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Limb movement frequency is a significant modulator of the ventilatory response during submaximal cycling exercise in humans

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ABSTRACT

Human experimentation investigating the contribution of limb movement frequency in determining the fast exercise drive to breathe has produced controversial findings. To evaluate the role of limb movement frequency in determining the fast exercise drive to breathe, endurance runners and recreationally-active controls performed two sinusoidal exercise protocols on a cycle ergometer. One protocol was performed at constant workload with sinusoidal pedaling cadence, and a second with sinusoidal workload at constant cadence. Metabolic rate (VO_2) increases and means were matched between these two experiments. The ventilatory response was significantly faster when limb movement speed was varied, compared to when pedal loading was varied (18.49 ± 15.6 s vs. 50.5 ± 14.5 s, $p < 0.05$). Ventilation response amplitudes were significantly higher during pedal cadence variation versus pedal loading variation (3.99 ± 0.25 vs. 2.58 ± 0.17 L/min, $p < 0.05$). Similar findings were obtained for endurance athletes, with significantly attenuated ventilation responses to exercise versus control subjects. We conclude that fast changes in limb movement frequency are a potent stimulus for ventilation at submaximal workloads, and that this response is susceptible to attenuation through training.

1. Introduction

The rapid increase in breathing observed at the onset of exercise and the slow increase as exercise continues is called the exercise hyperpnoea (Krogh and Lindhard, 1913). The sudden increase in ventilation at the onset of exercise is termed the 'fast neural drive' (Mateika and Duffin, 1995; Duffin, 2014), because this response occurs too rapidly for a metabolic signal to travel through the blood and increase ventilation through central or peripheral chemoreception (Barr et al., 1964). The fast neural drive originates from peripheral feedback from the muscles of exercising limbs that can be mechnoreceptive (Amann et al., 2011) or metaboreceptive (Haouzi, 2006). Additionally, central command generation from higher brain centres contributes to the fast neural drive to breathe (Bell, 2006).

It has long been hypothesized that limb movement frequency may have a significant role in the magnitude and speed of the ventilatory response (Dejours, 1967). Increasing limb movement by suddenly increasing treadmill speed will evoke a greater increase in ventilation than sudden changes in treadmill grade at the same metabolic workload (Duffin and Bechbache, 1983). Additionally, sinusoidal changes in treadmill speed result in a faster ventilatory response and greater amplitude of increase in ventilation than sinusoidal changes in grade (Wells et al., 2007). The shorter lag during sinusoidal changes in treadmill speed suggest that changes in limb movement frequency significantly contribute to the fast exercise drive to breathe (Wells et al., 2007). However, some investigators have demonstrated that ventilation couples with metabolism rather than limb movement speed, especially during the slow ventilatory response component (Wigertz, 1970). Therefore, the magnitude of the contribution of limb movement to exercise hyperpnoea is unclear, and its persistence throughout exercise has been debated (Casaburi et al., 1978). Furthermore, the amount of exercise training that an individual partakes in can affect exercise hyperpnoea through attenuation of neural drive that is either feedforward or feedback in nature (Miyamoto et al., 2012).

Research involving the fast exercise drive to breathe in humans has been extensive yet marked with experimental difficulties due to the complex relationship between feedforward and feedback inputs that affect the respiratory response to exercise (Forster,

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2014). Sinusoidal exercise protocols present a robust method to examine factors affecting the ventilatory response in humans non-invasively.

These experiments aimed to specifically determine if limb movement frequency controls the magnitude of the fast exercise drive to breathe in humans. A sinusoidal exercise protocol was selected in order to repeatedly observe the cardiorespiratory responses to a given exercise stimulus, and to avoid the possibility of entrainment of breathing frequency to limb movement (Bechbache and Duffin, 1977). Measurement of ventilation lags during sinusoidal exercise have been performed previously using treadmill exercise (Wells et al., 2007), and cycle ergometry (Casaburi et al., 1977, 1978). The use of cycle ergometry is an improved exercise modality versus treadmill exercise, as it mitigates confounding vestibular and upper body movement contributions to ventilation. Additionally, metabolic workloads (VO_2 and VCO_2) were not controlled for between sinusoidal exercise tests in earlier cycle ergometry experiments (Casaburi et al., 1977, 1978). This experiment represents an improvement in isolating the fast exercise drive to breathe in comparison to prior studies: we controlled for changes in metabolic gas exchange between tests, vestibular contributions, and potentially confounding upper limb movement.

These factors determining the drive to breathe during exercise were investigated in both recreationally active and endurance athlete populations, to establish if training can affect them. We hypothesized that ventilation would be affected more rapidly by changing cycling cadence than pedal loading, and that exercise training would diminish the fast exercise drive. These results would confirm that the fast exercise drive to breathe persists throughout exercise and is affected by limb movement speed.

2. Methods

2.1. Participant recruitment

Following approval from the University of Toronto ethics committee (protocol reference number 26396), 38 subjects participated in the experiment (16 female). Control participants were asked to participate in less than three hours of physical activity per week, and not be participating in a structured athletic training program. The athlete participants were endurance runners participating in races greater than 800 m, and training regularly in a structured running training program with race times within 10% of the qualifying standards for the Canadian National Championships. All participants gave their informed consent in writing prior to undertaking the study, and none reported health problems relevant to the experiment. Participants completed two study visits over a maximum time-span of two weeks. The first study visit included a familiarization session and ramp exercise testing, and the second study visit consisted of sinusoidal pedal cadence and pedal loading exercise. The two sinusoidal pedal loading protocols were performed in a randomly counterbalanced order with 40 min of recovery between tests.

2.2. Equipment

Participants breathed through a facemask connected to a portable breath-by-breath metabolic measurement system (Metamax 3B, CORTEX Biophysik, Germany). Breath-by-breath measures of the following physiological variables were collected from the device: ventilation (V), respiratory frequency (f_R), end-tidal partial pressure of oxygen ($P_{ET}O_2$), end-tidal partial pressure of carbon dioxide ($P_{ET}CO_2$), volume of carbon dioxide produced (VCO_2), and volume of oxygen consumed (VO_2). Beat-by-beat cardiac frequency (f_H) was measured using a heart rate monitor (Polar S810, Polar, Finland).

Participants exercised on an electromagnetically-braked cycle ergometer (Ergomedic 839e, Monark). Pedaling speed and cycling load data were collected using a specially-written software (LabVIEW 2012, National Instruments) that controlled and read data from the cycle ergometer. Ergometer pedal load changes were pre-programmed and controlled using a laptop computer. Participants followed ergometer cycling speed protocols on a screen that read out a pre-programmed cycling cadence. The heart rate monitor read data into the Metamax 3B system, and all physiological variables were then exported to spreadsheet software (Microsoft® Excel) for further analysis.

2.3. Ramp testing

Participants visited the laboratory to complete a modified VO_{2max} step test on the cycle ergometer. A low–wattage (30 W) workload was used for the first 5 min while the participant cycled at 75 r min^{-1}, followed by a ramp increase of 8 W min^{-1} for 10 min while the participant continued to cycle at 75 r min^{-1}. The 75 r min^{-1} pedaling speed was selected for ramp testing in order to replicate the mean limb movement speed performed during the sinusoidal exercise testing protocols. The first portion of the exercise test matched the amplitude of ventilation (V_E) and oxygen consumption (L min^{-1}) expected during the sinusoidal exercise tests. The second portion of the modified VO_{2max} test characterized their maximal aerobic capacity. When the ergometer reached 110 W, participants were permitted to volitionally select a cycling cadence, and the workload increased in steps of 40 W every minute until exhaustion.

2.4. Sinusoidal speed and load tests

The workload in watts (W) corresponding to half that of the first ventilatory threshold obtained during VO_{2max} testing was used to determine the workload for the sinusoidal exercise tests. The first ventilatory threshold was the time immediately prior to a maintained non-linear increase in ventilation, and had to be followed by a second threshold (Mateika and Duffin, 1994). At the beginning of the sinusoidal exercise tests, participants completed five minutes of steady-state exercise at the mean workload and cadence used for the sinusoidal exercise tests. Sinusoidal exercise protocol 1 consisted of participants volitionally altering their pedaling cadence to follow a sinusoidal variation, with a trough of 50 r min^{-1} and a peak of 100 r min^{-1} over a period of two minutes. Pedal loading on the cycle ergometer was set at a constant value during this test. Participants completed approximately ten sinusoidal cycles in total, with the final five cycles used for data analysis.

During the second sinusoidal protocol, participants first completed five minutes of exercise at the mean of the workload to be used during the test. Pedal loading was then altered sinusoidally with a two-minute period automated by the computer. Participants cycled at the mean of the cadence of the sine wave of protocol one (75 r min^{-1}) throughout the entire test. The first few sinusoidal cycles were used to adjust the pedal loading trough and peak to match metabolic workload (VO_2 and VCO_2) between the two tests as needed. This sinusoidal exercise was completed for ten cycles, with the final five cycles used for data analysis.

2.5. Matching VO_2 and VCO_2 between tests

Individual effort during cycling exercise is comprised of many factors including individual (external) effort to move the bicycle flywheel, as well as internal variables such as muscle fiber contraction speed and fiber type (Umberger et al., 2006). VO_2 and VCO_2