

Effects of Intermittent Hypoxia on Running Economy

Authors

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Key words

- running economy
- training phase
- intermittent hypoxia

Abstract

▼ We investigated the effects of two 5-wk periods of intermittent hypoxia on running economy (RE). 11 male and female middle-distance runners were randomly assigned to the intermittent hypoxia group (IHG) or to the control group (CG). All athletes trained for a 13-wk period starting at pre-season until the competition season. The IHG spent additionally 2 h at rest on 3 days/wk for the first and the last 5 weeks in normobaric hypoxia (15–11% FiO₂). RE, haematological parameters and body composition were determined at low altitude (600 m) at baseline, after the 5th, the 8th and the 13th week of training. RE,

determined by the relative oxygen consumption during submaximal running, (-2.3 ± 1.2 vs. -0.3 ± 0.7 ml/min/kg, $P < 0.05$) and total running time ($+1.0 \pm 0.9$ vs. $+0.4 \pm 0.5$ min, $P < 0.05$) changed significantly between the IHG and CG only during the first 5-wk period. Haematological and cardiorespiratory changes indicate that the improved RE was associated with decreased cardiorespiratory costs and greater reliance on carbohydrate. Intermittent hypoxia did not affect RE during the second 5-wk period. These findings suggest that the effects of intermittent hypoxia on RE strongly depend on the training phase.

Introduction

▼ For about 40 years, altitude training has been used to prepare for endurance competitions at altitude and to enhance sea level performance as well. The classic concept was to live high and to train high. Whereas this concept is generally accepted to be effective for performance improvement at altitude [6, 21, 30] it may not be advantageous for sea level performance, at least in elite athletes [7, 18, 26]. This is mainly due to the fact that the hypoxic environment compromises aerobic exercise performance and thus the training stimulus [4, 18].

In the nineties the “live high – train low” model was developed [18]. This type of altitude training is proposed to avoid the disadvantageous effects of hypoxic exercise and to profit from the increase of haemoglobin mass occurring during acclimatization which is associated with an enhancement of VO₂ max and performance [18, 26, 29, 32]. Several researchers propose that the improvement of work economy, i.e. running economy (RE), should contribute to the favourable effects of living high and training low [8, 9, 27]. Whereas some

recent studies confirmed improved RE after exposure to hypoxia [23, 28] others did not [20, 31]. This may at least partly be due to differences regarding the type, degree and duration of hypoxia applied. Most studies used intermittent hypoxia (IH) under hypobaric or normobaric conditions, defined as repeated episodes of hypoxia interspersed with normoxic periods [3]. It is also a common characteristic of all these studies that they evaluated the effects of hypoxic exposures before and after a single intervention period. Thus, it is unknown how repeated exposure periods to hypoxia would affect RE. Additionally, the most crucial factor is training per se. Also when the training is standardized individual responses may vary considerably during different training phases. It seems to be obvious that these training responses may greatly confound the hypoxia effects.

We hypothesised that RE increases during training from the beginning of the pre-season to the competition season and that the effects of hypoxia on RE are more distinct during the early pre-season compared to the competition season. Therefore, the main purpose of the present study

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Bibliography

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was to investigate the combined effects of training and 2 periods of hypoxic exposures on RE in well trained runners.

Methods

Subjects

11 male and female middle-distance runners volunteered to participate in this study. This was the complete group of runners who competed at least at a national level and were supervised by the same coach. They were informed about the experimental procedures and possible risks associated with participation before written consent was obtained. The study was performed according to the ethical standards of the International Journal of Sports Medicine [12] and was approved by our institutional review board.

The experimental protocol

The study was a between- and a within-subject repeated measures design. Subjects were assigned to 2 groups with each group

homogenous in VO_2 max, RE and training (● **Table 1**). The whole study consisted of a 13-wk training period with exercise testing before (pre-test), after 5 (re-test1), after 8 (re-test2), and after 13 weeks (re-test3) (for a schematic overview see ● **Fig. 1**). 6 subjects were randomly assigned to the intermittent hypoxia group (IHG) and 5 to the control group (CG). Both groups performed a very similar training during the 13-wk period (● **Table 1**). The training started after about 2 months recovery after finishing the competition season. Training volume and intensity increased continuously during the first 5 weeks at pre-season, were slightly reduced during the following 3 weeks and especially intensity was increased during the following 5-wk period up to the competition season (● **Table 1**). Training consisted for both groups mainly of running at an altitude of about 600m. The members of the IHG spent additionally 2h at rest on 3 days/wk for the first and the second 5-wk period in normobaric hypoxia (Hypoxico, Germany). During both periods the inspiratory oxygen concentration (FiO_2) was set at 15% (~ 3200m) at the beginning and was decreased by 1% per week being 11% (~ 5500m) during the 5th week. A similar course of hypoxia has been used in earlier studies, which has been well tolerated by both elderly subjects and highly trained distance runners [3, 15]. We decided not to apply a double blind design because we assumed, based on our experience of using hypoxia, that the members of the IHG would perceive the hypoxic exposure. The 4 exercise tests (see treadmill testing) were performed under normoxic conditions at the same altitude (600m) where training took place. During the whole study period all study participants abstained from exposures to real altitude >2500m.

Table 1 Subject characteristics and training.

	IHG (N=6)	CG (N=5)
age, yr	24.0±8.5	19.6±4.3
gender, m/f	5/1	3/2
height, cm	177.3±5.8	172.0±7.5
body mass, kg	62.9±5.3	61.4±6.4
HR _{max} , b/min	191±9	196±5
VO _{2max} , ml/min/kg	61.7±7.6	57.6±6.4
RE, ml/min/kg	46.5±6.6 ^a	45.7±5.8 ^a
training volume, km/wk		
wk 1–5	50–90 (105) ^b	50–85
wk 6–8	50–75 (105) ^b	50–75
wk 9–13	45–85 (100) ^b	50–75
training intensity, %>85% HR _{max}		
wk 1–5	10–25	10–30
wk 6–8	10–20	10–20
wk 9–13	20–35	20–40

Values are means ± SD, frequencies (gender) or ranges (training volume and intensity). Maximal heart rate (HR_{max}), maximal oxygen uptake (VO_{2max}), running economy (RE)

^aData are pooled values of the 3 submaximal running speeds: 12, 14, and 16 km/h for males and 9, 11, and 13 km/h for females

^bOne athlete of the IHG had somewhat higher training volumes
IHG: intermittent hypoxia group, CG: control group

Treadmill testing

Assessment of RE

Exercise tests were performed on a custom-built motorized treadmill (Proxomed Kardiomed Mill, H-P-Cosmos, Germany). Running economy (RE) was determined by measuring oxygen uptake for 4 min at 3 constant running speeds during the same session. The 3 running speeds, each with 1% gradient were set at 12, 14, and 16 km/h for males (n=8) or at 11, 13, and 15 km/h for females (n=3). The 1% gradient was used to compensate for the lack of air resistance when treadmill running [14]. The lower running speeds in females were applied because of their lower performance levels compared to the male runners.

After a 10–15 min warm-up on the field track, subjects started the exercise test where the running speed was gradually

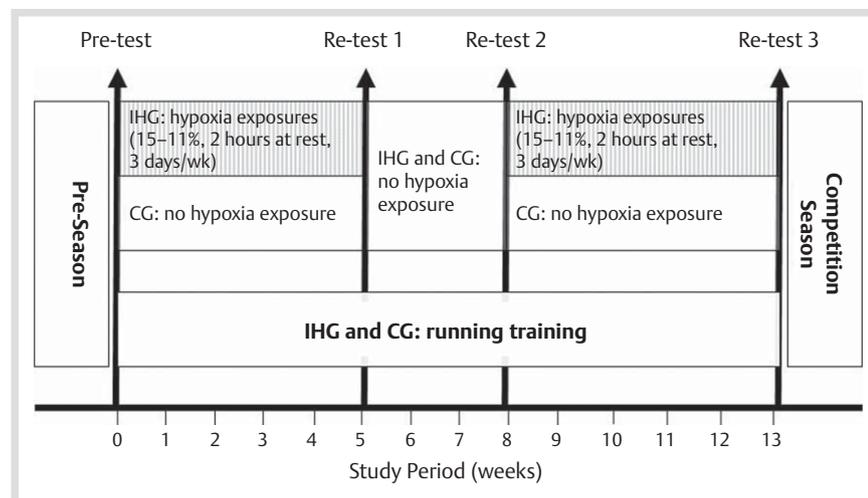


Fig. 1 Schematic diagram of the study protocol. IHG: intermittent hypoxia group, CG: control group.

increased within 3 min up to the first target speed. Oxygen consumption, minute ventilation, respiratory exchange ratio (RER) and heart rate were measured continuously during the RE tests.

Assessment of VO_2 max and maximal performance

VO_2 max and maximal performance were determined in the same session of RE assessment. After completing the 3 constant running speed levels for RE assessment, the running speed was increased by 1 km/h each minute for additional 4 min and then the treadmill gradient was increased by 2% each minute until volitional exhaustion was reached. Maximal performance was defined as the running time from the end of RE assessment up to exhaustion. The highest VO_2 -value (30-s average) measured during this time was defined as VO_2 max. Heart rate was recorded by short-range telemetry (Polar Vantage, NV, Kempele, Finland). No intense training was performed during the day prior to the tests. All athletes were properly hydrated without any indication of lowered glycogen storages. To limit typical error of measurement careful standardization of footwear, time of testing, ambient temperature, humidity and nutritional status was performed.

Gas analysis

Respiratory gases were analysed breath by breath using an open circuit system (Oxycon Alpha, Jaeger, Germany). Subjects ventilated via face mask and analyses of minute ventilation, oxygen consumption and carbon dioxide production were performed continuously throughout the exercise test. The oxygen, carbon dioxide and the ventilatory analysers were calibrated before each test according to the manufacturer's recommendation. The typical error of measurement for submaximal VO_2 in our laboratory, established in a pilot study on 5 runners, is 1.7% which is very similar to that reported by Katayama et al. [17].

Haematological parameters

To get a rough indication on possible changes of haemoglobin concentration and hematocrit capillary blood samples were drawn from a finger tip after 15 min rest in a sitting position before each exercise test. The capillary blood was stored in cuvettes (LKM 144 for Hct and LKM 134 for Hb, Hach Lange GmbH, Germany) and analysed by a Lange miniphotometer plus (LP-20, Hach Lange GmbH, Germany). The typical error of measurement for those determinations, established on 20 blood samples in duplicate, is 1.5%.

Body composition

Complex impedance measurements were taken using a multi-frequency bioimpedance analyser (BIA 2000-M, Data Input GmbH, Germany). The 2000-M device is a tetrapolar hand-to-foot bioimpedance analyser that provides values of resistance, reactance and phase angle at 3 fixed frequencies (5, 50, 100 kHz).

Percent body fat (%BF) and lean body mass (LBM) were estimated using the Nutri Plus Software (Data Input GmbH, Germany). The measurements were taken on the dominant side within the first minutes after subjects assumed the supine position. No intense training was performed during the day prior to the tests and the last meal was taken approximately 4 h before measurements.

Statistics

The primary target parameter was RE, the secondary were body composition and haematological data, maximum performance and cardiorespiratory responses to submaximal exercise. Values are reported as means \pm SD, frequencies or ranges. For quantitative data the Kolmogorov-Smirnov test was performed to assess normal distribution. In case of normal distributed data a two-way ANOVA for repeated measures was used to compare the effects of intermittent hypoxia between groups and one-way repeated measures ANOVA for within group changes followed by Scheffé post hoc tests. For the evaluation of the effects of the 2 hypoxia periods the results of each re-test were compared to baseline and those of re-test3 to that of re-test2. Unfortunately, 1 athlete of the CG missed re-test2 because of illness. Therefore, intention-to-treat analyses were performed additionally, using group means for the missing values. Mean values of RE and cardiorespiratory data at submaximal exercise are pooled values of the 3 running speeds, because differences were independent of speed, indicated by no group \times test \times speed interaction (cf. 27). Pearson's product-moment correlation coefficients were used to analyse the relationship between 2 quantitative variables. The level of significance was set at $P < 0.05$. All statistical analyses were performed using the SPSS, version 12.0.

Results



The hypoxic sessions and the training program were performed by all athletes as planned. The IHG completed a total of 60 h in hypoxia (30 h per one 5-wk period). Only one athlete was sick for several days and missed re-test2. No further complaints were reported. Because intention-to-treat analyses did not reveal any differences compared to the per-protocol analyses, only the results of the per-protocol analyses are shown.

Body composition and haematological data

No changes were observed between groups or within the CG. Within the IHG body mass (62.9 ± 5.3 kg vs. 61.9 ± 5.0 kg, $P < 0.05$) decreased and haemoglobin concentration (14.7 ± 1.4 g/dl vs. 15.4 ± 1.4 g/dl; $P < 0.05$) and hematocrit (43.3 ± 3.4 vs. 44.9 ± 4.9 ; $P < 0.05$) increased from pre-test to re-test1 ($P < 0.05$) (● **Table 2**).

Table 2 Body composition and haematological data.

	IHG				CG			
	Pre-Test	Re-Test1	Re-Test2	Re-Test3	Pre-Test	Re-Test1	Re-Test2	Re-Test3
body mass, kg	62.9 \pm 5.3	61.9 \pm 5.0 [§]	62.7 \pm 5.9	63.2 \pm 5.3	61.4 \pm 6.4	61.7 \pm 6.6	62.3 \pm 6.6	61.8 \pm 6.6
LBM, kg	53.5 \pm 6.8	52.4 \pm 6.9	53.0 \pm 7.0	54.2 \pm 7.1	50.8 \pm 8.0	50.6 \pm 8.1	50.8 \pm 8.2	51.1 \pm 8.8
% BF	15.1 \pm 4.7	15.6 \pm 5.2	15.6 \pm 4.2	14.6 \pm 4.9	17.5 \pm 7.3	18.3 \pm 6.7	18.8 \pm 6.3	17.7 \pm 7.5
Hb, g/dl	14.7 \pm 1.4	15.4 \pm 1.4 [§]	14.5 \pm 1.4	14.3 \pm 1.8	13.9 \pm 1.6	14.0 \pm 1.1	14.4 \pm 0.9	14.4 \pm 0.7
Hct, %	43.3 \pm 3.4	44.9 \pm 4.9 [§]	42.9 \pm 4.8	43.1 \pm 5.4	42.2 \pm 3.0	41.6 \pm 4.3	43.1 \pm 4.2	42.4 \pm 2.1

Values are means \pm SD. Lean body mass (LBM), percent body fat (%BF)

[§]denotes significant changes from baseline within groups; there are no significant changes from baseline between groups

IHG: intermittent hypoxia group, CG: control group

Running economy

Running economy, expressed as the relative oxygen consumption (ml/min/kg) across the 3 submaximal running speeds, improved within both groups during the 13-wk study period (IHG: -4.3 ± 2.3 , $P < 0.05$ vs. CG: -2.9 ± 2.1 ml/min/kg, $P < 0.05$; changes between groups are not significant), (Fig. 2–4). For the pooled data of the 3 submaximal running speeds significant changes in relative oxygen consumption between groups were only observed from pre-test to re-test1 (IHG: -2.3 ± 1.2 vs. CG: -0.3 ± 0.7 ml/min/kg, $P < 0.05$), (Fig. 2). Within the IHG RE improved from pre-test to re-test1, re-test2 and re-test3

($P < 0.05$), (Fig. 2, 4). Within the CG, RE improved from pre-test to re-test2 and re-test3 ($P < 0.05$) (Fig. 2, 4). RE improved within both groups during the second 5-wk IH period (re-test2 to re-test3), $P < 0.05$) (Fig. 3).

The regression data for both groups (Fig. 3) were fitted through the measured relative oxygen consumption at the 3 submaximal running speeds (12, 14, 16 km/h or 11, 13, 15 km/h). The slopes of relative oxygen consumption and running speed tended only to decrease between pre-test and re-test3 within the IHG ($P = 0.1$).

Cardiorespiratory responses to submaximal exercise

The presented data are pooled for the 3 stages of different running speeds. Significant changes between groups could only be observed for oxygen consumption as described above and the RER from pre-test to re-test1 (Fig. 4). Within the IHG the RER increased from 0.93 ± 0.02 to 0.95 ± 0.01 ($P < 0.05$) and within the CG it decreased from 0.94 ± 0.01 to 0.93 ± 0.01 (NS); $P < 0.05$ between groups. Minute ventilation decreased only within the IHG from pre-test to re-test1 and re-test3 ($P < 0.05$) (Fig. 4). Heart rates decreased within the IHG from pre-test to re-test1, re-test2 and re-test3 and within the CG from pre-test to re-test2 and re-test3 ($P < 0.05$) (Fig. 4). Within group changes during the second 5-wk period only occurred within the CG. Minute ventilation and heart rates decreased within this group from re-test2 to re-test3 significantly (Fig. 4).

VO₂ max and maximal performance

The running time, measured after the stage of the 3rd submaximal running speed up to exhaustion, changed significantly between groups from pre-test to re-test1 (IHG: 4.7 ± 0.5 vs. 5.7 ± 1.0 min ($P < 0.05$) and CG: 4.6 ± 0.9 vs. 5.0 ± 0.7 (NS) min; $P < 0.05$ between groups). Within the IHG running time changed also from pre-test to re-test2 and re-test3 (4.7 ± 0.5 vs. 6.0 ± 1.3 min and vs. 6.2 ± 1.3 min, $P < 0.05$) and within the CG from pre-test to re-test2 and re-test3 (4.6 ± 0.9 vs. 5.8 ± 0.4 min; $P < 0.05$). No changes between or within groups were observed regarding the maximum values of oxygen uptake, minute ventilation or heart rate (Table 3).

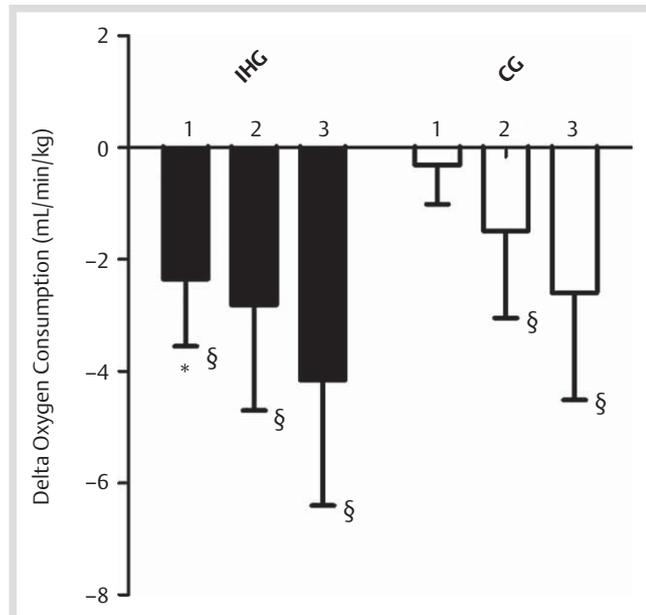


Fig. 2 Changes in the relative oxygen consumption for the submaximal running speeds (pooled data) of the intermittent hypoxia group (IHG) and the control group (CG) between pre-test and re-test1 (1), pre-test and re-test2 (2), pre-test and re-test3 (3). * denotes significant changes from baseline between groups; § denotes significant changes from baseline within groups. Error bars indicate SD.

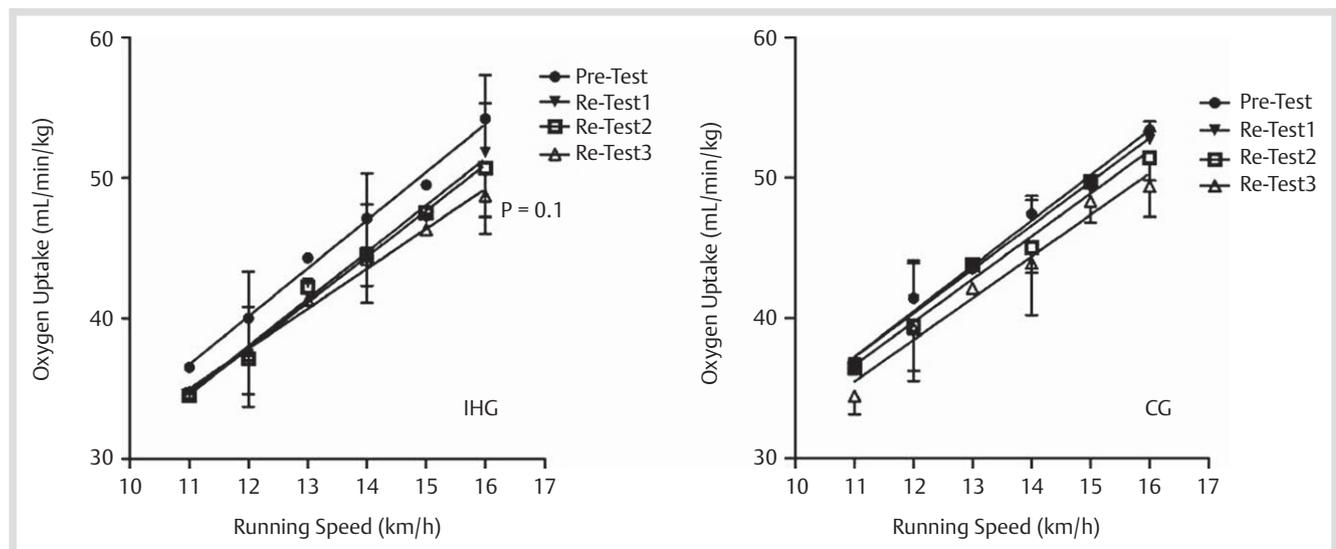


Fig. 3 The regression slopes between relative oxygen consumption and running speed at the pre-test, re-test1, re-test2 and re-test3 for the intermittent hypoxia group (IHG) and the control group (CG). $P = 0.1$ for differences in the slopes measures at the pre-test and re-test3. Error bars indicate SD.

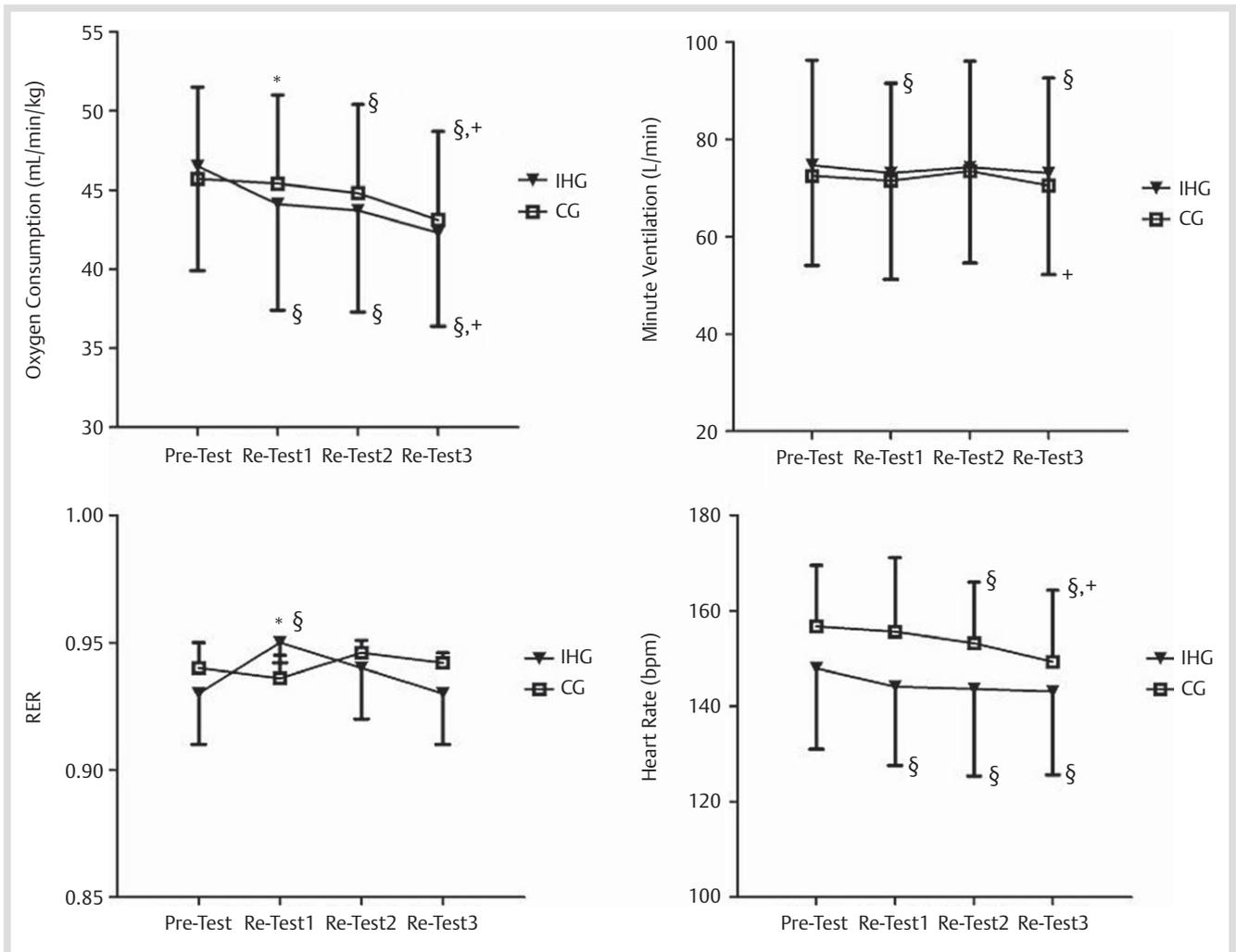


Fig. 4 Cardiorespiratory data of the intermittent hypoxia group (IHG) and the control group (CG) pooled for the submaximal running speeds at the 4 exercise tests. * denotes significant changes from baseline between groups; § denotes significant changes from baseline within groups; + denotes significant changes between re-test2 and re-test3. Error bars indicate SD.

Table 3 Responses to maximal exercise and running time above the 3 submaximal running speeds.

	IHG				CG			
	Pre-Test	Re-Test1	Re-Test2	Re-Test3	Pre-Test	Re-Test1	Re-Test2	Re-Test3
VO _{2max} , ml/min	61.7±7.6	62.9±7.8	63.4±8.7	62.5±6.7	57.6±6.4	61.2±6.1	60.3±6.5	58.7±4.3
VE _{max} , l/min	125.2±17.1	134.0±19.4	131.2±22.2	136.1±26.7	121.8±25.6	123.0±20.7	131.5±27.8	129.6±22.8
HR _{max} , b/min	191±9	192±10	192±10	192±10	196±5	195±5	196±6	196±6
RT, min	4.7±0.5	5.7±1.0*§	6.0±1.3§	6.2±1.3§	4.6±0.9	5.0±0.7	5.4±0.5§	5.8±0.4§

Values are means±SD. Maximal oxygen uptake (VO_{2max}), maximal ventilation (VE_{max}), maximal heart rate (HR_{max}), running time (RT)

* denotes significant changes from baseline between groups; § denotes significant changes from baseline within groups

IHG: intermittent hypoxia group, CG: control group

Correlation analyses

Correlation analyses revealed a close relationship between the decrease in oxygen uptake during submaximal running and the increase in haemoglobin concentration ($R^2=0.72$). (● Fig. 5) and the increase in hematocrit ($R^2=0.62$) within the IHG from the pre-test to re-test1. The decrease in relative oxygen consumption was also related to the increase in running time within the IHG from pre-test to re-test1 ($R^2=0.81$) (● Fig. 6).

Discussion

▼ The main finding of the present study was that RE improved only during the first 5-wk period of IH when compared to training alone. Although RE continuously improved during the 13-wk study period within both groups, no further differences between groups occurred after the first 5-wk period. These findings suggest that mainly IH must have been responsible for the RE improvement during the first 5 weeks and running training during the following 8 weeks. This emphasizes the importance of the training phase on the effectiveness of IH on RE. All those studies that did not find improved RE after IH were performed

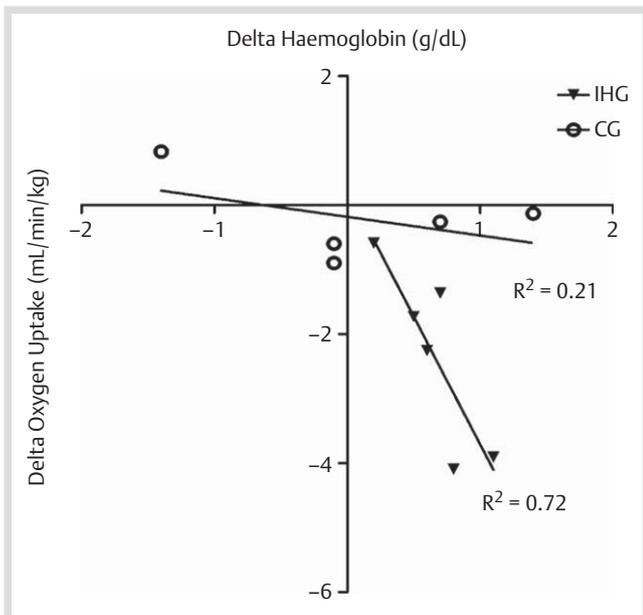


Fig. 5 Relationship between the changes in haemoglobin concentration and oxygen uptake during submaximal running from pre-test to re-test1 within the intermittent hypoxia group (IHG) and the control group (CG).

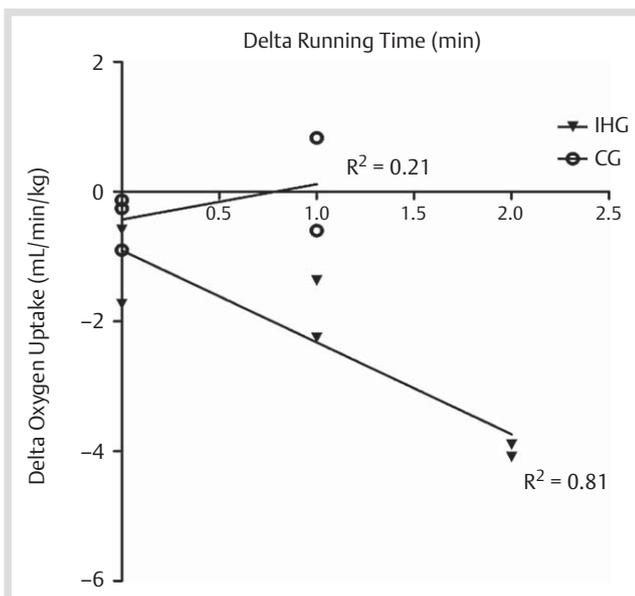


Fig. 6 Relationship between the changes in running time (after the submaximal running stages) and oxygen uptake during submaximal running from pre-test to re-test1 within the intermittent hypoxia group (IHG) and the control group (CG).

close to competition season [15,20,31] supporting the assumption that RE will be hardly affected by IH at that time. However, it can not be excluded that more severe hypoxia and longer durations of exposure would affect RE even close to competition season.

RE and haematological changes

Beside the training status, differences between study results may also arise from the applied exposure to hypoxia, i.e. real altitude, simulated altitude, degree of hypoxia, daily and total duration of hypoxic exposures. Whereas the dosing of hypoxia

for the enhancement of the total haemoglobin mass nowadays is well defined this does not apply to RE. About 400 h of hypoxia corresponding to an altitude >2 100 m seem to be necessary to increase total haemoglobin mass [28,29]. In the present study, however, the duration of hypoxic exposure was only 30 h during one 5-wk period which is unlikely sufficient to increase total haemoglobin mass but seems to be sufficient for the improvement of RE. The small increases in haemoglobin concentration and hematocrit were closely related to the improvement in RE. Because an increase in the total haemoglobin mass is unlikely to have occurred the exposures to hypoxia may have induced haemoconcentration [5,11] and optimization of the hematocrit at rest and during exercise. The increase in hematocrit results in linear increase of the oxygen carrying capacity and an exponential increase in blood viscosity [1]. Because blood viscosity is not highly dependent on hematocrit at high cardiac outputs [1] the enhanced oxygen carrying capacity could contribute to the improved RE and performance after intermittent hypoxia.

RE and cardiorespiratory and metabolic responses to submaximal exercise

Decreased cardiorespiratory costs [10,17,28], greater reliance on carbohydrates [8,25], and/or a decrease in the ATP cost of muscle contraction [24] have been proposed as major candidates for the reduced oxygen consumption after IH at submaximal work. Our findings indicate that a small increase in carbohydrate use and lower cardiorespiratory costs contributed to the improved RE after the first 5-wk IH period, which is supported by the increased submaximal RER and the decreased minute ventilation and heart rate values within the IHG. It remains unclear why IH caused this oxygen-sparing effect of a shift in metabolic substrate utilization from fatty acid to carbohydrate only during the first 5-wk period. Changes in ATP consumption needs at the muscular level are unlikely because the slope between oxygen uptake and running speed remained unchanged after the first 5-wk period of IH. Only after the second 5-wk IH period was there a tendency of a reduced slope between oxygen consumption and running speed within the IHG. Our findings are consistent with a growing number of studies which demonstrated that exposures to natural or simulated altitude improve running economy [8,23,27,28]. Why other studies did not find such improvements may mainly be attributed to the training phases of athletes [15,20,31]. This may simply be due to the fact that training stimuli provoke lower responses during the competitive season in comparison with pre-season [22]. This would also explain why the hypoxia-related RE improvements observed in this study occurred preferentially during the first 5-wk IH period. RE improvements during the second 5-wk study period were similar within both groups and may therefore be related to running training. The fact is interesting that associated decreases in submaximal heart rates and minute ventilation only occurred within the CG. The possible interactions between 2 periods of IH and running training are unclear.

RE and body composition

Although body mass decreased in the IHG during the first 5-wk IH period, no differences in body mass and body composition were found between the 2 groups during the whole study period. Training during IH has been shown to reduce body fat more efficiently compared to training in normoxia [13]. However, repeated passive short-term hypoxic exposures, as applied in our study, seem not to influence body composition [16].

RE and maximal performance and VO₂ max

The close relationship between the improvements in RE and running time within the IHG after the first 5-wk period suggests that mainly IH may have contributed to the improved maximal performance in this training phase. Interestingly, no VO₂max changes over the entire study period were observed neither in the IHG nor the CG. These findings may at least partly be explained by the assumption of an inverse relationship between RE and VO₂max [2, 19].

Limitations

The present study is the first demonstrating the course of RE with and without IH from the pre-season up to the competition season indicating that IH improvements occur more likely at the beginning of the pre-season. At least 2 limitations have to be considered. First, the study was not performed in a double-blind fashion. Thus, a placebo effect can not be entirely excluded but such an effect should have been visible also after the second 5-wk IH period. The second limitation arises from the small sample size. However, the fact that even in small groups statistical significant differences are evident indicates the potential of IH to improve RE during the pre-season.

Conclusion

In conclusion IH was accompanied by a more distinct response of RE at the beginning of the pre-season compared to the beginning of the competition season. This may have practical implications on the planning of training. Much shorter duration of hypoxic exposures seem to be sufficient for RE improvement compared to that necessary for the enhancement of total haemoglobin mass. But the optimal duration and degree of hypoxia have to be elucidated.

References

- Birchard GF. Optimal hematocrit: Theory, regulation and implications. *Am Zool* 1997; 37: 65–72
- Burtscher M, Förster H, Burtscher J. Superior endurance performance in aging mountain runners. *Gerontology* 2008; 54: 268–271
- Burtscher M, Haider T, Domej W, Linsler T, Gatterer H, Faulhaber M, Pocecco E, Ehrenburg I, Tkatchuk E, Koch R, Bernardi L. Intermittent hypoxia increases exercise tolerance in patients at risk for or with mild COPD. *Respir Physiol Neurobiol* 2009; 165: 97–103
- Cerretelli P. Muscle energetics and ultrastructure in chronic hypoxia. *Respiration* 1992; 59 (Suppl 2): 24–29
- Dill DB, Horvath SM, Dahms TE, Parker RE, Lynch JR. Hemoconcentration at altitude. *J Appl Physiol* 1969; 27: 514–518
- Fulco CS, Rock PB, Cymerman A. Improving athletic performance: is altitude residence or altitude training helpful? *Aviat Space Environ Med* 2000; 71: 162–171
- Gore CJ, Hahn AG, Burge CM, Telford RD. VO₂max and haemoglobin mass of trained athletes during high intensity training. *Int J Sports Med* 1997; 18: 477–482
- Gore CJ, Hahn AG, Aughey RJ, Martin DT, Ashenden MJ, Clark SA, Garnham AP, Roberts AD, Slater GJ, McKenna MJ. Live high:train low increases muscle buffer capacity and submaximal cycling efficiency. *Acta Physiol Scand* 2001; 173: 275–286
- Gore CJ, Hopkins WG. Counterpoint: Positive effects of intermittent hypoxia (live high:train low) on exercise performance are not mediated primarily by augmented red cell volume. *J Appl Physiol* 2005; 99: 2055–2057
- Green HJ, Roy B, Grant S, Hughson R, Burnett M, Otto C, Pipe A, McKenzie D, Johnson M. Increases in submaximal cycling efficiency mediated by altitude acclimatization. *J Appl Physiol* 2000; 89: 1189–1197
- Grover RF, Weil JV, Reeves JT. Cardiovascular adaptation to exercise at high altitude. *Exerc Sport Sci Rev* 1986; 14: 269–302
- Harriss DJ, Atkinson G. International Journal of Sports Medicine – Ethical Standards in Sport and Exercise Science Research. *Int J Sports Med* 2009; 30: 701–702
- Haufe S, Wiesner S, Engeli S, Luft FC, Jordan J. Influences of normobaric hypoxia training on metabolic risk markers in human subjects. *Med Sci Sports Exerc* 2008; 40: 1939–1944
- Jones AM, Doust JH. A 1% treadmill grade most accurately reflects the energetic cost of outdoor running. *J Sports Sci* 1996; 14: 321–327
- Julian CG, Gore CJ, Wilber RL, Daniels JT, Fredericson M, Stray-Gundersen J, Hahn AG, Parisotto R, Levine BD. Intermittent normobaric hypoxia does not alter performance or erythropoietic markers in highly trained distance runners. *J Appl Physiol* 2004; 96: 1800–1807
- Katayama K, Matsudo H, Ishida K, Mori S, Miyamura M. Intermittent hypoxia improves endurance performance and submaximal exercise efficiency. *High Alt Med Biol* 2003; 4: 291–304
- Katayama K, Sata K, Matsuo H, Ishida K, Iwasaki K, Miyamura M. Effect of intermittent hypoxia on oxygen uptake during submaximal exercise in endurance athletes. *Eur J Appl Physiol* 2004; 92: 75–83
- Levine BD, Stray Gundersen J. “Living high-training low”: effect of moderate altitude acclimatization with low-altitude training on performance. *J Appl Physiol* 1997; 83: 102–112
- Lucía A, Hoyos J, Pérez M, Santalla A, Chicharro JL. Inverse relationship between VO₂max and economy/efficiency in world class cyclists. *Med Sci Sports Exerc* 2002; 34: 2079–2084
- Lundby C, Calbet JA, Sander M, van Hall G, Mazzeo RS, Stray-Gundersen J, Stager JM, Chapman RF, Saltin B, Levine BD. Exercise economy does not change after acclimatization to moderate to very high altitude. *Scand J Med Sci Sports* 2007; 17: 281–291
- Maher JT, Jones LG, Hartley LH. Effects of high-altitude exposure on submaximal endurance capacity of men. *J Appl Physiol* 1974; 37: 895–898
- Midgley AW, McNaughton LR, Jones AM. Training to enhance the physiological determinants of long-distance running performance. Can valid recommendations be given to runners and coaches based on current scientific knowledge? *Sports Med* 2007; 37: 857–880
- Neya M, Enoki T, Kumai Y, Sugoh T, Kawahara T. The effects of nightly normobaric hypoxia and high intensity training under intermittent normobaric hypoxia on running economy and hemoglobin mass. *J Appl Physiol* 2007; 103: 828–834
- Ponsot E, Dufour SP, Zoll J, Doutrelau S, N’Guessan B, Geny B, Hoppeler H, Lampert E, Mettauer B, Ventura-Clapier R, Richard R. Exercise training in normobaric hypoxia in endurance runners. II. Improvement of mitochondrial properties in skeletal muscle. *J Appl Physiol* 2006; 100: 1249–1257
- Roberts AC, Reeves JT, Butterfield GE, Mazzeo RS, Sutton JR, Wolfel EE, Brooks GA. Altitude and beta-blockade augment glucose utilization during submaximal exercise. *J Appl Physiol* 1996; 80: 605–615
- Rusko HK, Tikkanen HO, Peltonen JE. Altitude and endurance training. *J Sports Sci* 2004; 22: 928–945
- Saunders PU, Telford RD, Pyne DB, Cunningham RB, Gore CJ, Hahn AG, Hawley JA. Improved running economy in elite runners after 20 days of moderate simulated altitude exposure. *J Appl Physiol* 2004; 96: 931–937
- Saunders PU, Telford RD, Pyne DB, Hahn AG, Gore CJ. Improved running economy and increased hemoglobin mass in elite runners after extended moderate altitude exposure. *J Sci Med Sport* 2009; 12: 67–72
- Schmidt W, Prommer N. Effects of various training modalities on blood volume. *Scand J Med Sci Sports* 2008; 18 (Suppl 1): 57–69
- Schuler B, Thomsen JJ, Gassmann M, Lundby C. Timing the arrival at 2340 m altitude for aerobic performance. *Scand J Med Sci Sports* 2007; 17: 588–594
- Truijens MJ, Rodríguez FA, Townsend NE, Stray-Gundersen J, Gore CJ, Levine BD. The effect of intermittent hypobaric hypoxic exposure and sea level training on submaximal economy in well-trained swimmers and runners. *J Appl Physiol* 2008; 104: 328–337
- Wehrli JP, Zuest P, Hallén J, Marti B. Live high-train low for 24 days increases hemoglobin mass and red cell volume in elite endurance athletes. *J Appl Physiol* 2006; 100: 1938–1945