©Journal of Sports Science and Medicine (2007) **6,** 526-531
http://www.jssm.org

Research article

No influence of hypoxia on coordination between respiratory and locomotor rhythms during rowing at moderate intensity

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Abstract

Besides neuro-mechanical constraints, chemical or metabolic stimuli have also been proposed to interfere with the coordination between respiratory and locomotor rhythms. In the light of the conflicting data observed in the literature, this study aimed to assess whether acute hypoxia modifies the degree of coordination between respiratory and locomotor rhythms during rowing exercises in order to investigate competitive interactions between neuro-mechanical (movement) and chemical (hypoxia) respiratory drives. Nine male healthy subjects performed one submaximal 6-min rowing exercise on a rowing ergometer in both normoxia (altitude: 304 m) and acute hypoxia (altitude: 2877 m). The exercise intensity was about 40 % and 35 % (for normoxia and hypoxia conditions, respectively) of the individual maximal power output measured during an incremental rowing test to volitional exhaustion carried out in normoxia. Metabolic rate and minute ventilation were continuously collected throughout exercise. Locomotor movement and breathing rhythms were continuously recorded and synchronized cycle-by-cycle. The degree of coordination was expressed as a percentage of breaths starting during the same phase of the locomotor cycle. For a same and a constant metabolic rate, acute hypoxia did not influence significantly the degree of coordination (mean ± SEM, normoxia: 20.0 ± 6.2 %, hypoxia: 21.3 ± 11.1 %, $p > 0.05$) while ventilation and breathing frequency were significantly greater in hypoxia. Our results may suggest that during rowing exercise at a moderate metabolic load, neuro-mechanical locomotion-linked respiratory stimuli appear "stronger" than peripheral chemoreceptors-linked respiratory stimuli induced by hypoxia, in the context of our study.

Key words: Control of breathing, locomotor-respiratory coupling, neuro-mechanical entrainment, chemical drive.

Introduction

Interactions between locomotion and ventilation have now been studied in several species of mammals, from a variety of perspectives. Among the mechanisms for this interaction are neural and mechanical interactions of separate controllers. Viala and Freton (1983) and Viala (1986) observed that direct central (subcortical and spinal areas) interactions do exist between the respiratory and the locomotor rhythms in decorticate rabbits. Iscoe and Polosa (1976) showed entrainment of the respiratory rate by repetitive somatic afferent stimulation of the hamstring nerve in cats. Moreover, in instrumented dogs and horses, Ainsworth et al. (1997) provided evidence that the exercise hyperpnea is neurally mediated. Further, it is now well established that locomotion entrains breathing rhythm, that is that the locomotor cycle contributes to the respiratory flow (Bernasconi et al., 1995; Bramble and Carrier, 1983; Hill et al., 1988; Rassler and Kohl, 1996) by mechanical linkage mechanisms. Locomotor muscles can cause airflow by acting directly on the chest wall (diaphragm, rib cage) or by generating inertial forces that accelerate tissue masses.

Interactions between rhythmic locomotor and respiratory patterns may lead to coordination, which can occur as an integer ratio of both frequencies and as a significant coincidence of certain phases of both cycles. When the nature of the locomotion involves a greater role for the forelimbs in humans as well as spinal flexion and extension, as occurs during rowing, then an entrainment of ventilation is reported to occur at integral multiples of stroke rate (1:1, 2:1 or 3:1). In rowing, periodic contraction of muscles and movement elevate pleural pressure (Siegmund et al., 1999). Also the increased intra-abdominal pressure impairs ventilation ($\dot{V}_E$) at stroke catch (Cunningham et al., 1975) or stroke finish (Siegmund et al., 1999). Furthermore, during the drive phase the knees and hips extend and $\dot{V}_E$ is assisted (Siegmund et al., 1999). In rowing, entrainment with various frequency ratios of 1:1, 2:1 or 3:1 (Maclennan et al., 1994; Mahler et al., 1991; Siegmund et al., 1999) appears to lead adequate $\dot{V}_E$ (Siegmund et al., 1999).

Besides neuro-mechanical constraints, chemical or metabolic stimuli have also been proposed to interfere with coordination between respiratory and locomotor rhythms (Paterson et al., 1987). For instance, an increase in chemical drive to breathe can occur under hypoxic conditions. To date, two independent studies (Paterson et al., 1987; Seebauer et al., 2003b) have tested the hypothesis that entrainment of breathing frequency (Bf) by exercise rhythm may be affected during conditions of an enhanced peripheral chemoreceptor activity in hypoxia. However, these two studies showed opposite findings. In running, Paterson et al. (1987) observed a decrease in degree of coordination with increasing hypoxia but more recently Seebauer et al. (2003b) observed no influence of hypoxia on coordination between breathing and cycling rhythms. Paterson et al. (1987) discussed their results in terms of an increased Bf in hypoxia beyond the fundamental frequencies that were locked to exercise rhythm in normoxia. It would seem that increased peripheral chemoreceptor activity during exercise in hypoxia decreases the degree of coordination as a consequence of hypoxic-

Received: 02 August 2007 / Accepted: 20 September 2007 / Published (online): 01 December 2007

induced increases in $\dot{V}_E$ (as seen in Bf), suggesting that the respiratory system is possibly no longer optimized.

Rowing presents a well established respiratory entrainment by limb movements during normoxia due to neuro-mechanical interactions especially with active upper-body limbs (Cunningham et al., 1975; Maclennan et al., 1994; Mahler et al., 1991; Siegmund et al., 1999). Considering the two previous contradictory findings of Paterson et al. (1987) and Seebauer et al. (2003b), we were interested to study whether chemical and neuromechanical respiratory drives competitively interact during submaximal rowing exercise. Therefore, the present study aimed to assess whether acute hypoxia (chemical respiratory drive) modifies the degree of coordination between respiratory and locomotor rhythms during rowing exercise.

Methods

Subjects

Nine male healthy students (age 25 ± 1.0 years, height 1.77 ± 0.02 m, and body weight 78.0 ± 3.6 kg) volunteered to participate to this study. Participants were not specialists in rowing activity but were regularly accustomed to rowing during the last three months before the testing period, twice a week. They were asked to refrain from ingesting caffeine and/or alcohol for at least 12 hours prior to testing. They were asked to eat a light meal 2 hours before testing. All participants were blind to the purpose of the experiment. The study protocol complies with the Helsinki declaration for human experimentation and was approved by the local Ethics Committee. Possible risks and benefits were explained and written informed consent was obtained from each subject prior to all testing.

Environmental conditions

Tests under normoxic conditions were undertaken at an altitude of 304 m and tests under hypoxic conditions were realized at an altitude of 2877 m (laboratory of the Pic du Midi de Bigorre, observatory, France). Subjects were transported by a cable-car and were tested immediately after their arrival. So, they were acutely exposed to hypoxia in order to induce marked alterations in Bf during exercise.

Determination of working intensity

Each subject underwent an incremental rowing test to volitional exhaustion on a rowing ergometer (Concept II, Morrisville, Vermont, USA) in normoxic conditions. The initial power output was set at 50 W, and each minute, the target intensity was increased by 25 W. Each subject continued to exercise until exhaustion or the inability to maintain the target level of power output. From this incremental test, a submaximal intensity corresponding to ~ 40 % of the individual maximal power output in normoxia was determined, that is with a negligible contribution of the anaerobic metabolism in total energy expenditure and allowing a large degree of freedom in the breathing regulation (Seebauer et al., 2003b). Due to the decrease in aerobic power output with the increase in altitude (Fulco et al., 1998), the submaximal intensity in hypoxia was adjusted in order to obtain the same metabolic rate (i.e., $\dot{V}O_2$) than during normoxic conditions. A decrease of about 13 % of the submaximal exercise power output in normoxia was necessary to reach the same absolute $\dot{V}O_2$ in both normoxia and hypoxia (that is for an equivalent absolute submaximal metabolic load).

Experimental protocol

During a second visit, subjects were asked to perform one submaximal 6-min rowing exercise in normoxia, and on a separate day, the same submaximal test with an adjusted exercise intensity (see above) was carried out in hypoxia. These tests were randomized.

Mechanical measurements

Upper-body movements were recorded with a custom-made load cell inserted between the ergometer handle and chain, and connected to a dedicated acquisition system (MP30, Biopac Systems Inc., Santa Barbara, CA, USA). Then, stroke rate (SR) values were calculated off-line.

Physiological measurements

Values of $\dot{V}_E$, tidal volume (VT) and $\dot{V}O_2$ were continuously determined breath-by-breath during all exercise testing (Cosmed K4b², Rome, Italy). Gas analyzers were calibrated before each test with ambient air (O_2: 20.93 % and CO_2: 0.03 %) and a gas mixture of known composition (O_2: 16.00 % and CO_2: 5.00 %). An O_2 analyzer with a polarographic electrode and a CO_2 analyzer with an infrared electrode sampled expired gases at the mouth. The facemask, that had a low dead space (70 mL) was equipped with a low-resistance, bidirectional digital turbine (28 mm diameter). This turbine was calibrated before each test with a 3 L syringe (Hans Rudolph Inc., Dallas, USA). Face masks allowed subjects to simultaneously breath with mouth and nose, for more comfort. It has been demonstrated that the use of a mouthpiece and nose clip may affect VT, $\dot{V}_E$, inspiratory flow and respiratory frequency (Weissman et al., 1984). Heart rate (HR) was continuously measured via a wireless Polar-monitoring system (Polar Electro Oy, Kempele, Finland), and mean HR over each breath was recorded.

Breathing frequency (Bf) was recorded using a thermocouple sensor (SS6L Temperature Transducer BSL, Biopac Systems Inc, Santa Barbara, USA) which determines nasal airflow by detecting the difference in air temperature. The temperature transducer was attached just under the nostril of the subject and connected to the Biopac MP100 acquisition unit. The respiratory flow and upper-body movement signals were continuously recorded and synchronized at 200 Hz during all exercises.

Data analysis

All values were recorded during metabolic steady state (after the initial 2 min of each constant-load submaximal exercise) and averaged during the last 4 min. Given the various inputs that may influence the central nervous system pattern generators for breathing and rowing, some cycle-to-cycle variability in the “tightness” of rhythm coordination is to be expected during entrainment. The

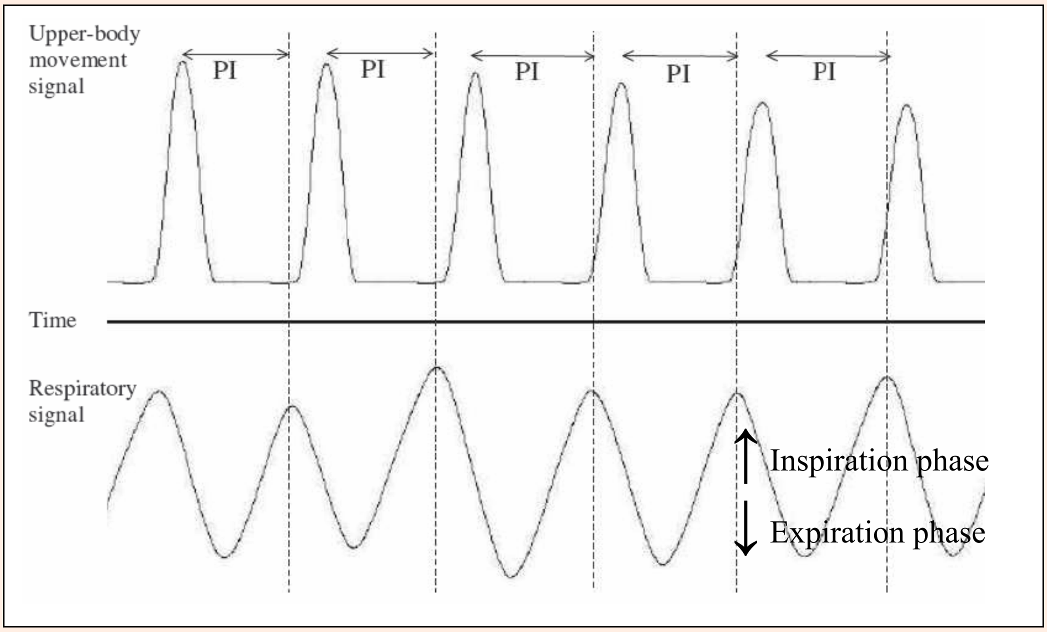

Figure 1. **Example of the evaluation of coordination between breathing and rowing rhythms. Respiratory (lower graph) and rhythmic upper-body movement (upper graph) signals were synchronized during submaximal rowing exercise. Dotted line represents the beginning of expiration. The signal between two dotted lines represents a full respiratory cycle (expiration and inspiration phases). Phase interval (PI) represents the time between an arbitrary chosen point of the stroke movement (i.e., the peak force during stroke) and the onset of expiration cycle by cycle. In the lower graph, the downward and the upward slopes represent the expiration and the inspiration phases, respectively.**

onset of the movement cycle and that of the expiration phase were determined cycle-by-cycle during the last 4 min of all submaximal exercise tests (Figure 1). Then, to estimate the degree of coordination, we used the rigorous method proposed by Seebauer et al. (2003a). We determined the time between the peak force during stroke and the onset of expiration during each cycle; this time is called phase interval. When the phase interval value is maintained constant ± 0.0725 sec for at least four consecutive breaths, coordination is considered to be present (Hill et al., 1988). The degree of coordination (%) corresponded to the percentage of breaths meeting this criteria compared with the total number of breaths recorded in the last 4 min of the respective test. This method takes into account the natural variability in coordination precision and is sensitive to changing patterns of coordination but also addresses the issue of how often apparent entrainment may arise by chance.

We also determined the mean integer ratio of frequencies (stroke frequency / breathing frequency) over the last 4 min of all exercise tests.

Statistical analysis

Data are reported as means ± SEM. Differences between environmental conditions (normoxia vs. hypxoxia) were assessed by using paired *t*-tests (SigmaStat, V2.03, SPSS Inc., USA). The level of significance was set at $p < 0.05$ for all tests.

Results

Mechanical power values during submaximal and incremental rowing exercises are given in Table 1. Physiological and mechanical variables during submaximal exercises are summarized in Table 2.

Table 1. **Power output values (n = 9) during submaximal and incremental rowing exercises. Data are means (±SEM).**

	Normoxia	Hypoxia
Mean power (W)	111.0 (4.5)	96.8 (3.9) *
Pmax (W)	277.4 (11.2)	-

Mean power, corresponding to 40 % of Pmax for the normoxia condition and to 35 % of Pmax for the hypoxia condition; Pmax, maximal power output value of the incremental rowing test to volitional exhaustion determined in normoxia. * Significantly different from normoxia ($p < 0.001$).

Table 2. **Physiological and mechanical variables (n = 9) during submaximal rowing exercises. Data are means (±SEM).**

	Normoxia	Hypoxia
$\dot{V}O_2$ (mL·min^{-1}·kg^{-1})	30.1 (1.5)	30.3 (1.6)
$\dot{V}_E$ (L·min^{-1})	56.5 (2.6)	66.9 (3.4) **
VT (L)	2.23 (.10)	2.16 (.09)
HR (beats·min^{-1})	129.7 (4.7)	140.1 (5.1) *
SR (strokes·min^{-1})	23.8 (1.4)	26.5 (1.1) *
Bf (breaths·min^{-1})	25.8 (1.6)	31.4 (1.8) **
Mean SR/Bf ratio	.93 (.04)	.86 (.05)

$\dot{V}O_2$, oxygen consumption; $\dot{V}_E$, ventilation.; VT, tidal volume, HR, heart rate; SR, stroke rate; Bf, breathing frequency; Mean SR/Bf ratio, mean stroke rate / breathing frequency ratio. $^{*, **}$ Significantly different from normoxia ($p < 0.05$ and $p < 0.01$).

Ventilatory and metabolic variables

During the rowing incremental test to volitional exhaustion, average peak $\dot{V}O_2$ value was about 53.3 ± 2.8 mL·min^{-1}·kg^{-1}. During submaximal exercises, $\dot{V}_E$ was significantly increased with altitude ($p < 0.01$) due to an increase in Bf ($p < 0.01$). An increase in HR was also observed with altitude ($p < 0.05$). Absolute $\dot{V}O_2$ values were not significantly different between normoxia and hypoxia conditions, and corresponded to 56.6 ± 1.4 % of peak $\dot{V}O_2$ measured in normoxia.

Mechanical variable

A significant effect of hypoxia was observed on the SR values: SR was significantly higher in hypoxia than in normoxia (Table 2, $p < 0.05$).

Degree of coordination and mean integer ratio

No effect of hypoxia was observed on the degree of coordination ($p = 0.9$) as on the mean integer ratio of both frequencies ($p = 0.1$, Table 2). The average degree of coordination was of 20.0 ± 6.2 % and of 21.3 ± 11.1 % in normoxia and in hypoxia, respectively.

Discussion

The degree of coordination observed during rowing exercise may be judged low. However, this value is completely dependent on the method of determination used. Different methods are proposed in the analysis of coordination between respiratory and locomotor rhythms but with variable results. Spectral analysis (MacDonald et al., 1992), nonlinear mathematical models like the Farey tree (Gonzalez and Piro, 1985) or the HKB model, a dynamical model first developed by Haken, Kelso and Bunz (Haken et al., 1985), or the percentage of recorded breaths in one phase of propulsion (Bernasconi and Kohl, 1993) have all been used. An integer frequency ratio is characteristic of coordination. It implies a tight phase locking during consecutive breaths. The base of any method for detecting coordination is to establish how often apparent phase locking may arise randomly. Previous studies suggest that coordination may often be intermittent; thus a detection method capable of discriminating short-term rhythm interactions is necessary to establish physiological interactions between breathing and moving limb patterns. We chose the method described by Hill et al. (1988), a rather well-identified method in the literature (Seebauer et al., 2003a; 2003b) allowing us to detect coordination even when it occurs sporadically, with varying coupling patterns, and in a not randomly fashion. However, since this method imposes strict criteria (see Methods) for coordination between two rhythms generators, it appears as a restrictive method and this may explain the low values of degree of coordination reported (about 20 %) in the present study and in the literature using the same method (Fabre et al., 2007; Seebauer et al., 2003a; 2003b).

The main goal of this study was to assess whether acute hypoxia modifies the degree of coordination between respiratory and locomotor rhythms during constant workload rowing exercise in order to investigate possible competitive interactions between neuro-mechanical (movement) and chemical (hypoxia) respiratory drives. The few studies (Paterson et al., 1987; Seebauer et al., 2003b) which have investigated this issue gave conflicting results. Paterson et al. (1987) observed a decrease in degree of coordination during running with hypoxia whereas Seebauer et al. (2003b) showed no influence of hypoxia on the coordination between breathing and cycling rhythms at three submaximal workloads. Rowing appears like a very different form of locomotion than running or cycling. Upper-body locomotor muscles implicated in rowing are in part the same as respiratory muscles and are acting directly on the chest wall (diaphragm, rib cage) in contrast to running or cycling activities. This type of mechanical links between respiratory and locomotory systems is further strengthened by the succession of cramped and extended body positions during rowing (Siegmund et al., 1999). Such an activity (with an important contribution of the upper-body limbs in propulsion) had never been investigated in this way.

When two rhythmic components of a system interact in a way so that one (locomotor rhythm) imposes its rhythm on the other (breathing), the first is said to have entrained the other (Bramble and Carrier, 1983; Hill et al., 1988; Rassler and Kohl, 1996; Seebauer et al., 2003a). So, coordination is determined by the relationships between the strength of attraction of the locomotor rhythm and the strength of the breathing rhythm in maintaining its intrinsic rate. Based on the control of breathing during exercise involving interactions between neuro-mechanical and chemical respiratory drives, it is possible that the hypoxic stimulus would decrease the degree of coordination between upper-body movement and breathing rhythms during rowing at a moderate metabolic load. But, our results suggest that the degree of coordination was not influenced by the increase in metabolic stimuli induced by the hypoxic-induced stress although we observed, as expected, a significant increase in both Bf and $\dot{V}_E$ in hypoxia for a same moderate metabolic load. Such an increase in Bf has been proposed by Paterson et al. (1987) as the main responsible factor of the hypoxic-induced decrease in degree of coordination. But, in the present study and contrary to Paterson's study (Paterson et al., 1987), the frequency of the second rhythm involved in the occurrence of coordination was also significantly affected by hypoxia, so that the mean integer ratio of both frequencies remained unchanged and close to a 1:1 coordination pattern whatever the condition (Table 2). However the impact of movement rate on the coordination is still a matter of debate. During rowing and contrary to running (Paterson et al., 1987), the respiratory and locomotor rhythms seem to be strongly locked in order to maintain homeostasis even when hypoxia induces an increase in chemical respiratory drive. This linkage between these two rhythms may have permitted to avoid a decrease of the degree of coordination. Nevertheless, our result is in agreement with a recent study (Seebauer et al., 2003b) involving different cycling exercise intensities where the authors proposed that the effect of hypoxia on the degree of coordination is in part dependent on the exercise intensity. In fact, Paterson et al. (1987) chose an exercise intensity at about 40 % of maximal $\dot{V}O_2$ whereas the lowest intensity used in Seebauer's study (Seebauer et al., 2003b) was of 56.1 ± 6.7 % of maximal $\dot{V}O_2$ and of 56.6 ± 1.4 % of peak $\dot{V}O_2$ in the present study. According to Seebauer et al. (2003b), lower intensities would permit higher degree of freedom in the breathing regulation and therefore, the breathing rhythm would be more vulnerable to other stimuli.

In our study, the absolute $\dot{V}O_2$ was deliberately the same in normoxia and hypoxia conditions. In the two previous studies concerning the influence of hypoxia on the degree of coordination (Paterson et al. 1987; Seebauer et al. 2003b), the subjects ran or cycled with the same relative $\dot{V}O_2$. So, the absolute $\dot{V}O_2$ in hypoxia was reduced (e.g. ~15 % in Seebauer et al., 2003b). The principle in the experimental design of these previous studies was to increase chemical stimuli with hypoxic condition in order to perturb the accepted concept of entrainment of the breathing rhythm by the movement rhythm. However, by reducing absolute $\dot{V}O_2$ in hypoxia, the metabolic demand and therefore the chemical stimuli are equally reduced. So, chemical stimuli are not necessarily increased by hypoxic conditions when the absolute $\dot{V}O_2$ is considerably reduced compared to normoxic condition. This is the reason why we chose to adjust the rowing ergometer workload in order to obtain the same absolute $\dot{V}O_2$ in hypoxia than in normoxia while keeping submaximal moderate intensities.

More than the metabolic load, it is likely that the neuro-mechanical-linked respiratory stimuli induced by the cramped position in rowing can exert more influence on breathing compared to the peripheral chemoreceptors-linked respiratory stimuli; this was likely less in cycling (Seebauer et al., 2003b) and running (Paterson et al., 1987) tasks. In rowing, Cunningham et al. (1975) speculated that, at catch, the body is in a cramped position with both knees and hips flexed. Increased intra-abdominal pressure in this position may impair downward excursion of the diaphragm and therefore inspiration. Conversely, during the drive phase of the rowing stroke, the knees and hips extend and inspiration may be assisted (Siegmund et al., 1999). Moreover, the respiratory muscles are used to perform a valsalva-like manoeuvre at the onset of each stroke in order to increase back strength. Very tight coordination between limb and breathing rhythms due to mechanical constraints in the thoracic region may account for our findings in rowing. Another explicative hypothesis could be that the hypoxic stimulus induced by altitude (i.e., 2877 m) was not important enough to alter the degree of coordination. We are fully conscious that we should have measured the arterial O_2 saturation and / or the arterial O_2 pressure in order to verify the direct effect of the hypoxic stimulus. But, in Paterson's study (Paterson et al., 1987), an effect of hypoxic stimulus on the degree of coordination was already observed as soon as subjects reached the altitude of 2135 m.

However, we need to emphasize that these results could be distorted by an important inter-individual difference in ventilatory response to hypoxia (VRH) (Weil et al., 1970; Reeves et al., 1993). But, in a previous study no correlation was found between individual VRH and the degree of coordination (Seebauer et al., 2003b). Finally, the degree of coordination is known to show large inter-individual differences. Combined with the low number of subjects in our study (n = 9) this might have masked real effects (i.e., type II error) and so have induced failure to detect significant differences (i.e., too low experimental power).

Conclusion

In conclusion, this study demonstrated that acute hypoxia did not influence the degree of coordination between breathing and locomotor rhythm during rowing at a moderate metabolic load. Neuro-mechanical locomotion-linked respiratory stimuli appear stronger than peripheral chemoreceptors-linked respiratory stimuli induced by hypoxia during rowing in the context of our study. It might be quite different during activities such as cycling or running, where the coupling between movement and ventilation is less required.

Acknowledgements

The authors gratefully acknowledge the assistance of all those who took part in this study, Nicolas Peluhet (Engineer) for technical help on determination of the degree of coordination, Catherine Capitan for her contribution and Jean-Marc Abbadie, Technical Department Director of the Pic du Midi de Bigorre observatory (France).

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Key points

- Changes in breathing frequency and ventilation induced by altitude have no effect on the degree of coordination between locomotor and breathing rhythms during moderate rowing exercise.
- During moderate rowing exercise in hypoxia, the neuro-mechanical drives still dominate over chemoreceptive stimuli.
- These above statements have to be taken carefully because it might be quite different during activities where the coupling between locomotor and breathing rhythms is less constrained (e.g., running, cycling).

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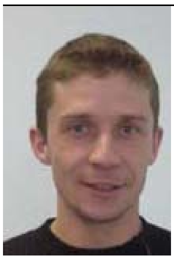

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