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Quadrupedal Locomotion-Respiration Entrainment and Metabolic Economy in Cross-Country Skiers

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Abstract

A 1:1 locomotion-respiration entrainment is observed in galloping quadrupeds, and is thought to improve running economy. However, this has not been tested directly in animals as animals cannot voluntarily disrupt this entrainment. The purpose of this study was to evaluate metabolic economy in a human gait involving all four limbs, cross-country skiing, in natural entrainment and forced non-entrainment. Nine elite cross-country skiers roller skied at constant speed using the 2-skate technique. In the first and last conditions, athletes used the natural entrained breathing pattern: inhaling with arm recovery and exhaling with arm propulsion, and in the second condition, the athletes dis-entrained their breathing pattern. The rate of oxygen uptake ($\dot{V}O_2$) and metabolic rate (MR) were measured via expired gas analysis. Propulsive forces were measured with instrumented skis and poles. $\dot{V}O_2$ and MR increased by 4% and 5% respectively when skiers used the dis-entrained compared to the entrained breathing pattern. There were no differences in ski or pole forces or in timing of the gait cycle between conditions. We conclude that breathing entrainment reduces metabolic cost of cross-country skiing by approximately 4%. Further, this reduction is likely a result of the entrainment rather than alterations in gait mechanics.

Key Words: Metabolic economy, entrainment, animal locomotion, cross-country skiing, oxygen consumption,

Abbreviations

$\dot{V}O_2$: Rate of oxygen consumption

RER: Respiratory exchange ratio

MR: Metabolic rate

STPD: Standard temperature and pressure, dry

Word Count: 3031

Introduction

When quadrupedal animals transition from a trot to a gallop, they exhibit a very particular locomotion-respiration coupling, or entrainment, between their breathing and movement patterns[1]. That is, animals exhale as they draw their forelimbs back and inhale as they extend their forelimbs. This coupling typically presents as a 1:1 ratio between breaths and strides, where the animal breathes once every stride. This phenomenon has been observed in quadrupedal animals such as horses[2], rabbits[3], rats[4], cats[5], and dogs[6]. Similarly, there is also an entrainment in humans, especially when the arms are involved in locomotion. For example, breathing entrainment has been observed in wheelchair use[7], rowing[8], cycling[9], and of particular interest, cross-country skiing[10,11]. When using a particular technique of cross country skiing, the two-skate (also known as V2 alternate or G4) technique, athletes move their skis in a skating motion while pushing with both poles simultaneously on every second ski plant (i.e. with either the left or the right ski). Using this distinctly four-limbed human gait, a natural breathing entrainment occurs with skiers inhaling as they recover the poles and exhaling as they push back with the poles[11].

It has been suggested that breathing entrainment in quadrupedal gaits leads to improved metabolic economy by reducing the work that needs to be done by the respiratory muscles, as they are assisted by the locomotor movements of the forelimbs (arms): expanding the chest cavity when forelimbs swing forward and compressing the chest cavity when moving the forelimbs backward[1,12]. This hypothesis cannot be tested directly in quadrupedal animals, as it is not possible to interrupt the naturally occurring entrained breathing patterns that non-human animals exhibit while galloping. However, the similarity of the two-skate cross-country skiing technique to a galloping animal, and the observed breathing entrainment during this activity[11] offers an interesting model to test this hypothesis directly. Therefore, the purpose of this study was to measure oxygen requirements and metabolic cost while skiing at a given speed using the naturally occurring entrained breathing patterns and using a dis-entrained breathing pattern. We hypothesized that skiers would naturally select the most economical breathing pattern and therefore skiers would be less economical when asked to abandon the breathing entrainment. In order to determine if the expected increase in metabolic cost was a result of a change in skiing mechanics associated with a shift of concentration to the athlete's breathing, we also evaluated the movement patterns created by a subset (n=4) of the skiers involved.

Methods

Subjects

Nine nationally and internationally ranked cross-country skiers (8 males, 1 female) were recruited to participate in this study (Table 1). Ethical approval was granted through the University of Calgary Conjoint Research Ethics Board and written informed consent was collected.

Materials

A ParvoMedics TrueOne 2400 Metabolic Measurement System was used to collect and analyze expired air every thirty seconds while skiers roller-skied on a custom made 3.5m long by 2.5m wide nordic treadmill (Treadsport Training Systems). Expired air was converted to standard temperature, pressure and dry (STPD) conditions, and analyzed to determine rate of oxygen consumption ($\dot{V}O_2$), metabolic rate (MR) in calories consumed per minute, minute ventilation ($\dot{V}_E$), and respiratory exchange ratio (RER), the ratio between the rate of carbon dioxide produced ($\dot{V}CO_2$) and $\dot{V}O_2$.

In addition to metabolic measurements, force data were also collected in Subjects 1-4 in order to confirm that changes in movement kinetics did not occur between trials. To do so, the roller-skis and poles were instrumented with resistive, foil type strain gauges to measure the instantaneous forces produced by each limb continuously at 128Hz. The strain gauges were mounted on a custom bracket between the wheels and shaft of the roller skis to measure forces in the vertical and mediolateral directions with respect to the ski. High-performance, carbon fiber poles were instrumented with strain gauges by bolting an aluminum cylinder between the handle and shaft of the pole. Six strain gauges were equally spaced around the cylinder such that force was measured in the direction of the long axis of the pole while eliminating cross-talk caused by pole bending. All skiers performed the tests using the same equipment.

Procedure

Skiers warmed up by roller skiing at an individually set pace at a flat (zero percent) grade on a Nordic treadmill. The entire test was conducted with the skiers using the two-skate technique on their self-selected dominant side, at consistent speed and grade. During the warm-up, skiers became familiar with the equipment and the test speed, which ranged between 21 and 27 km·hour^{-1} and was determined individually for each skier (Table 1). Once set, this speed remained constant across the conditions and the grade remained at zero percent. The test speed had to be sufficiently fast to elicit a consistent entrained breathing pattern, but not too fast to recruit anaerobic metabolism. During warm-up, skiers also practiced reversing their breathing patterns to familiarize themselves with the technique. Breathing entrainment was assessed by one of the researchers by observing the airflow out of the mixing chamber of the metabolic measurement system and matching to the strides of the skier. Using this method, proper entrained and dis-entrained breathing could be easily verified. Once the test speed had been determined, the test began and athletes skied as they normally would comfortably: that is, inhaling during pole recovery and exhaling during pole propulsion. Following this initial condition, athletes continued skiing exactly as they were, except that they were asked to reverse their breathing pattern (exhaling during pole recovery and inhaling during pole propulsion). Again, their breathing pattern was carefully monitored during the test by a researcher. The final condition was identical to the first and acted as a second control. Each test condition lasted four minutes to ensure that subjects had reached a metabolic steady-state. If monitoring suggested that a skier may not have reached a steady-state, the test was prolonged until steady-state metabolic conditions were achieved.

Analysis

Once athletes had reached steady-state metabolic conditions (change in absolute $\dot{V}O_2$ of less than 0.15 $L \cdot min^{-1}$ between consecutive 30s measurements), the expired air was analyzed. Metabolic economy was determined using $\dot{V}O_2$, where a higher $\dot{V}O_2$ indicates higher energy consumption through oxidative metabolism. Mechanical work rate is a function of treadmill speed, grade, and roller ski friction. Since the same skis were used in all trials and treadmill grade and speed was held constant across conditions, work rate was assumed to be constant. With work rate not changing between conditions, a higher consumption of energy therefore represents a worse economy. Additionally, we used the Weir equation[13],

$$MR\left(\frac{Kcal}{min}\right) = ((1.1 * RER) + 3.9)\left(\frac{Kcal}{L}\right) * \dot{V}O2\left(\frac{L}{min}\right)$$

to calculate MR in terms of calories, where a greater number of calories metabolized each minute at an equal intensity also would indicate a worsened economy.

Forces collected from the poles and skis were used to analyze changes in gait mechanics between the entrained and the dis-entrained breathing conditions. A gait cycle was defined from left pole touchdown to subsequent left pole touchdown. Once steady state oxygen consumption had been assessed, seven subsequent cycles were taken during that time and mean cycle frequency, mean cycle timing, and cycle characteristics were calculated. Changes in gait mechanics were assessed by comparing the impulse produced along the long axis of the poles and in the vertical and mediolateral direction of the skis, as well as the timing of ground contact and recovery for all four limbs between the entrained and dis-entrained breathing conditions. Metabolic data were analyzed using individual repeated measures analysis of variance (ANOVA; SPSS Statistics 20) and Bonferroni post hoc tests to determine differences between conditions. Friedman's tests were used to analyze the kinetics data.

Results

$\dot{V}O_2$ was significantly lower in the first control (5.3%, $p=.035$) and the second control (2.6%, $p=.040$) conditions when compared to the dis-entrained breathing condition (Table 2). Consequently, MR increased significantly in the dis-entrained breathing condition compared to the first (5.6%, $p=.045$) and second (3.9%, $p=.004$) control conditions (Table 2). RER increased significantly in the dis-entrained breathing condition compared to the first ($p=.013$) and the second ($p=.006$) control condition (Table 3). On average, RER remained below 0.93 and below 1.0 for all subjects in each condition. $\dot{V}_E$ was significantly greater in the dis-entrained condition than the first ($p=.029$), but not the second control ($p=.114$) condition (Table 3). Increases in $\dot{V}_E$ resulted primarily from increases in tidal volume as breathing frequency was not significantly different between conditions ($p>.05$) (Table 3). The two control conditions were not significantly different from each other in any of the metabolic variables.

Regarding skiing mechanics of the four subjects assessed, the impulse produced by each limb did not change significantly between the entrained and dis-entrained breathing conditions (Figure 1). Similarly, the duration of ground contact of each limb (Figure 2), mean cycle rate (cycles per minute) (Table 4), and timing of each contact and lift-off relative to left pole strike (Figure 2) were not significantly different for the entrained and dis-entrained breathing conditions for all limbs ($p>.05$).

Discussion

The purpose of this study was to measure oxygen requirements and metabolic cost using the naturally occurring entrained breathing patterns and using a dis-entrained breathing pattern. The primary finding of this study was that dis-entrained breathing was associated with a significant increase in $\dot{V}O_2$ compared to the entrained breathing condition. Given that the treadmill speed (skiing speed) and grade were identical for the control and experimental conditions, it can be concluded that there was a worsening of gait economy when subjects inversed their breathing pattern. Calculating the caloric cost using the Weir equation also gave an increase in MR (Table 2) for the dis-entrained breathing compared to the entrained breathing condition, also indicating a worse economy. Therefore, the findings of this study provide support for the previously proposed hypothesis[1] that the naturally occurring entrainment is metabolically more economical than for conditions when this entrainment is not present.

Despite careful collection, this study does have several limitations. Full mechanical data were only obtained from four of the nine subjects, and although these participants showed no change in skiing mechanics between the entrained and dis-entrained breathing conditions, there is the possibility that some of the other subjects might have changed gait patterns that we did not observe. Since there was still approximately a 4% increase in $\dot{V}O_2$ in the subjects with no differences in gait, we contend that these four would likely be representative of the whole group, however this is not fully known. Furthermore, there was a consistent increase in oxygen uptake, $\dot{V}_E$, and MR between the first and second control (entrained breathing) conditions, indicating some fatigue over the course of the test. However, this should not have affected our results and conclusions, as the metabolic economy was still significantly better in the second control experiment compared to dis-entrained breathing condition, although numerically the difference was smaller than that observed between the dis-entrained breathing and the first control experiment. The learning effect of new breathing patterns could certainly have contributed to the worsening of economy in the dis-entrained breathing pattern. To minimize this, skiers were allowed a warm-up and brief acclimatization period to familiarize themselves with dis-entrained breathing. Still, it is possible with further training of non-entrained breathing that the energy cost associated with the condition might be decreased.

It was observed that the RER increased when skiers switched from the first control condition (entrained breathing) to the dis-entrained breathing condition. However, of particular importance are the RER values, which remained below 0.93 on average and below 1.0 for every subject under all test conditions. An RER below 1.0, and particularly below 0.93, is often used to indicate that the intensity of exercise is below the anaerobic threshold, a work rate below which lactate accumulation does not occur and aerobic systems account predominantly for energy expenditure[14]. This is an important result because if the athletes were relying on anaerobic energy supply systems during the test, the recordings of $\dot{V}O_2$ would not necessarily be indicative of total energy consumption. Therefore, we are confident that the $\dot{V}O_2$ and MR findings in our study are representative of total energy consumption and therefore economy.

It is possible that changing the breathing patterns may result in distracting the skiers, leading to alterations in gait. For example, increased asymmetries in stride duration or impulse production, or longer/shorter strides may occur. These changes in gait mechanics might then produce changes in the metabolic cost of skiing independent of the actual entrainment. However, analysis of the impulses produced by each limb, as well as the coordination of limb contact times and cycle frequencies from Subjects 1-4, did not reveal significant changes in gait mechanics between the entrained and non-entrained breathing conditions. When $\dot{V}O_2$ from these four subjects alone are analyzed, they still consume 4% more oxygen than when breathing was not entrained. Since there do not appear to be differences in gait, but there are distinct differences in oxygen consumption, we are confident that the findings observed for the first four skiers are representative of the remaining five skiers. This strengthens the argument that the dis-entrained breathing did not affect skiing mechanics, and thus is the primary contributor to the worsening of economy compared to the entrained breathing. Novice skiers, with less training and competence than the elite level athletes used in this study, might not have been able to maintain skiing mechanics when required to focus on their breathing, and thus might have shown even greater increases in metabolic energy consumption for skiing with the dis-entrained breathing than were observed here with the elite athlete population[15]. All participants in this study were national or international level athletes and were well practised to the point of automation in the particular movement patterns they performed[16]. Additionally, the sub-anaerobic threshold speeds of skiing utilized (21-27 $km\cdot hour^{-1}$), and the athletes' familiarity with roller skiing made the testing a simple task physiologically and mechanically. Based on these data, the changes in economy observed in this study can likely be attributed to the interruption of the entrainment, rather than a transition to a less mechanically economical gait.

There are a number of possible mechanisms underlying the metabolic economy associated with respiration-locomotion entrainment that might explain our findings. Previous research identified changes in intra-abdominal pressure as a result of movement[6,17]. For example, Attenburrow and Goss[2] recorded pressure changes within the abdomen of horses while galloping. They found that when the animals brought their forelimbs back, pressure increased, and when the horses extended their forelimbs pressure decreased. These changes in pressure were coordinated with a 1:1 coupling between breathing and steps suggesting that the locomotion-induced changes in intra-abdominal pressure controlled the inspiration/expiration timing[2,8]. Specifically, as animals drew their forelimbs back, the chest cavity decreased in size resulting in an increase in pressure that compressed the lungs resulting in natural expiration. Conversely, when the forelimbs were moved forward, the chest cavity increased in volume, which resulted in a drop in intra-abdominal pressure causing natural inspiration. During quiet standing in horses, the changes in abdominal pressure are a result of inspiratory and expiratory muscle contraction. During galloping, the mechanical alteration of pressure caused by forelimb movement drives these changes, and as a result, respiratory muscles are less active and perform less work to cause breathing, thereby producing a decrease in energy consumption[6]. Though not measured in this study, it is possible that movement of the limbs and compression of the chest cavity with poling leads to pressure changes and results in improved economy. This breathing-movement coupling would likely only lead to a small drop in overall energy consumption, as breathing is associated with a small amount of the total energy requirements during galloping, thus causing the small (2-5%) but consistent energy savings for the entrained compared to the dis-entrained breathing pattern we observed in this study (Table 2).

However, the improved economy associated with the breathing entrainment may not be entirely due to mechanical changes. Several studies have identified neural characteristics that contribute to entrainment. For example, Corio et al[3] found that the expected 1:1 breathing-locomotion entrainment disappeared in decerebrate rabbits, despite the mechanical alterations of intra-abdominal pressure, which were still present. Similarly, Morin and Viala[4] observed an entrainment of simulated movement and breathing by stimulation of sensory pathways in rat hind limbs without actual locomotion. These findings suggest an interplay between proprioceptors in the hind limbs and the respiratory centres of the brain in the entrainment of respiration and locomotion. Viala and Freton[18] also identified that locomotion pattern generators in the rabbit spinal cord were responsible for the pacing of respiration. Purely as an anecdotal observation, many of the skiers in our study had some difficulty in performing the dis-entrained breathing condition during the initial warm-up, which might indicate a neural entrainment between breathing and locomotion that needed conscious inhibition. Regardless of whether the observed entrainment of respiration and movement is due to mechanical or neural factors, or a combination of the two, our findings suggest that these mechanisms exist and they cause an improvement of metabolic economy in animal and human gait.

Breathing entrainment has been previously attributed to an increase in metabolic economy. To date, this hypothesis was untested, as animals cannot produce entrained and uncoupled breathing patterns at will. The present study took a novel approach to directly test this hypothesis by using two-skate cross-country skiing, which has been shown to exhibit breathing entrainment similar to that observed in galloping animals. Breathing entrainment was associated with a 4% improvement in metabolic economy, without a detected change in gait characteristics, compared to skiing where breathing was uncoupled from its natural pattern. Therefore, we conclude that breathing entrainment independently contributes to improved metabolic economy, as has been suggested through indirect evidence in animal gait.

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Conflicts of Interest

The Authors declare that they have no conflict of interest.

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Abbreviations

$\dot{V}O_2$: Rate of oxygen consumption

RER: Respiratory exchange ratio

MR: Metabolic rate

STPD: Standard temperature and pressure, dry

Tables

Table 1. *Subject Characteristics for Skiers in Breathing Entrainment Testing*

Subject	Age (years)	Gender	Height (cm)	Weight (kg)	Test Speed (km·hour^{-1})
1	24	Male	178	80.3	24
2	26	Male	180	72.7	23
3	24	Male	176	68.7	27
4	22	Male	188	86.3	27
5	30	Male	170	71.7	27
6	21	Male	178	78.5	27
7	19	Male	175	70.7	23
8	21	Male	175	78.7	21
9	26	Female	175	64.8	22
Mean	24	-	177	74.7	24.6

Table 2. *Metabolic Data for Skiers When Breathing is Entrained and Dis-Entrained*

Subject	$\dot{V}O_2$ (ml·kg^{-1}·min^{-1})			MR (Kcal·min^{-1})		
	Control 1	Dis-Entrained Breathing	Control 2	Control 1	Dis-Entrained Breathing	Control 2
1	44.1	47.1	46.1	17.1	18.5	18.0
2	43.8	43.8	40.2	15.6	15.7	14.2
3	49.9	51.7	50.5	16.9	17.3	16.8
4	51.8	55.1	53.5	21.9	23.2	22.3
5	44.3	46.5	47.1	15.7	16.5	16.2
6	46.2	45.6	44.6	17.8	17.6	16.8
7	45.4	48.5	46.8	15.8	17.3	16.3
8	38.5	45.0	44.8	14.8	17.6	17.5
9	37.1	38.0	36.9	11.6	12.0	11.5
Mean	44.6*	46.8	45.6*	16.3*	17.3	16.6*
SE	1.6	1.6	1.7	0.9	1.0	1.0

*indicates significance at the 0.05 level compared to the dis-entrained breathing condition

Table 3. *Metabolic Data for Skiers When Breathing is Entrained and Dis-Entrained*

Subject	RER			Minute Ventilation ($L \cdot min^{-1}$)		
	Control 1	Dis-Entrained Breathing	Control 2	Control 1	Dis-Entrained Breathing	Control 2
1	0.83	0.90	0.87	100.7	109.7	108.0
2	0.91	0.95	0.92	81.4	91.6	76.8
3	0.87	0.88	0.86	87.9	102.4	99.2
4	0.82	0.89	0.86	94.8	98.8	98.5
5	0.95	0.94	0.95	109.4	106.6	101.2
6	0.92	0.93	0.91	105.2	134.2	126.0
7	0.92	0.96	0.92	96.1	119.7	123.8
8	0.90	0.97	0.96	67.4	71.0	66.7
9	0.83	0.88	0.85	87.9	97.4	92.0
Mean	0.88*	0.92	0.90*	92.3*	103.5	99.1*
SE	0.02	0.02	0.01	4.3	5.9	6.5

*indicates significance at the 0.05 level compared to the dis-entrained breathing condition

Table 4. *Mean Cycle and Breathing Frequencies for Skiers in all Conditions*

		Control	Dis-Entrained Breathing	Control
Cycle Frequency	Mean	40.6	41.0	38.7
	SE	0.7	0.4	0.7
Breathing Frequency	Mean	37.5	39.7	39.9
	SE	2.1	0.7	1.5

Figure 1- Mean impulse produced by each limb during skate cross-country skiing in four subjects. White bars indicate the dis-entrained breathing condition and dark bars indicate the first control and second control conditions, respectively.

Figure 2- Mean gait cycles during skate cross-country skiing for each limb in four subjects. Lines indicate percent of a cycle in which the limb was in contact with the ground. Vertical line indicates the touchdown of the left pole and onset of next gait cycle.