$ fluctuations shows a greater cumulated $\dot{V}O_2$ amplitude for the INT modality ($L \cdot \text{min}^{-1}$: 202 ± 40 vs. 88 ± 30 , respectively for INT vs. CON, $P < 0.01$) as well as a higher averaged derivative (in $\text{ml} \cdot \text{sec}^{-2}$: 2.94 ± 0.62 vs. 1.99 ± 0.67 , respectively for the INT and CON, $P < 0.01$). Similarly, the index of metabolic fluctuation showed 4-fold higher values for the INT modality (in $\text{mL}^2 \cdot \text{sec}^{-3}$: 10270 ± 4349 vs. 3237 ± 2113 , $P < 0.01$, figure 1).

Muscular oxygenation

The INT modality led to a shorter time spent over 90% of maximal HHb (sec: 76 ± 120 vs. 644 ± 591 , $P = 0.04$), a greater HHb amplitude (in A.U.: 2945 ± 1306 vs. 218 ± 99 , $P < 0.01$) and a higher average HHb derivative (in $\text{AU} \cdot \text{sec}^{-1}$: 1.91 ± 0.84 vs. 0.29 ± 0.12 , $P < 0.01$). The same pattern was observed for the metabolic fluctuation index with values 122-fold greater for INT (modality $\text{A.U.} \cdot \text{sec}^{-1}$: 6582 ± 6034 vs. 73 ± 68 , $P < 0.01$, figure 2).

EMG activity

The time course of RMS for the VL and VM was different between the modality ($P < 0.01$). There was an increase in the RMS from baseline to the 10th minute during CON (point 2) for the VL ($P < 0.01$) and a tendency for an increase for the VM ($P = 0.051$, figure 3). No change was observed during INT. The change over time in MPF for the VL was also dependent on the exercise modality ($P = 0.02$): during CON, the averaged MPF values were significantly lower at the 10th and 20th minute when compared to the 1st and last minute ($P < 0.01$, figure 3). Values remained steady during INT and were significantly lower compared to CON from the 10th min to the end of the exercise ($P < 0.05$, figure 3). No change in the MPF response was depicted for the VM.

Blood lactate concentration and RPE

$[\text{La}]_b$ was significantly greater at the end of CON compared to the measure at the 30th minute and at the end of INT ($P < 0.01$). No difference was observed between the latter two. RPE was

higher during CON compared to INT ($P < 0.01$, table 1). RPE increased during CON exercise while remaining constant during INT ($P < 0.01$, table 1).

Discussion

This study compared the respiratory and muscular responses (NIRS and EMG) during two exercises of different modalities but matched for work (30 min vs. 30 x 1 min of exercise) and intensity (70% WR_{peak}). During CON, the muscle fibre recruitment increased with a shift towards a recruitment of slow twitch fibres whereas the EMG response remained constant during INT. INT exhibited greater $\dot{V}O_2$ and muscle oxygenation fluctuations alongside lower $[La]_b$ and RPE scores compared to CON. We should take in consideration that small differences can be confused with the methodological error measurement, therefore data should be interpreted accordingly.

Metabolic responses

The OFI was 4-fold greater during the intermittent exercise compared to the continuous exercise ($P < 0.01$). This is due to the repeated transitions from rest to exercise causing repeated changes in the $\dot{V}O_2$ response, as reflected by a higher $\dot{V}O_2$ average derivative. Few studies have focused on the quantification of the magnitude of change in the $\dot{V}O_2$ signal during intermittent exercise (Combes, Dekerle, Bougault, & Daussin, 2016; Turner et al., 2006). In our study, the mean amplitude of the fluctuations (from lowest to highest point) is $1.48 \text{ L} \cdot \text{min}^{-1}$ and is similar to our previous work on similar population (Combes et al., 2015). Another study reported greater $\dot{V}O_2$ amplitudes ($2.38 \text{ L} \cdot \text{min}^{-1}$) for the same working time (60 min) (Turner et al., 2006). This difference can be mainly explained by a higher exercise intensity in the study of Turner et al. (2006), i.e. 120% of WR_{peak} . During exercise, mitochondrial ATP production is stimulated to match a demand. The kinetic control of $\dot{V}O_2$ is proposed to occur in response to an increase in [ADP] and [Pi], and a decrease in [PCr]. An increased delta between the starting $\dot{V}O_2$ and the $\dot{V}O_2$ in demand would speed up the “mitochondrial power” delivery (Bowen et al., 2011).

The $[La]_b$ response was greater during the CON exercise suggesting a higher contribution of the lactate anaerobic metabolism during this exercise modality. $[La]_b$ has been associated to an intracellular signal leading to muscular adaptations (Hoshino, Tamura, Masuda, Matsunaga, &

Hatta, 2015). In the current study, we observed moderate $[La]_b$ levels in the intermittent modality (2.32 ± 1.21 vs. 4.80 ± 1.50 mM). In line with the above-mentioned findings (Hoshino et al., 2015), our previous work, using the same bouts of exercise as those studied in the present paper, has demonstrated that the continuous modality did not induce stimulation of mitochondrial biogenesis signalling pathways while the intermittent modality did (Combes et al., 2015). We would speculate that transient accumulations of lactate within the muscle cells during exercise may promote muscle adaptations.

Muscular oxygenation

Few studies explored muscle oxygenation during intermittent exercise (Turner et al., 2006). In the present study, fluctuations were greater in the intermittent modality: amplitude, average derivative and IFH were respectively ~ 15 ~ 7 and ~ 122 -fold higher compared to the continuous exercise. Bhambhani et al. (1999) compared four intermittent exercises of different submaximal intensities. They observed a decrease in the percentage of muscular HbO_2 as the intensity increased, suggesting that the latter is a central factor in the amplitude of the muscular deoxygenation. Grassi et al. (s 2003), showed that, during a 5-min constant load exercise at a submaximal intensity, HbO_2 and HHb reached a steady state after about 60 sec. For an intermittent exercise realised at 120% WR_{peak} , Turner et al. (2006) also showed greater amplitude in the HHb variation in the 30- and 60-sec work compared to the 10-sec work duration suggesting that the muscle oxygenation amplitude follow an hyperbolic response as a function of the exercise duration. Taken together, these results suggest that during a submaximal exercise, an on-transient phase shorter than 60 sec provides maximum HHb variations. Moreover, there is a concordance between the $\dot{V}O_2$ and the HHb fluctuations ($r^2 = 0.36$, $P < 0.05$) suggesting that it is possible to evaluate muscle disturbances using different techniques.

Muscular recruitment

There is a change in the RMS for the VL over time but only for CON. The VM tends to follow the same trend. This may illustrate an increase in muscle fibre recruitment during CON to produce the same work rate over time. For the VL, the change in the MPF response over time depends on the exercise modality, with a difference between the two modalities for each time point and a decrease at the 10th and 20th min for CON. (Figure 3) This decrease suggests a

modification in the fibre type recruitment with a shift toward recruitment of slow twitch fibres. These results should be considered with caution. For instance, there is evidence that the change in MDF (median power frequency) or MPF may be observed, but not systematically (Scheuermann, Hoelting, Noble, & Barstow, 2001) during exercises underneath or above the ventilatory threshold. Several phenomena can affect the values of MPF: raise in intramuscular temperature (Petrofsky & Lind, 1980) and increase in slow twitch motoneurons firing frequency can increase MPF (Borrani et al., 2001) while increasing concentration of H^+ (Brody, Pollock, Roy, De Luca, & Celli, 1991) and the net loss of potassium (K^+) into the muscle (Sjøgaard, Adams, & Saltin, 1985) can decrease MPF. The two latter phenomena can be in part responsible for a shift towards fast twitch fibres. Our results suggest that fatigue developing during the CON modality leads to an increase in the recruitment of muscle fibres, and a possible use of larger motor units, so that the contribution of the slow fibres increases with time. Such adaptations do not happen during the INT exercise and fibre type II were recruited along all the exercise duration.

Practical considerations

As demonstrated by a lower RPE values throughout INT, subjects perceived exercise as less difficult when performed intermittently. The intermittent mode may therefore be a better choice for the exercise adherence of patients. However, our intermittent mode doubles the time commitment so the continuous exercise could be a good option when time for training is limited; the exercise shall feel marginally more effortful but for an effort of half duration compared to the intermittent exercise. Future studies should address the effect of short *vs.* long duration intermittent exercise. CON and INT do not share the same putative mechanisms and do not induce the same chronic adaptations because of the uniqueness in the physiological stresses induced. The intermittent modality seems to be a powerful stimulus for the mitochondrial biogenesis (Combes et al., 2015) and $\dot{V}O_{2max}$ development when performed at high intensities (Daussin et al., 2008); a continuous modality may be more effective for myogenesis (Daussin et al., 2008) when the exercise performed at low intensity.

Contrary to CON, INT is associated with a constant pattern of motor unit recruitment with greater recruitment of type II muscle fibres. Both mitochondrial content and oxidative capacity are lower in these muscle fibres. These fibres also respond better to endurance training with greater changes in their oxidative pathways when compared to type I muscle fibres. This suggests that type II muscle fibres are more sensitive to this training stimulus (Russell et al.,

2003). Therefore, INT may be used to stimulate this muscle fibre type to maximize the improvement of their muscle oxidative capacity.

In conclusion, two intermittent and continuous exercises of matched exercise intensity and energy expenditure showed different physiological responses. INT seems to lead to a greater recruitment of fast twitch fibres that have less mitochondrial equipment and are more prone to oxidative adaptations.

Disclosure statement:

No potential conflict of interest was reported by the authors.

Bibliography

- Bhambhani, Y., Buckley, S., & Susaki, T. (1999). Muscle oxygenation trends during constant work rate cycle exercise in men and women. *Medicine & Science in Sports & Exercise*, *31*(1), 90–98.
- Billat, L. V. (2001). Interval training for performance: a scientific and empirical practice. Special recommendations for middle- and long-distance running. Part I: aerobic interval training. *Sports Medicine*, *31*(1), 13–31.
- Borg, G. A. (1982). Psychophysical bases of perceived exertion. *Medicine & Science in Sports & Exercise*, *14*(5), 377–381.
- Borrani, F., Candau, R., Millet, G. Y., Perrey, S., Fuchslocher, J., & Rouillon, J. D. (2001). Is the VO₂ slow component dependent on progressive recruitment of fast-twitch fibers in trained runners? *Journal of Applied Physiology (Bethesda, Md. : 1985)*, *90*(6), 2212–2220.
- Bowen, T. S., Murgatroyd, S. R., Cannon, D. T., Cuff, T. J., Lainey, A. F., Marjerrison, A. D., et al. (2011). A raised metabolic rate slows pulmonary O₂ uptake kinetics on transition to moderate-intensity exercise in humans independently of work rate. *Experimental Physiology*, *96*(10), 1049–1061. <http://doi.org/10.1113/expphysiol.2011.058321>
- Brody, L. R., Pollock, M. T., Roy, S. H., De Luca, C. J., & Celli, B. (1991). pH-induced effects on median frequency and conduction velocity of the myoelectric signal. *Journal of Applied Physiology (Bethesda, Md. : 1985)*, *71*(5), 1878–1885.
- Burke, E. J., & Franks, D. (1975). Changes in VO₂ max Resulting from Bicycle Training at Different Intensities Holding Total Mechanical Work Constant. *Research Quarterly. American Alliance for Health, Physical Education and Recreation*, *46*(1), 31–37. <http://doi.org/10.1080/10671315.1975.10615302>
- Cochrane, K. C., Housh, T. J., Jenkins, N. D. M., Bergstrom, H. C., Smith, C. M., Hill, E. C., et al. (2015). Electromyographic, mechanomyographic, and metabolic responses during cycle ergometry at a constant rating of perceived exertion. *Applied Physiology, Nutrition, and Metabolism*, *40*(11), 1178–1185. <http://doi.org/10.1139/apnm-2015-0144>
- Combes, A., Dekerle, J., Bougault, V., & Daussin, F. N. (2016). Effect of work:rest cycle duration on fluctuations during intermittent exercise. *Journal of Sports Sciences*, 1–7. <http://doi.org/10.1080/02640414.2016.1154591>

- Combes, A., Dekerle, J., Webborn, N., Watt, P., Bougault, V., & Daussin, F. N. (2015). Exercise-induced metabolic fluctuations influence AMPK, p38-MAPK and CaMKII phosphorylation in human skeletal muscle. *Physiological Reports*, 3(9), e12462. <http://doi.org/10.14814/phy2.12462>
- Daussin, F. N., Zoll, J., Dufour, S. P., Ponsot, E., Lonsdorfer-Wolf, E., Doutreleau, S., et al. (2008). Effect of interval versus continuous training on cardiorespiratory and mitochondrial functions: relationship to aerobic performance improvements in sedentary subjects. *Am. J. Physiol. Regul. Integr. Comp. Physiol.*, 295(1), R264–72. <http://doi.org/10.1152/ajpregu.00875.2007>
- Gaesser, G. A., & RICH, R. G. (1984). Effects of high- and low-intensity exercise training on aerobic capacity and blood lipids. *Medicine & Science in Sports & Exercise*, 16(3), 269–274. <http://doi.org/10.1249/00005768-198406000-00012>
- Godin, R., Ascah, A., & Daussin, F. N. (2010). Intensity-dependent activation of intracellular signalling pathways in skeletal muscle: role of fibre type recruitment during exercise. *The Journal of Physiology*, 588(Pt 21), 4073–4074. <http://doi.org/10.1113/jphysiol.2010.195925>
- Gorostiaga, E. M., Walter, C. B., Foster, C., & Hickson, R. C. (1991). Uniqueness of interval and continuous training at the same maintained exercise intensity. *European Journal of Applied Physiology*, 63(2), 101–107. <http://doi.org/10.1007/BF00235177>
- Grassi, B., Pogliaghi, S., Rampichini, S., Quaresima, V., Ferrari, M., Marconi, C., & Cerretelli, P. (2003). Muscle oxygenation and pulmonary gas exchange kinetics during cycling exercise on-transitions in humans. *Journal of Applied Physiology (Bethesda, Md. : 1985)*, 95(1), 149–158. <http://doi.org/10.1152/jappphysiol.00695.2002>
- Harriss, D., & Atkinson, G. (2015). Ethical Standards in Sport and Exercise Science Research: 2016 Update. *International Journal of Sports Medicine*, 36(14), 1121–1124. <http://doi.org/10.1055/s-0035-1565186>
- Hermens, H. J., Freriks, B., Disselhorst-Klug, C., & Rau, G. (2000). Development of recommendations for SEMG sensors and sensor placement procedures. *Journal of Electromyography and Kinesiology : Official Journal of the International Society of Electrophysiological Kinesiology*, 10(5), 361–374.
- Hoshino, D., Tamura, Y., Masuda, H., Matsunaga, Y., & Hatta, H. (2015). Effects of decreased lactate accumulation after dichloroacetate administration on exercise training-induced mitochondrial adaptations in mouse skeletal muscle. *Physiological Reports*, 3(9), e12555. <http://doi.org/10.14814/phy2.12555>
- Howley, E. T., Bassett, D. R., & Welch, H. G. (1995). Criteria for maximal oxygen uptake: review and commentary. *Medicine & Science in Sports & Exercise*, 27(9), 1292–1301.
- Kunz, W. S. (2001). Control of oxidative phosphorylation in skeletal muscle. *Biochimica Et Biophysica Acta*, 1504(1), 12–19.
- MacDougall, J. D., Hicks, A. L., MacDonald, J. R., McKelvie, R. S., Green, H. J., & Smith, K. M. (1998). Muscle performance and enzymatic adaptations to sprint interval training. *Journal of Applied Physiology (Bethesda, Md. : 1985)*, 84(6), 2138–2142.
- Petrofsky, J. S., & Lind, A. R. (1980). Frequency analysis of the surface electromyogram during sustained isometric contractions. *European Journal of Applied Physiology and Occupational Physiology*, 43(2), 173–182.
- Russell, A. P., Feilchenfeldt, J., Schreiber, S., Praz, M., Crettenand, A., Gobelet, C., et al. (2003). Endurance training in humans leads to fiber type-specific increases in levels of peroxisome proliferator-activated receptor-gamma coactivator-1 and peroxisome proliferator-activated receptor-alpha in skeletal muscle. *Diabetes*, 52(12), 2874–2881.
- Scheuermann, B. W., Hoelting, B. D., Noble, M. L., & Barstow, T. J. (2001). The slow component of O₂ uptake is not accompanied by changes in muscle EMG during repeated

- bouts of heavy exercise in humans. *The Journal of Physiology*, 531(Pt 1), 245–256. <http://doi.org/10.1111/j.1469-7793.2001.0245j.x>
- Seiler, S., Jøranson, K., Olesen, B. V., & Hetlelid, K. J. (2013). Adaptations to aerobic interval training: interactive effects of exercise intensity and total work duration. *Scandinavian Journal of Medicine & Science in Sports*, 23(1), 74–83. <http://doi.org/10.1111/j.1600-0838.2011.01351.x>
- Sjøgaard, G., Adams, R. P., & Saltin, B. (1985). Water and ion shifts in skeletal muscle of humans with intense dynamic knee extension. *The American Journal of Physiology*, 248(2 Pt 2), R190–6.
- Swain, D. P. (2005). Moderate or vigorous intensity exercise: which is better for improving aerobic fitness? *Preventive Cardiology*, 8(1), 55–58.
- Tjønnå, A. E., Lee, S. J., Rognmo, Ø., Stølen, T. O., Bye, A., Haram, P. M., et al. (2008). Aerobic interval training versus continuous moderate exercise as a treatment for the metabolic syndrome: a pilot study. *Circulation*, 118(4), 346–354. <http://doi.org/10.1161/CIRCULATIONAHA.108.772822>
- Turner, A. P., Cathcart, A. J., Parker, M. E., Butterworth, C., Wilson, J., & Ward, S. A. (2006). Oxygen Uptake and Muscle Desaturation Kinetics during Intermittent Cycling. *Medicine & Science in Sports & Exercise*, 38(3), 492–503. <http://doi.org/10.1249/01.mss.0000188450.82733.f0>

Table

Table 1. Blood lactate concentration and Borg rating scale of perceived exertion during the 2 exercises (70% WR_{pic}).

Condition	CON	INT
<i>Blood lactate concentration (mM)</i>		
Rest	1.36 ± 0.91	1.39 ± 1.00
End/30 min	4.80 ± 1.50*#	2.36 ± 0.78*
End		2.32 ± 1.21*
<i>Borg rating scale of perceived exertion</i>		
Warm-up	10 ± 2	9 ± 2
10 min/20 min	14 ± 1*#§	13 ± 1*
20 min/40 min	15 ± 1*#§	13 ± 1*
30 min/60 min	16 ± 1*#§	13 ± 1*

Values are expressed as mean ± SD. n = 12 for each group.

*Significantly different from rest (blood lactate concentration) or warm-up (rate of perceived exertion) (P <0.01).

#Significantly different from INT (P <0.01).

§Significantly different from other points (P <0.01)

Figure legends

Figure 1. Quantification of $\dot{V}O_2$ fluctuations. Effect of modality (CON and INT) on cumulated amplitude (a), average derivative (b) and fluctuation index of $\dot{V}O_2$ (OFI, c). *Significantly different from CON ($P < 0.01$). $n = 12$ for each group. The line that goes through the box represents the group median, whereas the top and bottom of the box represent the 75th and 25th percentiles, respectively. Whiskers are extended to the most extreme data point that is no more than 1.5 interquartile range from the edge of the box (Tukey style). Dots beyond the whiskers represent outliers. The small thick line inside the box represents the mean.

Figure 2. Quantification of HHb fluctuations. Effect of modality (CON and INT) on cumulated amplitude (a), average derivative (b) and fluctuation index of HHb (HFI, c). *Significantly different from CON ($P < 0.01$). $n = 8$ for each group. The line that goes through the box represents the group median, whereas the top and bottom of the box represent the 75th and 25th percentiles, respectively. Whiskers are extended to the most extreme data point that is no more than 1.5 interquartile range from the edge of the box (Tukey style). Dots beyond the whiskers represent outliers. The small thick line inside the box represents the mean.

Figure 3. EMG values for the two conditions (CON and INT). Root mean square (RMS) for the vastus lateralis (VL) and vastus medialis (VM) (a), and mean power frequency (MPF) for VL and VM (b). Values are expressed as mean \pm SD. $n = 12$ for each group. *Significantly different from measure 1 for the same condition ($P < 0.01$). §Significantly different from INT at the same point ($P < 0.05$).

Supplemental data

Table 1. Mean difference, p-value, Effect Size (ES) and 95% Confidence Interval (CI) of mean differences.

	Difference	p-value	ES	95% CI
<i>EMG activity</i>				
RMS VL CON 1 vs. CON 10min	6.4 ± 5.1 %	0.0007	0.35	3.2, 9.7 %
RMS VM CON 1 vs. CON 10min	5.3 ± 3.4 %	0.01	0.28	3.1, 7.5 %
MPF VL CON 1 vs. CON 10min	-5.2 ± 4.8	0.0003	0.32	-8.2, -2.2
<i>Blood lactate concentration (mM)</i>				
CON Rest vs. CON End	3.45 ± 1.28	0.0002	1.61	2.6, 4.3
INT Rest vs. INT 30min	0.94 ± 1.03	0.02	0.96	0.3, 1.6
INT End vs. CON End	2.58 ± 1.50	0.002	1.42	1.6, 3.5
<i>Borg rating scale of perceived exertion</i>				
CON Warm-up vs. CON 10min	4.1 ± 1.5	0.002	1.65	3.1, 5.0
CON 10min vs. CON 20min	1.3 ± 1.0	0.008	0.89	0.6, 1.9
CON 20min vs. CON 30min	1.3 ± 0.9	0.005	0.89	0.8, 1.9
INT Warm-up vs. INT 20min	3.3 ± 1.5	0.002	1.53	2.4, 4.3
INT 20min vs. CON 10min	1.2 ± 1.1	0.008	1.03	0.5, 1.9
INT 40 min vs. CON 20min	2.0 ± 1.0	0.002	1.31	1.3, 2.7
INT 60min vs. CON 30min	3.3 ± 1.4	0.002	1.58	2.3, 4.2
<i>Energetic expenditure</i>				
Average $\dot{V}O_2$ INT vs. CON	1.146 ± 0.165	<0.0001	1.77	1.047, 1.246
Time spent >90% of target $\dot{V}O_2$ INT vs. CON	1288 ± 261	<0.0001	1.85	1130, 1446
<i>$\dot{V}O_2$ fluctuation</i>				
Cumulated $\dot{V}O_2$ amplitude CON vs. INT	113.7 ± 25.4	<0.0001	1.68	98.3, 129.1
Averaged derivative CON vs. INT	0.949 ± 0.350	<0.0001	1.19	0.733, 1.165
Index of metabolic fluctuation CON vs. INT	7032.5 ± 2769.9	<0.0001	1.43	5358.6, 8706.5
<i>Muscular oxygenation</i>				
Time spent >90% max HHb INT vs. CON	568 ± 632	0.04	1.12	39, 1096
HHb amplitude CON vs. INT	2727 ± 1294	<0.0001	1.63	1645, 3809

Average HHb derivative CON vs. INT	1.62 ± 0.82	<0.0001	1.59	0.94, 2.30
Metabolic fluctuation index CON vs. INT	6508 ± 6032	0.009	1.22	1464, 11552

Difference is expressed as mean ± SD. 95% CI is expressed as lower limit, upper limit.