The lower gross efficiency at altitude is mainly caused by a lower absolute power output

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Original Investigation

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Abstract

Although cyclists often compete at altitude, the effect of altitude on gross efficiency (GE) remains inconclusive. **Purpose** To investigate the effect of altitude on GE at the same relative exercise intensity and the same absolute power output (PO). Additionally, we sought to determine the effect of altitude on the change in GE during high-intensity exercise. **Methods** Twenty-one trained males performed three maximal incremental tests and five GE-tests, at sea level, 1500 m and 2500 m of acute simulated altitude. The GE-tests at altitude were performed once at the same relative exercise intensity and once at the same absolute PO as at sea level. **Results** Altitude resulted in an unclear effect at 1500 m (-3.8%; ±90% CL 3.3%) and most likely negative effect at 2500 m (-6.3%; ±1.7%) on pre-GE, when determined at the same relative exercise intensity. When pre-GE was determined at the same absolute PO unclear differences in GE were found (-1.5%; ±2.6% at 1500 m, -1.7%; ±2.4% at 2500 m). The effect of altitude on the decrease in GE during high-intensity exercise was unclear when determined at the same relative exercise intensity (-0.4%; ±2.8% at 1500 m, -0.7%; ±1.9% at 2500 m). When GE was determined at the same absolute PO, altitude resulted in a substantially smaller decrease in GE (2.8%; ±2.4% at 1500 m, 5.5%; ±2.9% at 2500 m). **Conclusion** The lower GE found at altitude, when exercise is performed at the same relative exercise intensity, is mainly caused by the lower PO at which cyclists exercise.

Keywords: exercise performance, hypoxia, economy, aerobic capacity

Introduction

To find the optimal altitude for each sporting event, it is important to know the effect of altitude on the main performance-determining variables. The main performance-determining variables, according to the model of Joyner and Coyle,[1] are performance oxygen uptake ($\dot{V}O_2$) (determined by the maximal oxygen uptake ($\dot{V}O_{2max}$) and $\dot{V}O_2$ at the lactate threshold), performance O_2 deficit, and gross mechanical efficiency (GE). GE, defined as the percentage of metabolic power input (PI) that is converted into mechanical power output (PO), is considered the most valid definition of whole-body efficiency.[2] Under hypoxic circumstances the respiratory exchange ratio (RER) increases,[3,4] while PO attained at $\dot{V}O_{2max}$ ($P\dot{V}O_{2max}$) declines.[5–8] The increased RER combined with the declined $P\dot{V}O_{2max}$ will likely affect the balance between PO and PI, leading to a change in GE. However, the effect of altitude on GE remains inconclusive.

Previous studies on the effect of simulated altitude on GE showed inconsistent results. Clark et al.[9] found a significant decrease in GE at a simulated altitude of 3200 m (16.8 ± 2.2%) compared to 200 m (17.3 ± 2.4%) and 1200 m (17.3 ± 2.4%), when GE was determined during a five minute exercise bout at similar absolute PO between 50 and 250 W. Clark et al.[9] however, discussed that the difference in GE was caused by the higher pedaling frequency at altitude, which is supported by the data summarized by Ettema and Lorås,[2] indicating that pedaling frequency influences GE measurements. Clark et al.[9] also investigated GE during a five minute time trial, but no significant differences in GE were found between trials performed at 200 m, 1200 m, 2200 m and 3200 m altitude. Schuler et al.[10] also found no significant effect of 2340 m altitude on GE compared to sea level (25.2 ± 1.0% and 25.3 ± 0.9%, respectively). Although unreported, it seems that in both studies two criteria for robust and reliable GE measurements were violated.[2,11,12] The RER was probably higher than 1.0 (not reported) and subjects probably did not attain steady state in both studies, since subjects had to cycle at 80% of sea level $P\dot{V}O_{2max}$ until exhaustion in the study of Schuler et al.[10] and participants had to perform a time trial in the study of Clark et al.[9] Niu et al.[13] found a negative effect of altitude on GE at 3680 m (13.2%) compared to 500 m (17.5%) during an exercise bout of three minutes performed at 90 W. So, currently it remains unclear if GE is negatively influenced by altitude or not.

A study that took the criteria of robust GE measurement into account was the study of Noordhof et al.[6] GE was determined during the final three minute of a six minute steady state exercise bout performed at 45%, 55%, and 65% $P\dot{V}O_{2max}$. Cycling tests were conducted at sea level and at a simulated altitude of 1500 m (hypobaric hypoxia). The conclusion of this study was that GE is lower at an altitude of 1500 m (20.7 ± 1.1%) with respect to sea level (21.4 ± 0.8%). The interesting difference between the study of Noordhof et al.[6] and the previous mentioned studies is that Noordhof et al.[6] determined GE at the same relative exercise intensity at sea level and altitude. The other studies determined GE at the same absolute PO at sea level and altitude. Since the study of Noordhof et al.[6] only took the relative exercise intensity into account, the change in GE could be a result of the lower absolute work load[2] and it is difficult to compare their results to the remaining body of literature.

Currently, no study has investigated the effect of altitude on GE both at the same relative exercise intensity and at the same absolute PO. Therefore, the main purpose of the present study was to investigate the effect of altitude on GE both at the same relative exercise intensity and the same absolute PO. Furthermore, multiple studies have shown a decrease in GE during a high-intensity exercise bout performed at sea level.[14–17] Thus far, it is unknown if the decrease in GE, observed during a high-intensity exercise bout,[14] is the same at acute altitude compared to sea level. Therefore, the second purpose of the study was to investigate the effect of altitude on the decrease in GE during a high-intensity exercise bout.

Methods

Subjects

Twenty-one trained,[18] non-acclimatized, male cyclists participated in this study. The three inclusion criteria were: 1) $\dot{V}O_{2max}$ at sea level above 55 mL·kg^{-1}·min^{-1}, 2) train at least twice a week, 3) previous experience with cycling time trials. Before the first test, participants received detailed information about the experimental protocol. In addition, each participant completed a health history form and provided written informed consent. Participants were also asked to avoid heavy exercise in the 24 h before the tests and not to use caffeine three hours before the tests. The characteristics of the participants are summarized in Table 1. The local ethics committee approved the study.

[Insert Table 1 about here]

Experimental protocol

Participants performed exercise tests at three different simulated altitudes: sea level ($F_iO_2 = 0.21$), 1500 m ($F_iO_2 = 0.17$) and 2500 m ($F_iO_2 = 0.15$). During the first visit, all participants performed a maximal incremental exercise test to determine if inclusion criteria regarding fitness were met. When participants met the inclusion criteria the GE test (see below) was practiced to diminish the effect of learning on subsequent tests.[19] GE tests were performed twice at each altitude: at sea level a familiarization trial and the actual GE test, and at 1500 m and 2500 m a GE test at the same relative exercise intensity as at sea level and at the same absolute PO as at sea level. All tests except the maximal incremental exercise test performed at sea level were performed in pseudo-random order. The only restriction was that the maximal incremental exercise test at a certain altitude had to be completed before the GE test at the same relative exercise intensity.

Maximal incremental exercise test

A maximal incremental test was performed to determine $\dot{V}O_{2max}$ and $P\dot{V}O_{2max}$. After one minute of rest participants started a three minute warm-up bout at 100 W. After the warm-up resistance increased stepwise by 25 W-min^{-1}. Participants were instructed to maintain a constant pedaling frequency of 90 revolutions per minute (rpm). The test ended if the pedaling frequency dropped below 80 rpm for more than five seconds.

Gross efficiency test

The protocol of the GE test is based on the protocol used by de Koning et al.[15] and Noordhof et al.[14] and is shown in Figure 1. The tests at the same absolute PO were performed at 55% $P\dot{V}O_{2max}$ obtained at sea level, while the tests at the same relative exercise intensity were performed at 55% $P\dot{V}O_{2max}$ determined at that particular altitude. During the submaximal exercise bouts participants received feedback on rpm on a screen in front of the bike. Participants were instructed to adjust their cadence if it deviated by more five rpm above or below 90. During the time trial participants were able to choose their own pedaling frequency and were instructed to finish the 4000 m as fast as possible. The resistance of the computer-controlled ergometer was corrected for the air-resistance at each altitude such that the power-speed relationship reflected natural altitude settings. During the entire time trial the gear ratio was set at 52/12 and participants received feedback on distance.

[Insert Figure 1 about here]

Data collection

All nine tests were performed on a custom-made electronically braked cycle ergometer (VU-MTO, Amsterdam, the Netherlands). Respiratory data were collected breath-by-breadth using open-circuit spirometry (Cosmed CPET, COSMED S.R.L., Rome, Italy), which was calibrated before each test, corresponding to the manufacturer's instructions. The mask, used to collect respiratory data, was also used to supply air to the participants. The mask was connected to a bag of air (hypoxic or normoxic), which contained air produced by the b-CAT High-Altitude (b-CAT BV, Tiel, the Netherlands). The inspired oxygen fraction was measured (Cosmed CPET, COSMED S.R.L., Rome, Italy) and checked throughout each test to make sure participants received the correct air mixture for each simulated altitude. Participants were blinded to the simulated altitude during the tests. Saddle height and handlebar height were set by participants' preference during their first visit and replicated during subsequent tests.

Data analysis

Breath-by-breath respiratory data were converted into second-by-second data using interpolation. The second-by-second data was filtered using a 30 s moving average filter to reduce breath-by-breath noise. GE was calculated using equation 1 and 2. The mean $\dot{V}O_2$, RER and PO of predetermined three minute blocks, pre, post1 and post2 (see Figure 1) were used to calculate GE. GE could not be determined when the criteria of robust GE measurement were violated.[2,11,12]

GE directly after the time trial was determined using the back-extrapolation method as described by Noordhof et al.[14] First, a linear regression line was fitted to the second-by-second GE data of the last nine minutes of the test. The linear regression line was determined using the least-squares method and was back-extrapolated to the end of the time trial (GE-extrap).

$$Gross\ Efficiency = \frac{Power\ Output}{Power\ Input} * 100 \qquad (1)$$

$$Power\ Input = \dot{V}O_2 * (4940 * RER + 16040) \qquad (2)$$

With $\dot{V}O_2$ expressed in $L \cdot s^{-1}$.

Statistics

Data were log transformed before analyses. Data are presented as means ± standard deviations (SD). The mean shown in this study is the back-transformed mean and the SD is a coefficient of variation expressed as a percentage.

The pre-post crossover spreadsheet[20] which also can be used for non-crossover studies, was used to determine the effect of altitude on GE, $\dot{V}O_2$, RER. The effect of altitude on PO during the time trial, $P\dot{V}O_{2max}$ and $\dot{V}O_{2max}$ was determined with the post-only spreadsheet,[20] which can be used for repeated measurements. With the pre-post crossover spreadsheet and post-only spreadsheet the probability that an intervention has a positive, negative or trivial effect can be determined.[21] The magnitude of the effect was determined using standardized Cohen units (0.2 times the between-subject SD), except for the average PO data of the time trial, for which we used 0.3 times the CV. A CV of 1.53%, reported by Hickey et al.[22] was used for this purpose . To interpret magnitudes of differences as small, moderate, large, very large, and extremely large, the following thresholds for standardized changes were reported: 0.20 (small), 0.60 (moderate), 1.2 (large), 2.0 (very large) and 4.0 (extremely large).[23] The uncertainty in the estimates is reported as 90% confidence limits (CL). The following scale is used to quantify how positive, negative or trivial the intervention is: < 0.5%: most unlikely, 0.5-5%: very unlikely, 5-25%: unlikely, 25-75%: possibly, 75-95%: likely, 95-99.5%: very likely, > 99.5%: most likely.[23]

Results

Gross efficiency test

GE values of the five GE tests are shown in Figure 2 and 3. To determine if GE was different between altitude and sea level all GE values (pre, extrap, post1, post2) at altitude were compared to sea level, at the corresponding time points, see Table 2. There are some missing values (for the corresponding *n* see Table 2 and Table 3) in the dataset due to violation of robust GE testing and errors of the equipment. Apart from two missing values at post1 during the absolute PO test at 2500 m that were caused by violation of robust GE testing or errors of the equipment, the other missing values were the result of participants that were unable to finish the post time trial exercise bout due to the high exercise intensity.

[Insert Table 2 about here]

To determine if the decline in GE during a high-intensity exercise bout was influenced by altitude, the difference between post1-GE and pre-GE was examined. Altitude resulted in an unclear effect on the change in GE during a high-intensity exercise bout of -0.4% (±90% CL 2.8%) at 1500 m and -0.7% (±1.9%) at 2500 m compared to sea level, when GE was determined at the same relative intensity (see Figure 2). Altitude resulted in a likely positive effect on the change in GE during a high-intensity exercise bout of 2.8% (±2.4%) at 1500 m and a very likely positive effect of 5.5% (±2.9%) at 2500 m with respect to sea level, when GE was determined at the same absolute PO (see Figure 3).

[Insert Figure 2 and Figure 3 about here]

To determine the underlying cause of the effect of altitude on GE, mean $\dot{V}O_2$ and RER values at altitude were compared to sea level values (see Table 3).

[Table 3 about here]

The mean PO during the 4000-m time trial was 317 ± 26 W at sea level, 286 ± 32 W at 1500 m and 255 ± 23 W at 2500 m, which corresponds to change scores of -11.5 ±2.4% at 1500 m and -19.9 ±1.9% at 2500 m compared to sea level. Both altitudes resulted in a most likely negative effect. Mean PO expressed relative to $P\dot{V}O_{2max}$ from the incremental test at equivalent altitude was 77 ± 7% at sea-level, 75 ± 8% at 1500 m, and 72 ± 7% at 2500 m. The corresponding change scores at 1500 m and 2500 m were -2.3 ±3.5, considered unclear (3% chance on a higher $\%P\dot{V}O_{2max}$, 38% chance on an insubstantial/trivial effect, and a 60% chance on a lower $\%P\dot{V}O_{2max}$), and -5.9 ±4.0%, considered likely negative.

Maximal incremental exercise test

Mean $\dot{V}O_{2max}$ decreased by 4.8% (±1.5%) at 1500 m and -12.9% (±2.0%) at 2500 m compared to sea level. The corresponding mean $P\dot{V}O_{2max}$ was 418 ± 37 W at sea level, 380 ± 44 W at 1500 m and 356 ± 29 W at 2500 m, which corresponds to change scores of -9.4% (±2.4%) at 1500m and -14.9% (±2.2%) at 2500 m. All effects were considered most likely negative.

Discussion

The main purpose of the present study was to investigate the effect of altitude on GE both at the same relative exercise intensity and the same absolute PO. The secondary purpose of the study was to investigate the effect of altitude on the decrease in GE during a high-intensity exercise bout. The main findings were: 1) The effect of altitude on pre-GE was unclear at 1500 m (1% chance on a higher GE, 10% chance on an insubstantial/trivial effect, and 90% chance of a lower GE), but GE was substantially lower at 2500 m when cyclists were cycling at the same relative exercise intensity as at sea level; 2) The effect of altitude on pre-GE was unclear (5%/33%/61% at 1500 m and 3%/33%/64% at 2500 m) when cyclists were cycling at the same PO; 3) altitude (1500 m and 2500 m) resulted in an unclear effect on the decline in GE during time trial exercise, when GE is determined at the same relative intensity; 4) GE decreases less at altitude (1500 m and 2500 m) during high-intensity exercise compared to sea level when GE was determined at the same PO.

The present study showed a 90% chance of a lower GE at 1500 m when cyclists were cycling at the same relative intensity as at sea level. The absolute decrease in GE found in the present study at 1500 m is of a comparable magnitude (-0.71 ± 0.6%) to the decrease in GE found by Noordhof et al.[6] (0.77 ± 1.1%). Multiple studies[2,11,12,24] have shown that the PO at which GE is determined influences GE. PO influences GE, because the relative contribution of the baseline energy expenditure becomes smaller as PO increases.[2] Ettema and Lorås[2] combined the data of several studies and concluded that 90% of the change in GE can be explained by PO. The data of the present study fits on this relationship between PO and GE. Participants performed submaximal exercise at 230 ± 20 W at sea level, 209 ± 24 W at 1500 m and 196 ± 16 W at 2500 m. According to the review of Ettema and Lorås[2] the decline in GE is ~0.7%, when PO drops from 230 W to 209 W and ~0.9% when PO drops from 230 W to 196 W, which corresponds to the decrease in GE found in the present study (-0.71 ± 0.6% at 1500 m and -1.2 ± 0.3% at 2500 m). Despite the fact that the effect of PO on GE diminishes above 150 W, it seems that the decrease in GE can be explained by the lower PO during exercise performed at the same relative exercise intensity.[2,11] The decreased PO as an explanation for the lower GE at altitude, is also supported by the GE data of the PO trials (see Figure 4). At the same PO no clear difference was found in GE between sea level and altitude, which suggests that altitude alone does not affect GE substantially. Comparable results were found in the study of Clark et al.[9]

[Insert Figure 4 about here]

The decrease in GE during a high-intensity exercise bout found in the present study is comparable to the findings from earlier studies. Noordhof et al.[14] also determined the difference in GE before and after a 4000-m time trial and found at sea level a decrease in GE of 1.7% when pre-GE and post1-GE were compared. The same magnitude decrease in GE was found in the current study during the trials performed at the same relative intensity (-2.0 ± 0.7%, -2.1 ± 1.0% and -2.0 ± 0.8% for sea level, 1500 m and 2500 m). the decrease in GE was smaller when exercise was performed at the same PO at altitude (-1.5 ± 0.6% and -1.1 ± 1.1% for 1500 m and 2500 m). Since PO remained constant between trials, it is unclear what caused these differences in the magnitude of decrease in GE. Several studies concluded that $\dot{V}O_2$ is similar at different altitudes when exercise is performed at the same PO.[3,4,9] A similar result was found in the present study; $\dot{V}O_2$ before the time trial (pre) was not different at altitude compared to sea level, when exercising at 2500 m . However, after the time trial there was a meaningful difference in $\dot{V}O_2$ at the same PO. At 1500 m and 2500 m $\dot{V}O_2$ increased between pre and post1 by 0.34 ± 0.13 $L \cdot min^{-1}$ and 0.21 ± 0.19 $L \cdot min^{-1}$, while at sea level there was a substantially larger increase in $\dot{V}O_2$ of 0.45 ± 0.13 $L \cdot min^{-1}$ between pre and post1. So, it seems that high-intensity exercise results in a difference in $\dot{V}O_2$ between sea level and altitude. A difference in $\dot{V}O_2$ during high-intensity exercise at altitude has been found in previous studies.[7,25] In Peltonen et al.[7] participants performed an exercise bout until exhaustion, which started at a submaximal exercise intensity and increased every five minutes by 100 W. At the lower submaximal exercise intensities there was no difference in $\dot{V}O_2$ between altitude and sea level, but at the higher exercise intensities, close to $\dot{V}O_{2max}$, there was a significant difference. The lower $\dot{V}O_2$ at altitude during a performance test at the same absolute PO is supported by the study of Romer et al.,[25] who found a decrease in $\dot{V}O_2$ during exercise performed at 92% $P\dot{V}O_{2max}$ until exhaustion. Especially at the end of the trial when participants were fatigued, the lower oxygen uptake at altitude became apparent. In the present study, cyclists were probably unable to increase $\dot{V}O_2$ after the time trial, because to increase $\dot{V}O_2$ in a similar degree between altitude and sea level some participants had to perform above 100% $\dot{V}O_{2max}$ when 0.45 $L \cdot min^{-1}$ was added to the $\dot{V}O_2$ of the pre-exercise bout. At 2500 m, 36% of the participants who met all the criteria of robust GE measurement and finished the final submaximal exercise bout this was the case. The number of participants (29%) who had to quit during the exercise bout after the time trial also supports the theory that participants performed at or close to their maximum capacity. In conclusion, the difference in relative intensity makes it hard to compare GE determined at the same absolute PO between sea level and 2500 m. In addition, multiple subjects were unable to finish this trial, which also complicated the data analysis.

Practical applications

PO delivered during cycling time trials at altitude is closer when considered at the same relative exercise intensity than the same absolute PO as at sea level. When a sport scientist or a coach wants to make a pacing plan or estimate the end time of a time trial at altitude, the lower GE at altitude needs to be taken into account. The lower GE for example affects the calculations to estimate the optimal altitude to perform the world hour record in track-cycling or speed skating. The lower GE during high-intensity exercise performed at altitude results in a lower optimal altitude for record performance.

Conclusions

The present study showed that GE was lower at altitude when cyclists were cycling at the same relative exercise intensity as at sea level. However, GE was not affected by altitude when the same absolute PO was produced. During a time trial athletes do not deliver the same absolute PO as at sea level, but perform closer to the same relative exercise intensity, which implies that GE is lower during time trials at altitude. In addition, it was shown that altitude resulted in an unclear effect on the decline in GE during time trial exercise when GE was determined at the same relative intensity. Finally, the effect of altitude on the decline in GE during time trial exercise, when GE is determined at the same power output, was considered substantially positive. However, this finding is most likely caused by the lower $\dot{V}O_2$.

References

1. Joyner MJ, Coyle EF. Endurance exercise performance: the physiology of champions: factors that make champions. *J Physiol.* 2008;586;35–44.
2. Ettema G, Lorås, HW. Efficiency in cycling: a review. *Eur J Appl Physiol.* 2009;106:1–14.
3. Wehrlin JP, Hallén J. Linear decrease in VO_{2max} and performance with increasing altitude in endurance athletes. *Eur J Appl Physiol.* 2006;96:404–412.
4. Katayama K, Goto K, Ishida K, Ogita F. Substrate utilization during exercise and recovery at moderate altitude. *Metabolism* 2010;59, 959–966.5.
5. Lawler J, Powers SK, Thompson D. Linear relationship between VO_{2max} and VO_{2max} decrement during exposure to acute hypoxia. *J Appl Physiol*. 1988;64:1486–1492.
6. Noordhof DA, Schoots T, Hoekert DH, de Koning JJ. Is gross efficiency lower at acute simulated altitude than at sea level? *Int J Sports Physiol Perform*. 2013;8:319–322
7. Peltonen JE, Tikkanen HO, Rusko HK. Cardiorespiratory responses to exercise in acute hypoxia, hyperoxia and normoxia. *Eur J Appl Physiol.* 2001;85:82–88.
8. Amann M, Pegelow DF, Jacques AJ, Dempsey JA. Inspiratory muscle work in acute hypoxia influences locomotor muscle fatigue and exercise performance of healthy humans. *AJP Regul Integr Comp Physiol.* 2007;293:R2036–R2045.
9. Clark SA, Bourdon PC, Schmidt W, et al. The effect of acute simulated moderate altitude on power, performance and pacing strategies in well-trained cyclists. *Eur J Appl Physiol.* 2007;102:45–55.
10. Schuler B, Thomsen JJ, Gassmann M, Lundby C. Timing the arrival at 2340 m altitude for aerobic performance: Performance and acclimatization to altitude. *Scand J Med Sci Sports* 2007;17:588–594.
11. de Koning JJ, Noordhof DA, Lucia A, Foster C. Factors affecting gross efficiency in cycling. *Int J Sports Med.* 2012;33:880–885.
12. Moseley L, Jeukendrup AE. The reliability of cycling efficiency. *Med Sci Sports Exerc.* 2001;33:621–627.
13. Niu W, Wu Y, Li B, Chen N, Song S. Effects of long-term acclimatization in lowlanders migrating to high altitude: comparison with high altitude residents. *Eur J Appl Physiol.* 1995;71:543–548.
14. Noordhof DA, Mulder RCM, Malterer KR, Foster C, de Koning JJ. The decline in gross efficiency in relation to cycling time-trial length. *Int J Sports Physiol Perform.* 2015;10:64–70.
15. de Koning JJ, Noordhof DA, Tom PU, Galiart RE, Dodge C, Foster C. An approach to estimating gross efficiency during high-intensity exercise. *Int J Sports Physiol Perform.* 2013;8:682–684.
16. Sahlin K, Sorensen J, Gladden L, Rositter H, Pedersen P. Prior heavy exercise eliminates VO_2 slow component and reduces efficiency during submaximal exercise in humans. *J Physiol.* 2005;564:765–773.
17. Grasaas CÅ, Ettema G, Hegge AM, Skovereng K, Sandbakk Ø. Changes in technique and efficiency after high-intensity exercise in cross-country skiers. *Int J Sports Physiol Perform.* 2014;9:19–24.

18. de Pauw KD, Roelands B, Cheung SS, de Geus B, Rietjens G, Meeusen R. Guidelines to classify subject groups in sport-science research. *Int J Sports Physiol Perform.* 2013;8:111–122.
19. Foster C, Schrager M, Snyder AC, Thompson NN. Pacing strategy and athletic performance*.* *Sports Med.* 1994;17:77–85.
20. Hopkins WG. Spreadsheets for analysis of controlled trials, with adjustment for a subject characteristic. *Sportsci.* 2006;10:46–50.
21. Hopkins WG, Hawley JA, Burke LM. Design and analysis of research on sport performance enhancement. *Med Sci Sports Exerc.* 1999;31:472-485.
22. Hickey MS, Costill DL, McConell GK, Widrick JJ, Tanaka H. Day to day variation in time trial cycling performance. *Int. J. Sports Med.* 1992;13:467–470.
23. Hopkins WG, Marshall SW, Batterham AM, Hanin J. Progressive statistics for studies in sports medicine and exercise science: *Med Sci Sports Exerc.* 2009;41:3–13.
24. Chavarren, J, Calbet JAL. Cycling efficiency and pedalling frequency in road cyclists. *Eur J Appl Physiol.* 1999;80:555–563.
25. Romer LM, Haverkamp HC, Amann M, Lovering AT, Pegelow DF, Dempsey JA. Effect of acute severe hypoxia on peripheral fatigue and endurance capacity in healthy humans. *AJP Regul Integr Comp Physiol.* 2006;292, R598–R606

Figure captions

Figure 1. Experimental protocol of the GE test. The dark grey shaded area represents the 4000-m time trial, the light gray shaded areas represent the three minute blocks over which data was averaged to calculate GE (pre, post1, post2, respectively). ft, finish time.

Figure 2. Gross efficiency values before and after the 4000-m time trial, determined at the same relative exercise intensity at sea level and altitude. Black squares, sea level; dark grey triangles, 1500 m; light grey diamonds, 2500 m.

Figure 3. Gross efficiency values before and after the 4000-m time trial, determined at the same absolute power output at sea level and altitude. Black squares, sea level; dark grey triangles, 1500 m; light grey diamonds, 2500 m.

Figure 4. Gross efficiency (pre) determined at the same absolute power output and the same relative exercise intensity. Black square, sea level; dark grey triangles, 1500 m; light grey diamonds, 2500 m.