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Influence of extreme pedal rates on pulmonary O_2 uptake kinetics during transitions to high-intensity exercise from an elevated baseline

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ABSTRACT

We used extreme pedal rates to investigate the influence of muscle fibre recruitment on pulmonary $\dot{V}_{O_2}$ kinetics during unloaded-to-moderate-intensity (U → M), unloaded-to-high-intensity (U → H), and moderate-intensity to high-intensity (M → H) cycling transitions. Seven healthy men completed transitions to 60% of the difference between gas-exchange threshold and peak $\dot{V}_{O_2}$ from both an unloaded and a moderate-intensity (95% GET) baseline at cadences of 35 and 115 rpm. Pulmonary gas exchange was measured breath-by-breath and iEMG of the *m. vastus lateralis* and *m. gluteus maximus* was measured during all tests. At 35 rpm, the phase II time constant (τ_p) values for U → M, U → H, and M → H were 26 ± 7, 31 ± 7 and 36 ± 8 s with the value for M → H being longer than for U → M ($P < 0.05$). At 115 rpm, the τ_p values for U → M, U → H, and M → H were 29 ± 8, 48 ± 16 and 53 ± 20 s with the value for U → M being shorter than for the other two conditions ($P < 0.05$). The $\dot{V}_{O_2}$ slow component was similar at both cadences, but iEMG only increased beyond minute 2 during high-intensity cycling at 115 rpm. These results demonstrate that $\dot{V}_{O_2}$ kinetics are influenced by an interaction of exercise intensity and pedal rate and are consistent with the notion that changes in muscle fibre recruitment are responsible for slower phase II $\dot{V}_{O_2}$ kinetics during high-intensity and work-to-work exercise transitions.

1. Introduction

When muscular work is abruptly increased to an intensity that does not engender a sustained elevation in blood lactate concentration ([lactate], i.e. moderate-intensity exercise below the lactate threshold; LT), pulmonary oxygen uptake ($\dot{V}_{O_2}$) rises exponentially to achieve a new steady state after a short delay (Whipp and Mahler, 1980; Whipp et al., 1982). In healthy, young subjects, an 'unloaded'-to-moderate cycling transition is typically characterised by a $\dot{V}_{O_2}$ time constant (τ; time to achieve 63% of the response) of 20–35 s, which indicates that the response is functionally complete within 2–3 min. However, when a similar transition is made to a work rate above LT (i.e. heavy/severe exercise), this 'fundamental' response is accompanied by an additional component that elevates $\dot{V}_{O_2}$ above the value predicted for the work rate (Whipp and Wasserman, 1972; Linnarsson, 1974; Barstow and Mole, 1991). The mechanistic basis of this '$\dot{V}_{O_2}$ slow component' is still debated (Borrani et al., 2009; Zoladz et al., 2008; see Poole and Jones, 2005 for review).

The phase II $\dot{V}_{O_2}$ kinetics are known to be slower when both moderate and heavy/severe transitions are initiated from an elevated baseline work rate (i.e. during 'work-to-work' transitions) (Hughson and Morrissey, 1982, 1983; di Prampero et al., 1989; Brittain et al., 2001; MacPhee et al., 2005; Wilkerson and Jones, 2006, 2007; DiMenna et al., 2008). The original explanation for slower $\dot{V}_{O_2}$ kinetics in these circumstances was that muscle O_2 delivery was limiting O_2 consumption (Hughson and Morrissey, 1982, 1983; Hughson, 2005). However, further investigation has shown that prior exercise that increases muscle O_2 availability does not reduce τ_p during subsequent work-to-work transitions spanning moderate-to-high intensities (DiMenna et al., 2008).

The lengthening of phase II $\dot{V}_{O_2}$ kinetics during work-to-work transitions might be explained by differences in muscle fibre recruitment (Brittain et al., 2001; Wilkerson and Jones, 2006, 2007; DiMenna et al., 2008). Henneman's size principle indicates that fibres are recruited in a hierarchical manner depending primarily upon the intensity of the activity being undertaken (Henneman and Mendell, 1981). The smallest motoneurons that typically innervate fibres with the highest oxidative capacity are recruited first and would, therefore, be expected to contribute substantially in the moderate region where $\dot{V}_{O_2}$ kinetics is most rapid (Brittain et al., 2001). Conversely, larger motor units that are positioned higher in the recruitment hierarchy comprise type II fibres which might be expected to exhibit slower $\dot{V}_{O_2}$ kinetics (Crow and Kushmerick, 1982). This recruitment hierarchy is exemplified by the measured profile of muscle glycogen depletion, which indicates exclusive type I fibre involvement during

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moderate exercise compared with the activation of both principal fibre types during more intense efforts (Gollnick et al., 1974; Krustrup et al., 2004). On this basis, it is likely that higher order fibres would make a proportionately greater contribution to force production during transitions to high-intensity exercise initiated from a moderate-intensity baseline (Wilkerson and Jones, 2007; DiMenna et al., 2008). With the assumption that muscle fibres that are positioned higher in the recruitment hierarchy have an innately slower oxidative metabolic response (Crow and Kushmerick, 1982), it might be predicted that phase II $\dot{V}_{O_2}$ kinetics would be relatively fast for low-intensity exercise, relatively slow during work-to-work transitions (such as in the transition from low-intensity to high-intensity exercise) and intermediate for high-intensity exercise, i.e. unloaded-to-moderate τ_p < unloaded-to-high-intensity τ_p < moderate-to-high-intensity τ_p.

In addition to work intensity, progression through the fibre recruitment hierarchy is influenced by muscle contraction frequency and it is generally accepted that the proportional contribution of higher order fibres is greater at higher compared to lower pedal rates (Sargeant, 1999; MacIntosh et al., 2000; Ferguson et al., 2001). Therefore, at the same relative exercise intensity, manipulation of pedal rate would be expected to alter the oxidative response heterogeneity by causing a shift toward a greater contribution of low-order fibres at extremely slow cadences and toward a greater contribution of high-order fibres at extremely rapid ones. The use of cadence extremes in conjunction with the work-to-work model could, therefore, provide further insight into the degree to which the altered $\dot{V}_{O_2}$ kinetics during work-to-work high-intensity transitions are related to the metabolic properties of the recruited muscle fibres, as has been suggested by us and others (Brittain et al., 2001; Poole and Jones, 2005; Wilkerson and Jones, 2006, 2007; DiMenna et al., 2008).

On the basis of the expected motor unit recruitment profiles (see above), we tested the hypotheses that: (1) at 35 rpm, τ_p would be similar for U → M and U → H (i.e. unloaded-to-moderate-intensity τ_p = unloaded-to-high-intensity τ_p < moderate-to-high-intensity τ_p); and (2) at 115 rpm, τ_p would be similar for U → H and M → H (i.e. unloaded-to-moderate-intensity τ_p < unloaded-to-high-intensity τ_p = moderate-to-high-intensity τ_p). We used EMG to assess the degree to which motor unit activation was altered at extreme pedal rates.

2. Methods

2.1. Subjects

Seven male subjects (mean ± SD age 31 ± 8 years, stature 1.79 ± 0.02 m, mass 81.5 ± 7.5 kg) volunteered and gave written informed consent to participate in this study, which had been approved by the local Research Ethics Committee. The subjects were all recreationally active and were familiar with the exercise mode and experimental procedures used in the present study. On test days, subjects were instructed to report to the laboratory in a rested state, having completed no strenuous exercise within the previous 24 h, and having abstained from food, alcohol and caffeine for the preceding 3 h.

2.2. Experimental overview

In the present study, we combined previously published data for high-intensity transitions (U → H) at extreme pedal rates (see DiMenna et al., 2009; conditions '35 Unprimed' and '115 Unprimed') with additional data characterizing similar transitions completed in two steps (U → M, unloaded-to-moderate-intensity exercise; and M → H, moderate-to-high-intensity exercise) to examine the effect of pedal rate on $\dot{V}_{O_2}$ kinetics during work-to-work transitions.

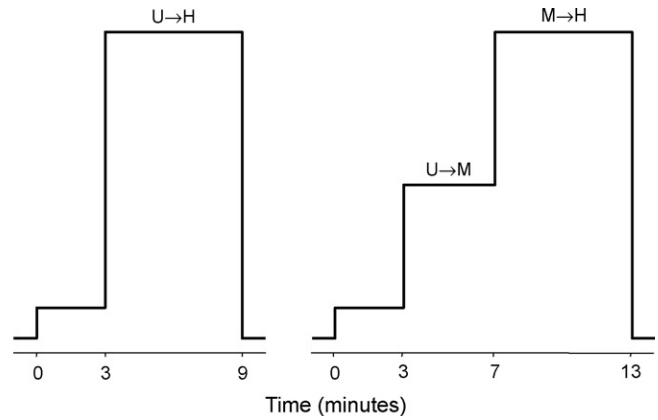

Fig. 1. Schematic illustration of the two experimental protocols. The protocol depicted on the left involved an abrupt transition from unloaded cycling to a high-intensity work rate that was completed in one full step (U → H). The protocol depicted on the right involved the same transition divided into two separate steps (i.e. lower step, U → M; upper step, M → H). U → H was performed four times at each pedal rate; U → M/M → H was performed three times at each pedal rate.

All testing was completed in an air-conditioned laboratory at a temperature of 20–22 °C. The subjects visited the laboratory on 16 occasions over a 6-week period to perform exercise tests on an electronically braked cycle ergometer (Lode Excalibur Sport, Groningen, the Netherlands). This device allows for the maintenance of a prescribed constant power output across a wide range of pedal cadences by instantaneously adjusting flywheel resistance via electrical braking.

Testing was conducted at the same time of day (±2 h) for each subject. On each of the first two visits, the subjects completed a ramp incremental exercise test for determination of cadence-specific peak $\dot{V}_{O_2}$ ($\dot{V}_{O_2\,peak}$) and gas-exchange threshold (GET). One test was performed at a pedal rate of 35 rpm, the other at a pedal rate of 115 rpm, and test order was alternated among subjects. On each of the 14 subsequent visits, subjects completed a bout of high-intensity exercise (at a work rate calculated to require 60% of the difference between the GET and $\dot{V}_{O_2\,peak}$, i.e., 60% "Δ") initiated from either 'unloaded' (20 W) cycling or moderate (95% GET) cycling (work-to-work transition). Four repetitions of the full transition (from an unloaded baseline) and three repetitions of the work-to-work transition were performed at both 35 and 115 rpm. Each laboratory visit was separated by at least 48 h. The two protocols are depicted in Fig. 1.

2.3. Experimental procedures

The ramp incremental exercise tests consisted of 3 min of pedaling at 0 W, followed by a continuous ramped increase in work rate of 30 W/min until the subject was unable to continue. The subjects were asked to maintain the prescribed cadence and instruction was given if/when they deviated by more than ±5 rpm. Saddle and handlebar heights were recorded and the same settings were reproduced on subsequent tests. The $\dot{V}_{O_2\,peak}$ was defined as the highest 30 s mean value recorded before the subject's volitional termination of the test. The GET was determined from a cluster of measures including: (1) the first disproportionate increase in carbon dioxide output ($\dot{V}_{CO_2}$) from visual inspection of individual plots of $\dot{V}_{CO_2}$ vs. $\dot{V}_{O_2}$; (2) an increase in $\dot{V}_E/\dot{V}_{O_2}$ ($\dot{V}_E$, expiratory ventilation) with no increase in $\dot{V}_E/\dot{V}_{CO_2}$; (3) an increase in end-tidal O_2 tension with no fall in end-tidal CO_2 tension. When there was lack of agreement between these measures, the more conservative estimate was