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ORIGINAL ARTICLE

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Breathing pattern and exercise endurance time after exhausting cycling or breathing

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Abstract The aim of the present study was to investigate whether the changes in breathing pattern that frequently occur towards the end of exhaustive exercise (i.e., increased breathing frequency, f_b, with or without decreased tidal volume) may be caused by the respiratory work itself rather than by leg muscle work. Eight healthy, trained subjects performed the following three sessions in random order: (A) two sequential cycling endurance tests at 78% peak O_2 consumption ($\dot{V}O_{2peak}$) to exhaustion (A1, A2); (B) isolated, isocapnic hyperpnea (B1) at a minute ventilation ($\dot{V}_E$) and an exercise duration similar to that attained during a preliminary cycling endurance test at 78% $\dot{V}O_{2peak}$, followed by a cycling endurance test at 78% $\dot{V}O_{2peak}$ (B2); (C) isolated, isocapnic hyperpnea (C1) at a $\dot{V}_E$ at least 20% higher than that of the preliminary cycling test and the same exercise duration as the preliminary cycling test, followed by a cycling endurance test at 78% $\dot{V}O_{2peak}$ (C2). Neither of the two isocapnic hyperventilation tasks (B1 or C1) affected either the breathing pattern or the endurance times of the subsequent cycling tests. Only cycling test A2 was significantly shorter [mean (SD) 26.5 (8.3) min] than tests A1 [41.0 (9.0) min], B2 [41.9 (6.0) min], and C2 [42.0 (7.5) min]. In addition, compared to test A1, only the breathing pattern of test A2 was significantly different [i.e., $\dot{V}_E$: +10.5 (7.6) l min^{-1}, and f_b: +12.1 (8.5) breaths min^{-1}], in contrast to the breathing patterns of cycling tests B2 [$\dot{V}_E$: −2.5 (6.2) l min^{-1}, f_b: +0.2 (3.6) breaths min^{-1}] and C2 [$\dot{V}_E$: −3.0 (7.0) l min^{-1}, f_b: +0.6 (6.1) breaths min^{-1}]. In summary, these results suggest that the changes in breathing pattern that occur towards the end of an exhaustive exercise test are a result of changes in the leg muscles rather than in the respiratory muscles themselves.

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Introduction

During constant-load cycling at a high load, a change in breathing pattern (i.e., an increase in breathing frequency, f_b) with a small, or no decrease in tidal volume (V_T), resulting in an increase in minute ventilation ($\dot{V}_E$), is frequently observed towards the end of an exhausting test (Kearon et al. 1991; Boutellier et al. 1992; Johnson et al. 1993). We wondered whether this change might be a result of fatiguing respiratory muscles due to exercise hyperpnea rather than to fatiguing leg muscles.

Recently two groups showed, independently (Johnson et al. 1993; Mador et al. 1993; Babcock et al. 1995, 1996), that diaphragmatic fatigue, measured as a reduction of transdiaphragmatic pressure during phrenic nerve stimulation ($P_{di,tw}$), can occur in subjects who perform exhausting constant-load exercise at an intensity of at least 80% of maximal O_2 consumption ($\dot{V}O_{2max}$). Fatigue of the respiratory muscles induced by inspiratory resistive or threshold loading, in turn, can alter the breathing pattern during a subsequent exercise test. In particular, f_b is increased (Mador 1991; Mador and Acevedo 1991a; Sliwinski et al. 1996). In addition, exercise performance is impaired (Mador and Acevedo 1991b). These data suggest that the respiratory muscles themselves are important in determining the pattern of breathing during exercise and the duration of endurance exercise.

The aim of the present study was to investigate whether the changes in breathing pattern that occur towards the end of an exhaustive exercise bout result from the respiratory rather than the leg muscle work performed during that exercise. We chose the following protocol to address this question: (A) two cycling endurance tests separated by a 15-min break; (B) an isocapnic hyperpnea (with a $\dot{V}_E$ and duration similar to that experienced in a preliminary cycling endurance test) followed by a 15-min break and then another cycling

endurance test; (C) isocapnic hyperpnea (with $\dot{V}_E$ +20%, and the same duration as the preliminary cycling endurance test) followed by a 15-min break and then another cycling endurance test.

Methods

Subjects

Eight healthy, trained subjects (one female, seven males) participated in the study. The subjects' characteristics are given in Table 1. All subjects were informed in detail about the study, with the exception of the main purpose of the experiments (i.e., the examination of breathing pattern and cycling time). They gave their written, informed consent to participate. The study complies with the Helsinki declaration for human experimentation.

Equipment

The following parameters were measured during the exercise tests, with the aid of a metabolic cart (OxyconBeta, Jaeger, Würzburg, Germany): vital capacity (VC), peak expiratory flow (PEF), forced expiratory volume in 1 s (FEV_1), and 20-s maximal voluntary ventilation (MVV), as well as $\dot{V}_E$, V_T, f_b, O_2 uptake ($\dot{V}O_2$), CO_2 elimination ($\dot{V}CO_2$) and end-tidal partial pressure of CO_2 ($P_{ET\text{-}CO_2}$).

A special device was used to perform isocapnic hyperpnea. This device is similar to that described in detail by Boutellier and Farhi (1986). In brief, the device consists of a gas-mixing unit and indicators for f_b and V_T. CO_2 was added to the inspired air to maintain normocapnia. A gas sampling line was connected to the mouthpiece and CO_2 was measured continuously by an infrared method (medical gas analyzer LB-2, Beckman Instruments, Fullerton, Calif., USA). The inspired CO_2 concentration was continuously adjusted to maintain end-tidal CO_2 concentrations at 5.4%. Air flow was measured using a pneumotachograph (no. 3, Fleisch, Metabo, Epalinges, Switzerland) connected to a differential pressure transducer (MP 45–1, Validyne, Northridge, Calif., USA). Flow was integrated and displayed to the subject using a horizontal series of 35 green light-emitting diodes (LED). For each experiment, the system was calibrated with a syringe so that each LED represented 1/35 of the target V_T. Three red LEDs at the end of the scale warned the subject if his or her V_T exceeded the target value. A metronome was used to pace f_b.

A cycle ergometer, Ergometrics 800S (Ergoline, Bitz, Germany) was used for the incremental exercise test and the cycling endurance test. Heart rate (f_c) was recorded in parallel with respiratory variables using a f_c monitor, PE3000 (Polar Electro, Kempele, Finland).

Blood lactate concentrations were measured with an automatic analyzer, ESAT6661 (Eppendorf, Hamburg, Germany) using 20 µl blood taken from an earlobe. Total perceived exertion (PE_{TOT}) as well as perceived respiratory exertion (PE_{RESP}) and perceived leg exertion (PE_{LEG}) were measured separately using a modified Borg scale (Wilson and Jones 1991) which was translated into German.

Protocol

Preliminary testing

First, the subjects were familiarized with the different testing devices. Then, VC, PEF, FEV_1, and MVV were measured. After these measurements, subjects performed an incremental cycling test to determine their anaerobic threshold, peak O_2 consumption ($\dot{V}O_{2peak}$) and maximal aerobic power (W_{max}). Subjects started pedaling at 100 W and the workload was then increased by 30 W every 2 min until the subjects were exhausted. The workload for the cycling endurance test (W_{CET}) was calculated for each individual by determining their ventilatory anaerobic threshold. At least 2 days later, a cycling endurance test to exhaustion was performed at the individual's W_{CET} which, on average, corresponded to [mean (SD)] 73 (4)% of W_{max} and 78 (6)% of $\dot{V}O_{2peak}$. After 5 min at 150 W (males) or 120 W (female), the workload was increased to W_{CET}. Every 5 min, blood was taken from an earlobe for determination of blood lactate concentration, and perceived exertion (PE) scores were determined. Respiratory variables and f_c were recorded continuously throughout the tests. The $\dot{V}_E$ of this preliminary cycling endurance test was used to determine target ventilations for isocapnic hyperpnea tasks in sessions B and C (see below).

Experimental phase (Fig. 1)

Three test sessions (A, B, and C) were performed in random order with at least 4 days between single sessions (Fig. 1). Session A consisted of two sequential cycling endurance tests (A1 and A2) at W_{CET} with a 15-min break between them. During session B, subjects first performed isocapnic hyperpnea at a $\dot{V}_E$ corresponding to that of the preliminary cycling endurance test (same V_T, same f_b, and same duration), but without cycling (test B1). After a break of 15 min, they performed a cycling endurance test at W_{CET} (B2). During session C, subjects performed isocapnic hyperpnea without cycling, at a $\dot{V}_E$ that was at least 20% higher than the average $\dot{V}_E$ of the preliminary cycling endurance test (test C1). After a break of 15 min, they performed a cycling endurance test at W_{CET} (C2). Blood lactate concentrations as well as PE scores were measured every 5 min during all of the tests. Respiratory variables and f_c were recorded continuously throughout the tests.

Statistics

To detect changes in blood lactate concentrations and in f_c during the tests A1, B1, and C1, values averaged over 1 min at rest were

Table 1 Characteristics of the subjects. ($\dot{V}O_{2peak}$ Peak O_2 consumption, W_{max} maximal aerobic power, W_{CET} workload of the cycling endurance test, *VC* vital capacity, *PEF* peak expiratory flow, FEV_1 forced expiratory volume in 1 s, *MVV* maximal voluntary ventilation in 20 s, *m* male, *f* female)

Subject	Gender	Age (years)	Height (cm)	Mass (kg)	$\dot{V}O_{2peak}$ ($ml \cdot kg^{-1} \cdot min^{-1}$)	W_{max} (W)	W_{CET} (W)	VC (l)	PEF ($l \cdot s^{-1}$)	FEV_1 (l)	MVV ($l \cdot min^{-1}$)
1	m	24	184	79	65.6	400	300	6.4	12.0	5.3	198
2	m	23	180	70	76.1	370	270	7.6	13.5	5.5	236
3	f	28	178	64	51.9	280	180	5.1	7.6	4.1	140
4	m	26	176	66	58.2	280	220	5.7	8.9	4.6	180
5	m	32	183	67	58.5	340	240	5.7	9.1	4.5	157
6	m	26	181	70	59.4	340	240	5.7	9.3	4.3	192
7	m	27	187	71	62.2	370	280	6.6	10.2	5.5	253
8	m	29	179	68	65.5	340	250	5.8	12.0	4.9	218
Mean		26.9	181.0	69.4	62.2	340.0	247.5	6.1	10.3	4.8	196.8
SD		2.9	3.5	4.5	7.2	42.4	37.3	0.8	2.0	0.6	38.3

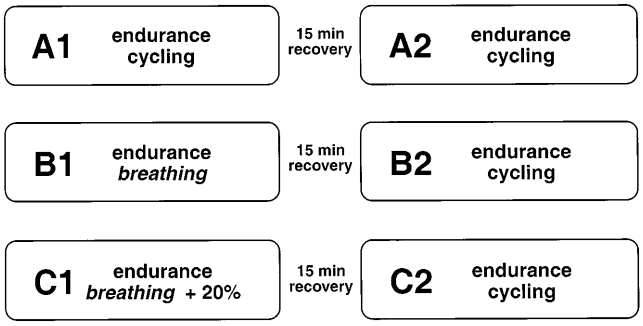

Fig. 1 Experimental sessions A, B, and C were performed in random order on different days. In each session, a period of endurance cycling (A2, B2, C2) was preceded by either endurance cycling (A1) or by hyperpnea (B1, C1)

compared with the mean values of the last minute of exercise, and statistical significance was determined using the paired Wilcoxon signed-rank test.

Variables from the cycling endurance tests A1, A2, B2, and C2, and the PE of tests A1, B1, and C1 were compared at three exercise times, t_1, t_2 and t_3. t_1: To compare variables shortly after the beginning of exercise, respiratory variables and f_c were averaged over 5 min (the 10th to the 14th min of the total exercise time, i.e., the 5th to the 9th min of exercise at W_{CET}) for each subject. As blood lactate concentrations and PE scores were measured every 5 min, comparable values were obtained at the 15th min of exercise. t_2: Since test durations differed between subjects, t_2 was more individually chosen: minute values of the 5th min before the end of the shortest test (always test A2) were compared. This particular minute was chosen to exclude a final hyperventilation in test A2. For blood lactate and PE measurements, values closest to the 5th min from the end were taken. t_3: Finally, we compared all variables at the time of exhaustion (the last exercise minute for respiratory variables and f_c; blood lactate concentrations and PE scores were measured immediately after termination of the test).

The variables of tests A1, A2, B2, and C2 or A1, B1, and C1 were tested for significant differences using the analysis of variance introduced by Friedman. When a significant difference was found, tests A2, B2, and C2 or B1 and C1 were compared individually with test A1 using the paired Wilcoxon signed-rank test (StatView 4.01, Abacus Concepts, Berkeley, Calif., USA). For all tests, the null hypothesis (H_o: no difference between the data sets) was rejected if $P < 0.05$. Data are presented as the mean (SD).

Results

As indicated in Table 1, all subjects had normal lung functions. As expected from the study design, the mean $\dot{V}_E$ was similar in cycling endurance test A1 [101.5 (8.4) l min^{-1}] and the isocapnic hyperpnea test, B1 [100.5 (9.3) l min^{-1}]. In addition, the duration of the two tests did not differ significantly [A1: 41.0 (9.0) min, B1: 42.9 (5.4) min]. During the isocapnic hyperpnea (+20%) test C1, $\dot{V}_E$ was significantly higher than in the other two tests [122.4 (10.2) l min^{-1}], as intended. During cycling endurance test A1, blood lactate concentration increased significantly from 1.2 (0.4) mmol l^{-1} (rest) to 5.2 (1.7) mmol l^{-1} (end of the test), whereas there was no significant change during breathing tests B1 [rest: 1.6 (0.5) mmol l^{-1}, end: 1.4 (0.3) mmol l^{-1}] and C1 [rest: 1.7 (0.6) mmol l^{-1}, end: 1.9 (0.9) mmol l^{-1}]. At t_1, steady state PE_{RESP} and PE_{TOT} were similar in all three tests (Table 2), whereas PE_{LEG} was significantly lower during tests B1 and C1. At the end of exercise, PE_{RESP} was similar in all three tests (Table 2), whereas PE_{LEG} and PE_{TOT} were significantly lower in B1 and C1 compared to A1. In all three tests, f_c increased significantly from resting values. However, in test A1 the increase [from 67.6 (11.4) to 176.1 (6.4) beats min^{-1}] was much higher than during test B1 [from 70.3 (8.0) to 89.6 (14.2) beats min^{-1}] and test C1 [from 73.1 (7.0) to 94.3 (11.8) beats min^{-1}].

Table 2 Scores of perceived exertion during either steady state (15th min, t_1), 5 min before the end (t_2), or at the end (t_3) of constant-load cycling endurance exercise (A1) or isocapnic hyperpnea (B1 and C1) for $n = 8$ subjects. (PE_{RESP} Perceived exertion of respiration, PE_{LEG} perceived exertion of legs, PE_{TOT} total perceived exertion)

Time point	Variable	Test A1		Test B1		Test C1	
		Mean	SD	Mean	SD	Mean	SD
t_1	PE_{RESP} (points)	3.8	1.6	4.1	2.1	5.0	1.8
	PE_{LEG} (points)	4.9	1.6	0.8	1.0*	0.6	0.7*
	PE_{TOT} (points)	4.3	1.9	3.5	1.9	4.1	1.6
t_2	PE_{RESP} (points)	5.2	1.8	4.9	2.5	6.0	2.5
	PE_{LEG} (points)	6.5	2.1	0.8	1.0*	0.6	0.7*
	PE_{TOT} (points)	5.9	2.6	3.8	1.7	4.9	2.3
t_3	PE_{RESP} (points)	8.1	2.3	6.4	3.1	7.0	2.9
	PE_{LEG} (points)	9.4	0.7	0.8	1.0*	0.6	0.7*
	PE_{TOT} (points)	9.2	1.0	5.5	2.4*	6.0	2.4*

* Significant differences vs A1, $P < 0.05$

Comparisons of cycling endurance tests A2, B2, and C2 with A1 revealed that the exercise times of tests A1 [41.0 (9.0) min], B2 [41.9 (6.0) min], and C2 [42.0 (7.5) min] were similar, whereas test A2 [26.5 (8.3) min] was significantly shorter than test A1 ($P < 0.05$). There were no significant differences between tests A1, B2, and C2 at any time (t_1, t_2 and t_3) in any of the variables except for f_c, which was significantly lower during tests B2 and C2 at t_1 (Table 3). At t_2, f_c was significantly lower only in test C2 (Table 4).

Since no significant differences were observed between tests B2, C2 and A1 (except for f_c), the following results concentrate on comparisons between tests A1 and A2 at three different times (t_1, t_2 and t_3). At t_1, averages of the 10th to the 14th min of cycling revealed that the following variables of test A2 differed significantly from test A1 (Table 3): $\dot{V}_E$ was higher in test A2, V_T was lower, f_b was higher, $P_{ET}CO_2$ was lower, f_c was higher, and PE_{RESP}, PE_{LEG} and PE_{TOT} were all higher. Blood lactate concentrations tended to be lower in test A2 than in test A1, but the difference did not quite reach significance ($P = 0.058$). The changes in $\dot{V}_E$ and breathing pattern were not only seen at W_{CET}, but were already apparent at the very beginning of the cycling endurance test when subjects were cycling with a load of only 120–150 W (Figs. 2, 3, and 4). $\dot{V}O_2$ (Fig. 5) and $\dot{V}CO_2$ were identical in tests A1 and A2. At t_2, during the 5th min preceding the end of test A2 compared with the

Table 3 Respiratory variables and heart rate (averages of the 10th–14th min; t_1); blood lactate concentrations, and scores of perceived exertion (of the 15th min) during constant-load cycling endurance exercise in $n = 8$ subjects. ($\dot{V}_E$ Minute ventilation, V_T tidal volume, f_b breathing frequency, $\dot{V}O_2$ O_2 consumption, $\dot{V}CO_2$ CO_2 output, $P_{ET}CO_2$ end-tidal partial pressure of CO_2, f_c heart rate)

Variable	Test A1		Test A2		Test B2		Test C2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
$\dot{V}_E$ ($l \cdot min^{-1}$)	101.5	8.4	112.0	14.6*	99.0	5.8	98.5	5.3
V_T (ml)	2689	479	2261	381*	2608	478	2679	562
f_b (breaths $\cdot$ min^{-1})	38.7	6.5	50.8	10.9*	38.9	5.9	38.0	7.0
$\dot{V}O_2$ ($ml \cdot min^{-1}$)	3328	408	3374	425	3328	437	3357	409
$\dot{V}CO_2$ ($ml \cdot min^{-1}$)	3407	380	3361	370	3379	443	3429	439
$P_{ET}CO_2$ (mmHg)	38.4	4.1	35.7	4.1*	38.7	3.0	38.8	3.4
f_c (beats $\cdot$ min^{-1})	158.5	7.7	166.3	4.5*	154.4	8.8*	150.2	9.7*
lactate ($mmol \cdot l^{-1}$)	4.6	1.4	3.4	1.2	4.1	1.3	4.4	1.2
PE_{RESP} (points)	3.8	1.6	6.1	2.0*	4.4	1.6	4.3	1.3
PE_{LEG} (points)	4.9	1.6	8.1	1.7*	5.3	0.9	5.5	1.2
PE_{TOT} (points)	4.3	1.9	7.1	2.0*	4.4	1.2	4.6	1.6

* Significant differences vs A1, $P < 0.05$

Table 4 Respiratory variables and heart rate (5th min before the end of test A2; t_2); blood lactate concentrations and scores of perceived exertion (closest to the 5th min before the end of test A2) during constant-load cycling endurance exercise in $n = 8$ subjects. For abbreviations see Table 3

Variable	Test A1		Test A2		Test B2		Test C2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
$\dot{V}_E$ ($l \cdot min^{-1}$)	107.6	7.6	115.6	13.0	107.6	11.2	107.2	13.5
V_T (ml)	2544	387	2260	327*	2526	515	2606	605
f_b (breaths $\cdot$ min^{-1})	42.9	5.1	53.7	8.7*	38.7	13.0	42.7	8.5
$\dot{V}O_2$ ($ml \cdot min^{-1}$)	3370	426	3410	459	3430	552	3417	453
$\dot{V}CO_2$ ($ml \cdot min^{-1}$)	3395	398	3340	387	3449	531	3454	479
$P_{ET}CO_2$ (mmHg)	36.4	2.7	34.6	2.9	36.6	1.7	36.5	3.1
f_c (beats $\cdot$ min^{-1})	165.4	9.5	171.3	5.2*	161.4	12.5	156.3	10.4*
Lactate ($mmol \cdot l^{-1}$)	4.8	1.5	3.6	1.0*	4.4	1.5	4.6	1.1
PE_{RESP} (points)	5.2	1.8	7.4	2.2*	5.6	2.1	5.4	2.2
PE_{LEG} (points)	6.5	2.1	9.0	1.4*	6.5	1.3	6.5	2.2
PE_{TOT} (points)	5.9	2.6	8.8	1.5*	5.5	1.8	5.8	2.6

* Significant differences vs A1, $P < 0.05$

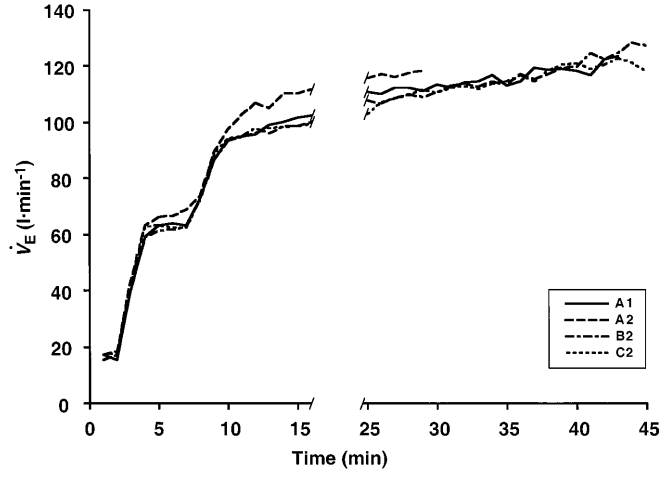

Fig. 2 Minute ventilation ($\dot{V}_E$). The *lines* are the mean values of eight subjects. Standard deviations have been omitted to preserve clarity. Since individual tests were of different durations, there is a gap in the data in order to align the average responses at both the start and the end of exercise. The curves after the gap end at the averaged end-times of the particular tests

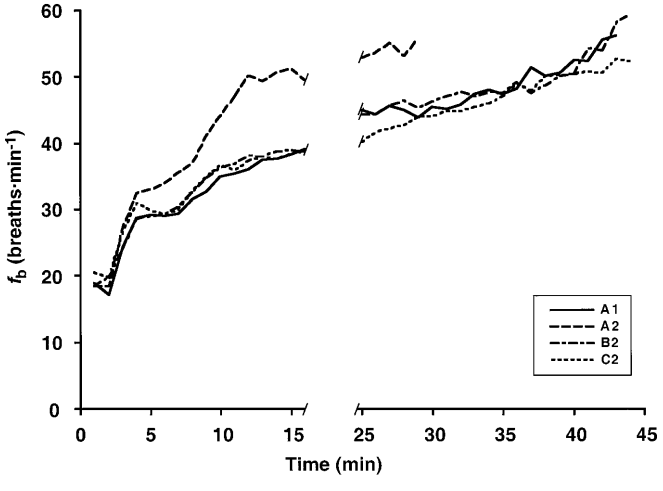

Fig. 3 Breathing frequency (f_b). The *lines* are the mean values of eight subjects. Standard deviations have been omitted to preserve clarity. Since individual tests were of different durations, there is a gap in the data in order to align the average responses at both the start and the end of exercise. The curves after the gap end at the averaged end-times of the particular tests

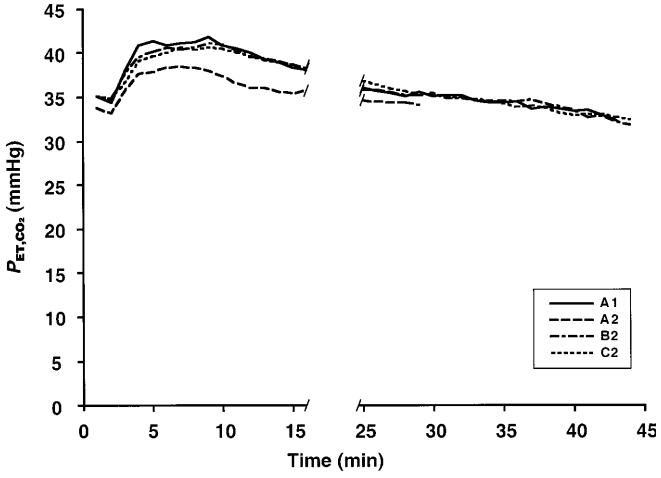

Fig. 4 End-tidal CO_2 partial pressure ($P_{ET}CO_2$). The *lines* are the mean values of eight subjects. Standard deviations have been omitted to preserve clarity. Since individual tests were of different durations, there is a gap in the data in order to align the average responses at both the start and the end of exercise. The curves after the gap end at the averaged end-times of the particular tests

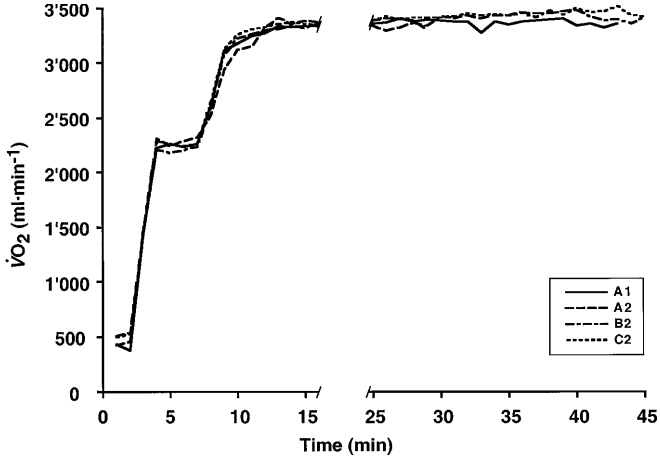

Fig. 5 O_2 consumption ($\dot{V}O_2$). The *lines* are the mean values of eight subjects. Standard deviations have been omitted to preserve clarity. Since individual tests were of different durations, there is a gap in the data in order to align the average responses at both the start and the end of exercise. The curves after the gap end at the averaged end-times of the particular tests

Table 5 Respiratory variables and heart rate (last min of exercise; t_3); blood lactate concentrations and scores of perceived exertion (immediately after the end of the test) during constant-load cycling endurance exercise in $n = 8$ subjects. For abbreviations see Table 3

Variable	Test A1		Test A2		Test B2		Test C2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
$\dot{V}_E$ (l · min^{-1})	123.2	12.9	118.1	13.2	120.4	13.9	121.4	15.6
V_T (ml)	2213	348	2087	380	2236	491	2316	437
f_b (breaths · min^{-1})	56.4	7.3	56.5	9.8	55.6	6.0	53.1	5.0
$\dot{V}O_2$ (ml · min^{-1})	3341	443	3388	491	3422	573	3486	488
$\dot{V}CO_2$ (ml · min^{-1})	3337	401	3345	407	3381	598	3435	494
$P_{ET}CO_2$ (mmHg)	32.6	2.9	34.1	2.8	32.4	2.6	33.0	2.7
f_c (beats · min^{-1})	176.1	6.4	174.3	5.5	174.6	9.5	169.3	6.7
Lactate (mmol · l^{-1})	5.2	1.7	3.8	1.0*	5.0	1.3	5.3	1.0
PE_{RESP} (points)	8.1	2.3	7.9	2.0	8.4	2.1	8.1	2.0
PE_{LEG} (points)	9.4	0.7	9.5	0.5	9.1	1.0	8.8	1.7
PE_{TOT} (points)	9.2	1.0	9.1	1.0	8.8	1.5	8.4	1.9

* Significant differences vs A1, $P < 0.05$

corresponding minute of test A1, almost all differences seen at t_1 still persisted, except for $\dot{V}_E$, which was no longer elevated, and $P_{ET}CO_2$, which was no longer lower. In contrast, blood lactate concentrations were now significantly lower than in test A1 (Table 4). At t_3, during the last minute of exercise, all variables were similar in tests A1 and A2, except for blood lactate concentrations, which were still significantly lower in test A2 (Table 5).

Discussion

Isolated hyperpnea (B1) at a $\dot{V}_E$ similar to that attained during cycling had no influence on the breathing pattern or exercise duration of a subsequent exhausting cycling endurance test at 78% $\dot{V}O_{2peak}$ (B2). This was also true for cycling endurance test C2, where the $\dot{V}_E$ during the preceding hyperpnea (C1) was 20% higher than $\dot{V}_E$ during cycling. In contrast to cycling endurance tests B2 and C2, cycling endurance test A2 – which was preceded by another cycling endurance test (A1) – was shorter, and the breathing pattern was altered. The $\dot{V}_E$ and f_b in A2 were higher than in A1 from the beginning of exercise onward, whereas these variables were identical at the time of exhaustion for all four cycling endurance tests (A1, A2, B2, and C2).

The fact that the hyperpnea of tests B1 and C1 had no influence on the breathing pattern or the cycling time of the subsequent cycling endurance tests, B2 and C2, might suggest that the respiratory muscles did not fatigue during B1 and C1, or that they recovered during the 15-min break before the cycling tests. We believe it is rather unlikely that the respiratory muscles did not fatigue during isolated hyperpnea, in particular during test C1 where subjects breathed at 62% MVV. Mador et al.

(1996), for example, measured a significant reduction in $P_{di,tw}$ after about 9 min of voluntary hyperpnea at 60% MVV, indicating diaphragmatic fatigue, while the subjects in the present study breathed for 42 min at 62% MVV. Given that PE_{RESP} ratings were similar for tests A1 (cycling), B1 (breathing at 52% MVV), and C1 (breathing at 62% MVV), the degree of respiratory muscle fatigue in tests A1 and B1 was likely to be similar to that of test C1. In addition, we believe that the 15-min break between the end of hyperpnea (B1 and C1) and the beginning of the cycling tests (B2 and C2) was too short for the respiratory muscles to fully recover from fatigue, as Mador et al. (1996) have shown that fatigued respiratory muscles need more than 1 h to recover fully from exhaustive hyperpnea. It has been shown that after exhaustive whole-body exercise above 80% $\dot{V}O_{2max}$, similar conditions to test A1, diaphragmatic fatigue (measured as decreased $P_{di,tw}$) lasted for at least 30 min (Johnson et al. 1993; Mador et al. 1993; Babcock et al. 1995). In addition, the fact that f_c was significantly lower during most of B2 and C2 than during the exercise test that was not preceded by isolated breathing (A1) seems to indicate that hyperpnea did affect the subsequent cycling endurance test, at least in this respect. A similar effect was observed by Martin et al. (1982).

Assuming the presence of respiratory muscle fatigue at the start of cycling tests B2 and C2, why were breathing pattern and exercise time not affected in a similar way as they were after respiratory muscle fatigue in other studies (Mador and Acevedo 1991a, b; Sliwinski et al. 1996)? The difference might be explained by the different methods used to fatigue the respiratory muscles. While the authors cited above induced respiratory muscle fatigue by having their subjects breathe to exhaustion with an inspiratory threshold load of 80% maximal inspiratory pressure or an inspiratory resistance, the subjects in the present study performed isocapnic hyperpnea similar to exercise hyperpnea. McCool et al. (1992) have suggested that isolated hyperpnea predominantly fatigues the diaphragm, whereas resistive- or threshold-loaded breathing puts a bigger load on the inspiratory rib cage muscles than on the diaphragm. This suggests that fatigue of the ribcage muscles (Mador and Acevedo 1991a, b; Sliwinski et al. 1996), rather than fatigue of the diaphragm (if any, in the present study), affects the breathing pattern during exercise. Thus, even though the diaphragm was shown to fatigue during exhaustive cycling exercise (Johnson et al. 1993; Mador et al. 1993) and may also have fatigued during hyperpnea, changes in breathing pattern towards the end of exercise, or during cycling test A2 in the present study, may arise from a different source.

We suggest two possible mechanisms that do not need to be mutually exclusive:

1. The difference might be the result of increased central command, a cortical drive that irradiates the medullary respiratory center during voluntary muscle work. Ochwadt et al. (1959), Asmussen et al. (1965), and Innes et al. (1992) have demonstrated an increased ventilatory response to exercise in subjects who were cycling with a weak leg (compared with cycling with their healthy leg) and in subjects who were exercising with partially curarized legs compared to controls. The authors interpreted the higher $\dot{V}_E$ to be a result of increased collateral excitation of the respiratory center caused by the increased motor drive to the legs needed to keep up the same workload. In the present study, subjects were most likely to have been exercising with fatigued leg muscles during cycling test A2, which had been preceded by an exhaustive cycling test of 40 min duration and only a 15-min break. Thus, the fatigued leg muscles of the present study would correspond to weak or curarized leg muscles in the previously cited studies, and increased central command could also have increased $\dot{V}_E$ in the present study.
2. The difference between test A2 and the other cycling tests might be attributable to partially depleted glycogen stores in the leg muscles during cycling test A2. Heigenhauser et al. (1983) observed, for example, that $\dot{V}_E$ is increased during exercise after glycogen depletion compared to exercise with intact glycogen stores. The assumption that in the present study, subjects also cycled with partially depleted glycogen stores in test A2 is supported by the fact that blood lactate concentrations were lower at the same workload during test A2 than during test A1.

In conclusion, the results of the present study show that isolated hyperpnea similar to or larger than that which occurs during exercise does not affect either the breathing pattern or the exercise time of a subsequent exercise test, while exhaustive exercise does alter the breathing pattern and shortens the endurance time of a second exercise test. Thus, these results suggest that the changes in breathing pattern that occur towards the end of an exhaustive exercise test are attributable to changes in the leg muscles rather than changes in the respiratory muscles themselves.

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