## **ORIGINALIA**

Beneke R<sup>1</sup>, Leithäuser RM<sup>1</sup>

ACCEPTED: August 2017

PUBLISHED ONLINE: September 2017

DOI: 10.5960/dzsm.2017.296

Beneke R, Leithäuser RM. Energy Cost of Running Related to Running Intensity and Peak Oxygen Uptake. Dtsch Z Sportmed. 2017; 68: 196-202.

1. PHILIPPS UNIVERSITY MARBURG,
Department of Medicine, Training
and Health, Institute of Sports
Sciences and Motology, Marburg,
Germany

# **Energy Cost of Running Related to Running Intensity and Peak Oxygen Uptake**

Energieverbrauch beim Laufen in Abhängigkeit von Laufintensität und Peak-Sauerstoffaufnahme

#### Summary

- The hypotheses that a) a positive correlation between running oxygen uptake ( $\dot{V}O_{2\text{run}}$ ) and peak oxygen uptake ( $\dot{V}O_{2\text{peak}}$ ) is caused by a higher caloric equivalent and/or more reliance on anaerobic metabolic energy in subjects with lower  $\dot{V}O_{2\text{peak}}$  and that b) the energy cost per meter increases with relative intensity related to  $\dot{V}O_{2\text{neak}}$  were tested.
- > **Twenty-nine males** (mean±SD age: 24.4±2.7yrs; height: 179.0±5.6cm; bodymass: 74.5±6.8kg;  $\dot{VO}_{2peak}$ : 51.5±5.2mlkg  $^{\dagger}$ min  $^{\dagger}$ ) ran at 2.6 and 3.0m s  $^{\dagger}$ .  $\dot{VO}_{2run}$  oxygen uptake per meter distance ( $C_{vo2}$ ), energy cost per meter distance based on respiratory measures and indirect calorimetry ( $C_{AER}$ ), and net increase in blood lactate concentration ( $C_{ANAER}$ ), as well as total C ( $C_{TOT}$ = $C_{AER}$ + $C_{ANAER}$ ) were analyzed. Ad a)  $\dot{VO}_{2run}$  and  $C_{vo2}$  were positively, and  $C_{ANAER}$  negatively interrelated with  $\dot{VO}_{2peak}$  (all p<0.05).  $C_{TOT}$  was independent of  $\dot{VO}_{2peak}$ . Ad b)  $C_{vo2}$  was independent of relative intensity related to  $\dot{VO}_{2peak}$ , whilst  $C_{AER}$ .  $C_{ANAER}$  and  $C_{TOT}$  increased with relative intensity (all p<0.05).
- The frequently observed positive interrelationship between  $\dot{VO}_{2\text{run}}$  and  $\dot{VO}_{2\text{peak}}$  reflects less aerobic carbohydrate combustion and less reliance on anaerobic glycolysis in fitter subjects with higher  $\dot{VO}_{2\text{peak}}$ . Additionally, running economy decreases with increasing relative intensity.

## Zusammenfassung

- > **Die Hypothesen**, dass a) eine positive Korrelation zwischen Sauerstoffaufnahme beim Laufen ( $\dot{V}O_{2run}$ ) und der Peak-Sauerstoffaufnahme ( $\dot{V}O_{2peak}$ ) durch ein höheres kalorisches Äquivalent und/oder eine größere Abhängigkeit von anaerober metabolischer Energie bei Personen mit niedriger  $\dot{V}O_{2peak}$  verursacht wird und b) der Energieverbrauch pro Meter Laufstrecke mit relativer Intensität bezogen auf die  $\dot{V}O_{2peak}$  ansteigt, wurden getestet.
- > Neunundzwanzig Männer (Mittelwert±SD Alter: 24,4±2,7Jahrer; Größe: 179,0±5,6cm; Körpermasse: 74,5±6,8kg; VO $_{2peak}$ : 51,5±5,2ml kg $^1$  min $^1$ ) liefen mit Geschwindigkeiten von 2,6 und 3,0m s $^1$ . VO $_{2run}$ , der Sauerstoffverbrauch pro Meter (C $_{\rm Vo2}$ ), der Energieverbrauch pro Meter basierend auf respiratorischen Messgrößen und indirekter Kalorimetrie (C $_{\rm ARR}$ ), und Nettoanstieg der Blutlaktatkonzentration (C $_{\rm ANAER}$ ) sowie der Gesamtenergieverbrauch (C $_{\rm TOT}$ =C $_{\rm AER}$ +C $_{\rm ANAER}$ ) wurden analysiert. Zu Hypothese a) VO $_{\rm 2run}$  und C $_{\rm vo2}$  hingen positiv und C $_{\rm ANAER}$  negativ mit der VO $_{\rm 2peak}$ zusammen (alle p<0.05). C $_{\rm TOT}$  war unabhängig von der VO $_{\rm 2peak}$ . Zu Hypothese b) C $_{\rm vo2}$  war unabhängig von der relativen Intensität bezogen auf die VO $_{\rm 2peak}$ ; wohingegen C $_{\rm AER}$ , C $_{\rm ANAER}$  und C $_{\rm TOT}$  mit relativer Intensität zunahmen (alle p<0.05).
- Der häufig beobachtete positive Zusammenhang zwischen VO<sub>2run</sub> und VO<sub>2peak</sub> spiegelt eine geringere aerobe Kohlenhydratverwertung und eine geringere Abhängigkeit von anaerober Glykolyse bei fitteren Personen mit höherer VO<sub>2peak</sub> wider. Zusätzlich nimmt die Laufökonomie mit zunehmender relativer Intensität ab.

### **KEY WORDS:**

Terrestrial Locomotion, Human, Speed, Aerobic, Anaerobic

#### SCHLÜSSELWÖRTER:

Terrestrische Fortbewegung, Mensch, Geschwindigkeit, Aerob, Anaerob



Article incorporates the Creative Commons Attribution — Non Commercial License. https://creativecommons.org/licenses/by-nc-sa/4.0/



QR-Code scannen und Artikel online

#### CORRESPONDING ADDRESS

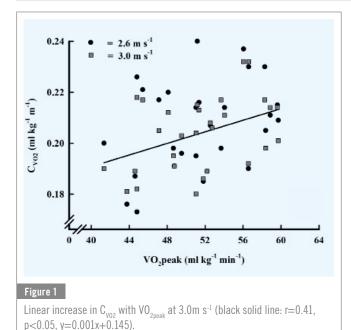
Prof. Dr. Ralph Beneke
Department of Medicine, Training and
Health, Institute of Sports Sciences and
Motology, Philipps University Marburg
Jahnstraße 12, 35037 Marburg, Germany

⇒: ralph.beneke@staff.uni-marburg.de

#### Introduction

Running performance of top class endurance athletes but also of recreational and non-specifically trained physically active individuals depends on the maximum aerobic metabolic rate and the energy cost of a unit of running distance (1, 5, 6, 7, 11, 12, 16, 29). There is evidence that elite runners have better running economy (RE) than good and less capable runners (13, 26), and that in untrained individuals RE improves if they take on running exercises (2).

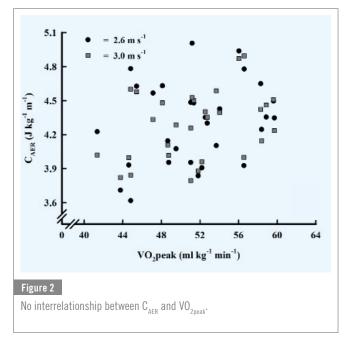
However, some other studies reported that RE is essentially the same in sedentary and athletic subjects (9, 11, 31) and independent of running velocity if air resistance can be neglected such as during running on the treadmill (11, 14, 18, 20, 21, 27). In contrast, other studies reported an increase in oxygen uptake ( $C_{\text{VO2}}$ ) or aerobic energy expenditure ( $C_{\text{AER}}$ ) per unit of running distance with increasing relative intensity (8, 13).



Peak oxygen uptake  $(\dot{VO}_{2peak})$  and oxygen uptake at given running velocities  $(\dot{VO}_{2run})$  are generally accepted measures of maximum aerobic metabolic rate and economy of exercise. Frequent reports that  $\dot{VO}_{2run}$  is positively correlated with  $\dot{VO}_{2peak}$  (13, 15, 19, 23, 25, 30) are at odds with the supposedly logical conclusion that the combination of high maximum aerobic metabolic rate and high RE is the best concept for best endurance running performance (2, 3, 11, 26, 28, 31, 33). Suggestions that among athletes with similar race performances a negative correlation between  $\dot{VO}_{2peak}$  and RE always reflects compensation of lower aerobic power by lower energy cost of a given task, is not fully convincing. Being the best athlete more likely combines high economy with high  $\dot{VO}_{2peak}$ . Attempts to explain the positive interrelationship between  $\dot{VO}_{2run}$  and  $\dot{VO}_{2peak}$  based on muscle fiber type and mitochondrial factors remained inconclusive (15, 25).

In previous studies analyzing the  $\dot{VO}_{2run}$  to  $\dot{VO}_{2peak}$  relationship in subjects with highly different VO<sub>2peak</sub>, the applied velocities in walking and running tests reflected substantially different relative intensities in the magnitude of between approximately 20 and above 90% of  $\dot{VO}_{2peak}$  (13, 25, 30). A consistent pattern of the  $\dot{VO}_{2\text{run}}$  to  $\dot{VO}_{2\text{peak}}$  interrelationship is that the correlation and regression coefficients become higher at velocities which reflect higher relative intensities (13, 30). Partly this may mirror differences in the respiratory exchange ratio (RER) between subjects with different  $\dot{VO}_{2peak}$ , which may vary the caloric equivalent and thus the metabolic energy per ml O<sub>2</sub> in favor of the less fit subjects (13). Additionally, the relative intensity at which anaerobic energy is required to perform, as indicated by an increase in the blood lactate concentration (BLC), is highly variable between subjects and independent of the absolute metabolic rate. Consequently, the higher correlation and regression coefficients of the  $\dot{VO}_{2run}$  to  $\dot{VO}_{2peak}$  relationship at the higher velocities may indicate that the less fit subjects had to rely on a higher fraction of carbohydrate combustion than the fitter subjects. Additionally, less fit subjects may rely to some extent on anaerobic energy shifting the metabolic demand from aerobic to partly anaerobic metabolism. These factors may result in utilizing less oxygen at a given metabolic cost of locomotion in less fitter subjects.

Therefore, we tested the hypotheses that a) the positive correlation between  $\dot{VO}_{2\text{run}}$  and  $\dot{VO}_{2\text{peak}}$  is caused by a higher reliance on carbohydrate utilization and/or anaerobic metabolic



energy in subjects with lower  $\dot{VO}_{\rm 2peak}$  and b) that RE in terms of the energy cost of a unit of running distance decreases with relative intensity if intensity related effects on carbohydrate and fat combustion, and anaerobic energy are considered.

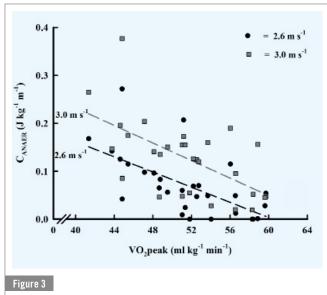
#### Methods

Twenty-nine male subjects (mean±SD age:  $24.4\pm2.7yrs$ ; height:  $179.0\pm5.6cm$ ; body mass:  $74.5\pm6.8kg$ ;  $\dot{VO}_{\rm 2peak}$ :  $51.5\pm5.2ml~kg^{-1}$  min<sup>-1</sup>) signed informed consent conforming to internationally accepted policy statements on the use of human subjects as approved by the local ethics committee. All participants were healthy and physically active but not specifically trained.

They performed an incremental running test on an electronically driven treadmill (Ergo XELG2, Woodway, Germany) in an air-conditioned room (21°C, 60% humidity). The test started with a 3min resting reference phase. The initial running velocity was set 2.2m s $^{-1}$ . The speed was increased stepwise by 0.4m s $^{-1}$  every 3min until exhaustion occurred. After each stage the running was interrupted for 30s for capillary blood sampling.

Respiratory gas exchange measures were taken continuously during the entire protocol (Oxycon Gamma, Mijnhard, Netherlands). The metabolic cart was calibrated using gases of known concentration and a syringe prior to each test. The breath-by-breath oxygen uptake data were reduced to stationary averages of the final 30s of each stage. Immediately before the start of a test, during each 30s break and after test-termination  $20\mu l$  capillary blood was drawn from the hyperemic earlobe (Finalgon\*, Thomae, Boehringer, Ingelheim, Germany) for the analysis of the BLC (Ebio plus, Eppendorf, Hamburg, Germany). The net lactate concentration ( $\Delta BLC$ ) was calculated as the difference between pre- and post-run at each running velocity.

RE at 2.6 and 3.0m s<sup>-1</sup> were analyzed in terms of:  $\dot{VO}_{2\text{run}}$ ,  $C_{VO2}$ ,  $C_{AER}$ , total energy cost above rest ( $C_{TOT}$ ) calculated via  $C_{AER}$  plus anaerobic glycolytic energy per meter running distance ( $C_{ANAER}$ ). Resting  $\dot{VO}_2$  can hardly be measured correctly pre-testing which never fulfills conditions of true rest. These are defined as measurements in the morning, fasting and at indifferent temperature. Pre-testing conditions always include pre-test activities and excitement. Therefore, resting was defined as standing still and set as a  $\dot{VO}_2$  of 4.5ml kg<sup>-1</sup> min<sup>-1</sup>, which reflects standing still in males (4).



Linear decrease in C  $_{\tt ANAER}$  with VO  $_{\tt 2peak}$  at 2.6m s $^{-1}$  (black dashed line: r=0.62, p<0.001, y=-0.008x+0.48) and at 3.0m s $^{-1}$  (dark gray dashed line: r=0.60, p<0.001, y=-0.009x+0.60).

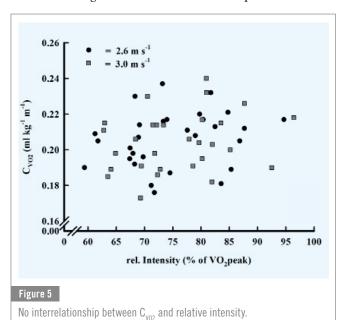
$$\begin{split} &C_{_{AER}},C_{_{ANAER}} \text{ and } C_{_{TOT}} \text{ were calculated by Eq.1, 2 and 3:} \\ &Eq.1: \quad C_{_{AER}}[J\,kg^{^1}\,m^{^{-1}}] = &(\dot{V}O_{_{2run}}\text{-resting }\dot{V}O_{_2})\,[ml\,s^{^{-1}}]\,\text{caloric equivalent }[J\,ml^{^{-1}}]\,\text{body mass}^{^{-1}}\,[kg^{^{-1}}]\,\text{speed}^{^{-1}}[s\,m^{^{-1}}],\\ \text{where the caloric equivalent was adjusted to the RER (32). A RER above 1.0, which clearly indicate respiratory compensation of a metabolic acidosis, was set 1.0 (2).} \end{split}$$

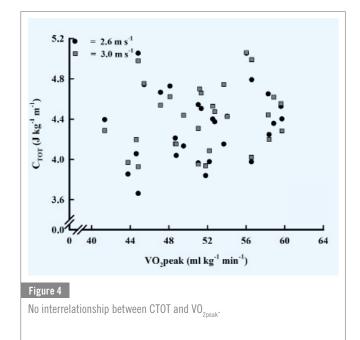
 $\begin{array}{ll} \mbox{Eq.2:} & \mbox{$C_{ANAER}$} \mbox{ [J $kg^1$ $m^{-1}$] = $\Delta BLC$ [mmol $l^1$] $O_2$-lactate equivalent [ml mmol^1 l $kg^1$] $21.131$ [J ml^1] running time $^{-1}$ [s^1] \\ & \mbox{speed} $^{-1}$ [s m^1], \end{array}$ 

where an  $\rm O_2$ -lactate equivalent of 3.0ml mmol<sup>-1</sup> l kg<sup>-1</sup> was used, which is compatible to a distribution space of lactate of approximately 45% of the body mass (2, 10); the factor 21.131 reflects the caloric equivalent of carbohydrate oxidation (2).

$$\label{eq:equation:eq:continuous} \text{Eq.3:} \qquad \text{$C_{_{TOT}}\left[J\,kg^{_{}^{-1}}\,m^{_{}^{-1}}\right] = C_{_{AER}}\left[J\,kg^{_{}^{-1}}\,m^{_{}^{-1}}\right] + C_{_{ANAER}}\left[J\,kg^{_{}^{-1}}\,m^{_{}^{-1}}\right]$.}$$

All results are described as mean±SD. Differences between running velocities were tested via repeated measure





ANOVA and Bonferroni post hoc test and effect sizes, in the form of partial eta squared ( $\eta^2$ ), were calculated. Linear and non-linear regression models were used to identify significant interrelationships between measures of running economy at given running velocities and  $\dot{VO}_{2peak}$  or relative intensity. The goodness of fits of different regression models were compared using the F-test (24). For all statistics the significance was set at P<0.05.

## Results

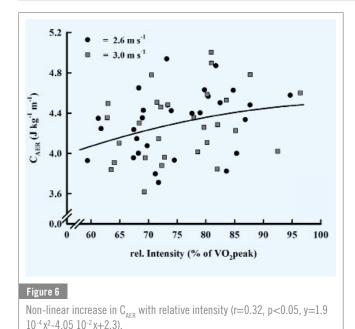
The  $\dot{VO}_{2run}$  at 2.6 and 3.0m s<sup>-1</sup> running reflected 71±8% and 80±8% of the  $\dot{VO}_{2peak}$ , respectively. There were significant main effects and medium to large effect sizes for running velocity in  $\dot{VO}_{2run}$ , BLC, RER,  $C_{\dot{VO2}}$ ,  $C_{AER}$ ,  $C_{ANAER}$  and  $C_{TOT}$ . Significant pair differences were confirmed in  $\dot{VO}_{2run}$ , BLC, RER and  $C_{ANAER}$  in terms of increases from 2.6 to 3.0m s<sup>-1</sup>. Furthermore,  $\dot{VO}_{2run}$ , BLC, RER and  $C_{ANAER}$  were lower at 2.6 and 3.0m s<sup>-1</sup> than at peak velocity whilst  $C_{\dot{VO2}}$  was lower at peak velocity than at 2.6 and 3.0m s<sup>-1</sup> (p<0.05; Tab.1).

At 3.0m s<sup>-1</sup>, VO $_{\rm 2run}$  (r=0.41, p<0.05, y=0.21x+30.0) as well as C $_{\rm VO2}$  were positively interrelated with VO $_{\rm 2peak}$  (Fig. 1). Irrespective of running speed, C $_{\rm AER}$  was independent of VO $_{\rm 2peak}$  (Fig. 2). C $_{\rm ANAER}$  was negatively interrelated with VO $_{\rm 2peak}$  at both given velocities (Fig. 3). C $_{\rm TOT}$  was independent of VO $_{\rm 2peak}$  (Fig. 4).

 $\rm C_{_{
m VO2}}$  was independent of relative intensity related to  $\rm \dot{VO}_{_{2peak}}$  (Fig. 5). A quadratic function best described (p<0.01) the positive interrelationship between  $\rm C_{_{AER}}$  and  $\rm C_{_{ANAER}}$ , and relative intensity which flattens in  $\rm C_{_{AER}}$  and increases progressively in  $\rm C_{_{ANAER}}$  (Fig. 6 and 7). The latter results in an interrelation between  $\rm C_{_{TOT}}$  and relative intensity which was best described by a linear fit (Fig. 8).

#### Discussion

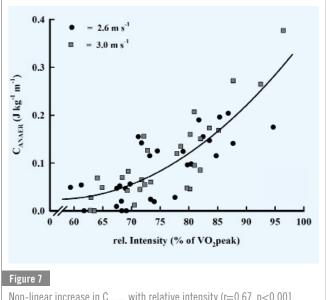
The main findings of the present study were a) that below peak running velocity,  $C_{\text{TOT}}$  is independent of  $\dot{VO}_{\text{2peak}}$  and b) that  $C_{\text{TOT}}$  increases with relative intensity related to  $\dot{VO}_{\text{2peak}}$ . Consequently the results support the hypothesis a) that the positive correlation between  $\dot{VO}_{\text{2run}}$  and  $\dot{VO}_{\text{2peak}}$  at given speeds is caused by the higher reliance on carbohydrate oxidation plus anaerobic me-



tabolic energy in subjects with lower  $\dot{VO}_{2\rm peak}$ . They also support the hypothesis b) that RE decreases with increasing relative intensity.

The present results clearly support but also extent recent suggestions that measuring RE in terms of  $C_{_{\! AER}}$  or  $C_{_{\! TOT}}$  is more appropriate than expressing RE as  $\dot{VO}_{2run}$  or  $C_{\dot{V}O2}$  (13). They also indicate that previous reports that  $\dot{VO}_{2run}$  was positively correlated with  $\dot{VO}_{2peak}$ , which becomes more obvious at higher running velocities and/or mechanical power and thus relative intensity (13, 15, 23, 25, 30), do not contradict the conclusion that a combination of high maximum aerobic metabolic rate and high RE is the best concept for a most successful endurance running performance (2, 3, 11, 26, 28, 31). However, they challenge suggestions that among athletes with similar race performances a positive correlation between  $\dot{VO}_{\rm 2peak}$  and  $\dot{VO}_{\rm 2run}$ always reflects compensation of lower aerobic power by less energy cost of a given task. The previously reported higher  $\dot{VO}_{2run}$  in athletes with higher  $\dot{VO}_{2peak}$  does not necessarily reflect lower RE. Alternatively it may indicate lower reliance on carbohydrate utilization and/or anaerobic energy. The positive interrelationship between  $\dot{VO}_{2run}$  and  $\dot{VO}_{2reak}$  does not require specific muscle fiber compositions or mitochondrial factors (15, 25). However, differences in the metabolic profile of slow- and fast-twitch muscle fibers may strongly contribute to a higher  $\dot{VO}_{2neak}$  in athletes with extremely high fractions of slow-twitch fibers. This allows less reliance on carbohydrate combustion and anaerobic energy including a reduced maximum glycolytic rate. These factors increase  $\dot{VO}_{2\mathrm{run}}$  and  $C_{\dot{V}O2}$  (Fig. 1). No corresponding interrelation between  $C_{AER}$  and  $\dot{VO}_{2peak}$  may reflect that higher  $\dot{VO}_{2run}$  and  $C_{\dot{VO}2}$  indicate either a higher lipid oxidation rate at a given C<sub>AER</sub> (identical RE) or even lower C<sub>AER</sub> (higher RE) and/or an increased  $C_{AER}$  (lower RE). Irrespective of RE the combination of higher  $\dot{V}O_{2peak}$  and reduced maximum glycolytic rate results in a lower  $C_{ANAER}$  (Fig. 3). On aggregate,  $C_{TOT}$ , the combination of all above effects, is independent of  $\dot{V}O_{\rm 2peak}$  and highly variable between individual subjects (Fig. 4).

Whilst considering for effects of aerobic substrate utilization, a potential contribution of anaerobic energy remains undetected when calculating  $\mathbf{C}_{\text{AER}}$  based on respiratory data only. The present findings clearly demonstrate that within the given range of the RER the aerobic fitness related effect on

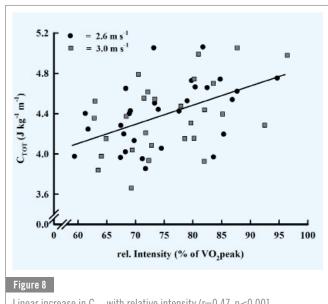


Non-linear increase in C  $_{\rm ANAER}$  with relative intensity (r=0.67, p<0.001, y=1.8  $10^{-4}\,x^2$ -2.010  $^{-2}\,x$ +0.6).

relative reliance of carbohydrate does not fully compensate for the underestimation of the energy cost of running based on  $\dot{V}O_{2\mathrm{run}}$  and  $C_{\dot{V}O_2}$  related to  $\dot{V}O_{2\mathrm{peak}}$  in less fit subjects (Fig. 1). The effect of changes of the caloric equivalent on  $C_{\mathrm{TOT}}$  was less than half the magnitude of that of  $C_{\mathrm{ANAER}}$ .

No interrelationship between C $_{\dot{v}02}$  and relative intensity (Fig. 5) was highly confirmatory of previous findings (11, 14, 18, 20, 21, 22, 27). However, in conjunction with growing evidence of an interrelationship between both C $_{\rm AER}$  and C $_{\rm TOT}$  and relative intensity (2, 9, 13; Fig. 6, 7 and 8) the independence between C $_{\dot{v}02}$  and relative intensity also indicates that purely  $\dot{V}O_{\rm 2run}$  based estimations of the energy cost of running may substantially underestimate the real metabolic cost at higher exercise intensities (Fig. 8).

This underestimation gets even more evident at peak velocity where  $C_{\dot{v}02}$  suggests a slight but significant increase in RE in the magnitude of 2 to 3% which at RER <1.0 is similar to that in  $C_{AER}$ . The latter clearly indicates that analyses of RE do not only require consideration of changes in the caloric equivalent



Linear increase in  $C_{TOT}$  with relative intensity (r=0.47, p<0.001, y=0.019x+3.0)

#### Table 1

Metabolic measures and corresponding energy costs per meter running (p-value and partial eta of main effects; a=Significant pair difference with 2.6m s<sup>-1</sup>, b=Significant pair difference with 3.0m s<sup>-1</sup>).

	2.6 M S <sup>-1</sup> (MEAN±SD)	3.0 M S <sup>-1</sup> (MEAN±SD)	PEAK (MEAN±SD)	SIG.	η²
VO <sub>2run</sub> (ml kg <sup>-1</sup> min <sup>-1</sup> )	36.3±2.7	40.7±2.6a	51.5±5.2a,b	<0.001	0.885
BLC (mmol I <sup>-1</sup> )	2.4±0.9	3.5±1.4a	9.8±2.3a,b	<0.001	0.891
RER	$0.94 \pm 0.05$	0.99±0.06a	1.11±0.04a,b	<0.001	0.856
C <sub>v02</sub> (ml kg <sup>-1</sup> m <sup>-1</sup> )	0.207±0.017	0.204±0.014	$0.198 \pm 0.014$ a,b	< 0.01	0.251
C <sub>AER</sub> (J kg <sup>-1</sup> m <sup>-1</sup> )	4.306±0.364	4.287±0.301	4.189±0.292	< 0.05	0.132
C <sub>ANAER</sub> (J kg <sup>-1</sup> m <sup>-1</sup> )	0.071±0.066	0.127±0.080a	0.319±0.082a,b	< 0.001	0.821
C <sub>TOT</sub> (J kg <sup>-1</sup> m <sup>-1</sup> )	4.377±0.387	4.414±0.327	4.507±0.283	<0.05	0.116

but also the potential use of anaerobic energy to prevent potentially substantial overestimations of RE at running velocities causing an increase in the BLC. In the present study at peak velocity the increase of  $C_{\rm ANAER}$  is approximately 2 and 2.5 times as high as the above mentioned decreases in  $C_{\rm \acute{V}O2}$  and  $C_{\rm AER}$  compared to 2.6 and 3.0m s $^{-1}$ , respectively. The latter furthermore stresses that estimations of the anaerobic fraction of energy required for a given performance based on estimations of the accumulated oxygen deficit (17) is likely to result in substantial underestimations of  $C_{\rm ANAER}$ .

In conclusion,  $C_{\text{TOT}}$  including  $C_{\text{AER}}$  plus  $C_{\text{ANAER}}$  is independent of  $\dot{VO}_{\text{2peak}}$ . The consistently observed positive interrelationships between  $\dot{VO}_{\text{2run}}$  and  $\dot{VO}_{\text{2peak}}$  as well as  $C_{\dot{VO}2}$  and  $\dot{VO}_{\text{2peak}}$  reflect less reliance on aerobic carbohydrate combustion and anaerobic glycolysis in fitter subjects with a higher  $\dot{VO}_{\text{2peak}}$ . Frequent observations of no interrelationship between  $C_{\dot{VO}2}$  and relative intensity do not support independence of RE and running velocity. The non-linear increases of  $C_{\text{AER}}$  and  $C_{\text{ANAER}}$  with the relative intensity are degressive (Fig. 6) and progressive (Fig. 7), respectively. In combination, these nonlinear increases resulted in a linear intensity related increase of  $C_{\text{TOT}}$  (Fig. 8).

## **Conflict of Interest**

The authors have no conflict of interest.

#### References

- (1) ABE D, YANAGAWA K, YAMANOBE K, TAMURA K. Assessment of middle distance running performance in sub-elite young runners using energy cost of running. Eur J Appl Physiol Occup Physiol. 1998; 77: 320-325. doi:10.1007/s004210050340
- (2) BENEKE R, HÜTLER M. The effect of training on running economy and performance in recreational athletes. Med Sci Sports Exerc. 2005; 37: 1794-1799. doi:10.1249/01.mss.0000176399.67121.02
- (3) BILLAT V, LEPRETRE PM, HEUGAS AM, LAURENCE MH, SALIM D, KORALSZTEIN JP. Training and bioenergetic characteristics in elite male and female Kenyan runners. Med Sci Sports Exerc. 2003; 35: 297-304. doi:10.1249/01.MSS.0000053556.59992.A9
- (4) GEIGY C. Wissenschaftliche Tabellen Geigy Teilband Körperflüssigkeiten. (Scientific Tables Geigy, Volume Body Fluids.) Ciba Geigy, Basel; 1985: 225-28.
- (5) COETZER P, NOAKES TD, SANDERS B, LAMBERT MI, BOSCH AN, WIGGINS T, DENNIS SC. Superior fatigue resistance of elite black South African distance runners. J Appl Physiol. 1993; 75: 1822-1827.
- (6) CONLEY DL, KRAHENBUHL GS. Running economy and distance running performance of highly trained athletes. Med Sci Sports Exerc. 1980; 12: 357-360. doi:10.1249/00005768-198025000-00010
- (7) COSTILL DL, WINROW E. Maximal oxygen intake among marathon runners. Arch Phys Med Rehabil. 1970; 51: 317-320.
- (8) DANIELS J, DANIELS N. Running economy of elite male and elite female runners. Med Sci Sports Exerc. 1992; 24: 483-489. doi:10.1249/00005768-199204000-00015
- (9) DILL DB. Oxygen used in horizontal and grade walking and running on the treadmill. J Appl Physiol. 1965; 20: 19-22.
- (10) DI PRAMPERO PE. Energetics of muscular exercise. Rev Physiol Biochem Pharmacol. 1981; 89: 143-222. doi:10.1007/BFb0035266
- (11) DI PRAMPERO PE. The energy cost of human locomotion on land and in water. Int J Sports Med. 1986; 07: 55-72. doi:10.1055/s-2008-1025736
- (12) DI PRAMPERO PE, CAPELLI C, PAGLIARO P, ANTONUTTO G, GIRARDIS M, ZAMPARO P, SOULE RG. Energetics of best performances in middledistance running. J Appl Physiol. 1993; 74: 2318-2324.
- (13) FLETCHER JR, ESAU SP, MACINTOSH BR. Economy of running: beyond the measurement of oxygen uptake. J Appl Physiol. 2009; 107: 1918–22. First published October 15, 2009
- (14) HAGBERG JM, COYLE EF. Physiological comparison of competitive race walking and running. Int J Sports Med. 1984; 05: 74-77. doi:10.1055/s-2008-1025883
- (15) HUNTER GR, BAMMAN MM, LARSON-MEYER DE, JOANISSE DR, MCCARTHY JP, BLAUDEAU TE, NEWCOMER BR. Inverse relationship between exercise economy and oxidative capacity in muscle. Eur J Appl Physiol. 2005; 94: 558-568. doi:10.1007/s00421-005-1370-z
- (16) JONES AM, CARTER H. The effect of endurance training on parameters of aerobic fitness. Sports Med. 2000; 29: 373-386. doi:10.2165/00007256-200029060-00001
- (17) KEIR DA, ZORY R, BOUDREAU-LARIVIÈRE C, SERRESSE O. Running exercise: Effect of anaerobic-energy contribution at various speeds. Int J Sports Physiol Perform. 2012; 7: 382-389. doi:10.1123/ijspp.7.4.382
- (18) KNUTTGEN HG. Oxygen uptake and pulse rate while running with undertermined and determined stride lengths at different speeds. Acta Physiol Scand. 1961; 52: 366-371. doi:10.1111/j.1748-1716.1961.tb02232.x

- (19) LUCIA A, ESTEVE-LANAO J, OLIVAN J, GOMEZ-GALLEGO F, SAN JUAN AF, SANTIAGO C, PEREZ M, CHAMORRO-VINA C, FOSTER C. Physiological characteristics of the best Eritrean runners-exceptional running economy. Appl Physiol Nutr Metab. 2006; 31: 530-540. doi:10.1139/h06-029
- (20) MARGARIA R, CERRETELLI P, AGHEMO P, SASSI G. Energy cost of running. J Appl Physiol. 1963; 18: 367-370.
- (21) MCMIKEN DF, DANIELS JT. Aerobic requirements and maximum aerobic power in treadmill and track running. Med Sci Sports. 1976: 8: 14-17.
- (22) MENIER DR, PUGH LGCE. The relation of oxygen intake and velocity of walking and running in competition walkers. J Physiol. 1968; 197: 717-721. doi:10.1113/jphysiol.1968.sp008584
- (23) MORGAN DW, DANIELS JT. Relationship between VO2max and the aerobic demand of running in elite distance runners. Int J Sports Med. 1994; 15: 426-429. doi:10.1055/s-2007-1021082
- (24) MOTULSKY HJ, RANSNAS LA. Fitting curves to data using nonlinear regression: a practical and nonmathematical review. FASEB J. 1987; 1: 365-374.
- (25) PATE RR, MACERA CA, BAILEY SP, BARTOLI WP, POWELL KE.
  Physiological, anthropometric, and training correlates of
  running economy. Med Sci Sports Exerc. 1992; 24: 1128-1133.
  doi:10.1249/00005768-199210000-00010
- (26) POLLOCK ML. Submaximal and maximal working capacity of elite distance runners. I. Cardiorespiratory aspects. Ann N Y Acad Sci. 1977; 301: 310-322. doi:10.1111/j.1749-6632.1977.tb38209.x
- (27) PUGH LGCE. Oxygen intake in track and treadmill running with observations on the effects of air resistance. J Physiol. 1970; 207: 823-835. doi:10.1113/jphysiol.1970.sp009097
- (28) SALTIN B, LARSEN H, TERRADOS N, BANGSBO J, BAK T, KIM CK, SVEDENHAG J, ROLF GJ. Aerobic exercise capacity at sea level and at altitude in Kenyan boys, junior and senior runners compared with Scandinavian runners. Scand J Med Sci Sports. 1995; 5: 209-221. doi:10.1111/j.1600-0838.1995.tb00037.x
- (29) SAUNDERS PU, PYNE DB, TELFORD RD, HAWLEY JA. Factors affecting running economy in trained distance runners. Sports Med. 2004; 34: 465-485. doi:10.2165/00007256-200434070-00005
- (30) SAWYER BJ, BLESSINGER JR, IRVING BA, WELTMAN A, PATRIE JT, GAESSER GA. Walking and running economy: inverse association with peak oxygen uptake. Med Sci Sports Exerc. 2010; 42: 2122-2127.
- (31) SLAWINSKI JS, BILLAT VL. Difference in mechanical and energy cost between highly, well and non-trained runners. Med Sci Sports Exerc. 2004; 36: 1440-1446. doi:10.1249/01. MSS.0000135785.68760.96
- (32) STEGEMENN J. Leistungsphysiologie: physiologische Grundlagen der Arbeit und des Sports. 4. überarb. Aufl. Stuttgart, New York, Thieme, 1991; pp. 65-60
- (33) WESTON AR, MBAMBO Z, MYBURGH KH. Running economy of African and Caucasian distance runners. Med Sci Sports Exerc. 2000; 32: 1130-1134. doi:10.1097/00005768-200006000-00015