

REVIEW

Open Access

Running economy: measurement, norms, and determining factors

Kyle R Barnes^{1,2*} and Andrew E Kilding¹

Abstract

Running economy (RE) is considered an important physiological measure for endurance athletes, especially distance runners. This review considers 1) how RE is defined and measured and 2) physiological and biomechanical factors that determine or influence RE. It is difficult to accurately ascertain what is good, average, and poor RE between athletes and studies due to variation in protocols, gas-analysis systems, and data averaging techniques. However, representative RE values for different caliber of male and female runners can be identified from existing literature with mostly clear delineations in oxygen uptake across a range of speeds in moderately and highly trained and elite runners. Despite being simple to measure and acceptably reliable, it is evident that RE is a complex, multifactorial concept that reflects the integrated composite of a variety of metabolic, cardiorespiratory, biomechanical and neuromuscular characteristics that are unique to the individual. Metabolic efficiency refers to the utilization of available energy to facilitate optimal performance, whereas cardiopulmonary efficiency refers to a reduced work output for the processes related to oxygen transport and utilization. Biomechanical and neuromuscular characteristics refer to the interaction between the neural and musculoskeletal systems and their ability to convert power output into translocation and therefore performance. Of the numerous metabolic, cardiopulmonary, biomechanical and neuromuscular characteristics contributing to RE, many of these are able to adapt through training or other interventions resulting in improved RE.

Key points

- Running economy is a complex, multifactorial concept that represents the sum of various metabolic, cardiorespiratory, biomechanical and neuromuscular characteristics during submaximal running.
- Many of the determining factors of running economy are able to adapt through training or other interventions, however an economical change in one athlete may be uneconomical in another athlete because of differences in other physiological or biomechanical characteristics.
- Representative running economy values for different caliber of runners running at various speeds are presented.

Introduction

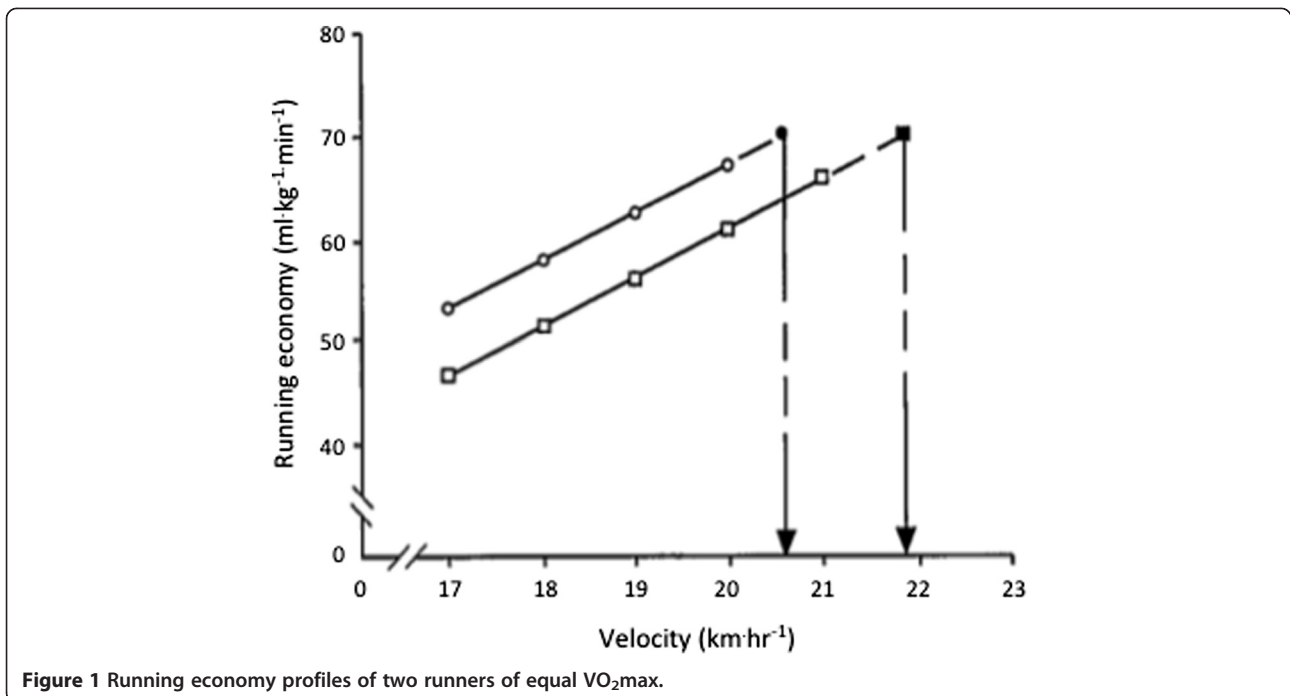
The steady-state oxygen consumption (VO_2) at a given running velocity, which is often referred to as running economy (RE) [1-3], reflects the energy demand of running at a constant submaximal speed. Runners with good economy use less oxygen than runners with poor economy at the same steady-state speed (Figure 1) [4]. It has been reported that RE can vary by as much as 30% among trained runners with similar VO_{2max} [2]. Running economy has also been shown to be a useful predictor of endurance running performance [1,2,5-8] especially in athletes who are homogenous with respect to VO_{2max} (Figure 1) [1,6,9].

While the measurement of RE is often perceived as a simple concept, it is actually a multifactorial measure which reflects the combined functioning of the metabolic, cardiopulmonary, biomechanical and neuromuscular systems (Figure 2) [2,3,5,10]. Metabolic efficiency refers to the utilization of available energy to facilitate optimal performance [2,3], whereas cardiopulmonary efficiency refers to a reduced work output for the processes related to oxygen transport and utilization. Lastly, neuromuscular and biomechanical characteristics refer to the interaction between the neural and musculoskeletal systems and their

* Correspondence: kyle.barnes@yahoo.com

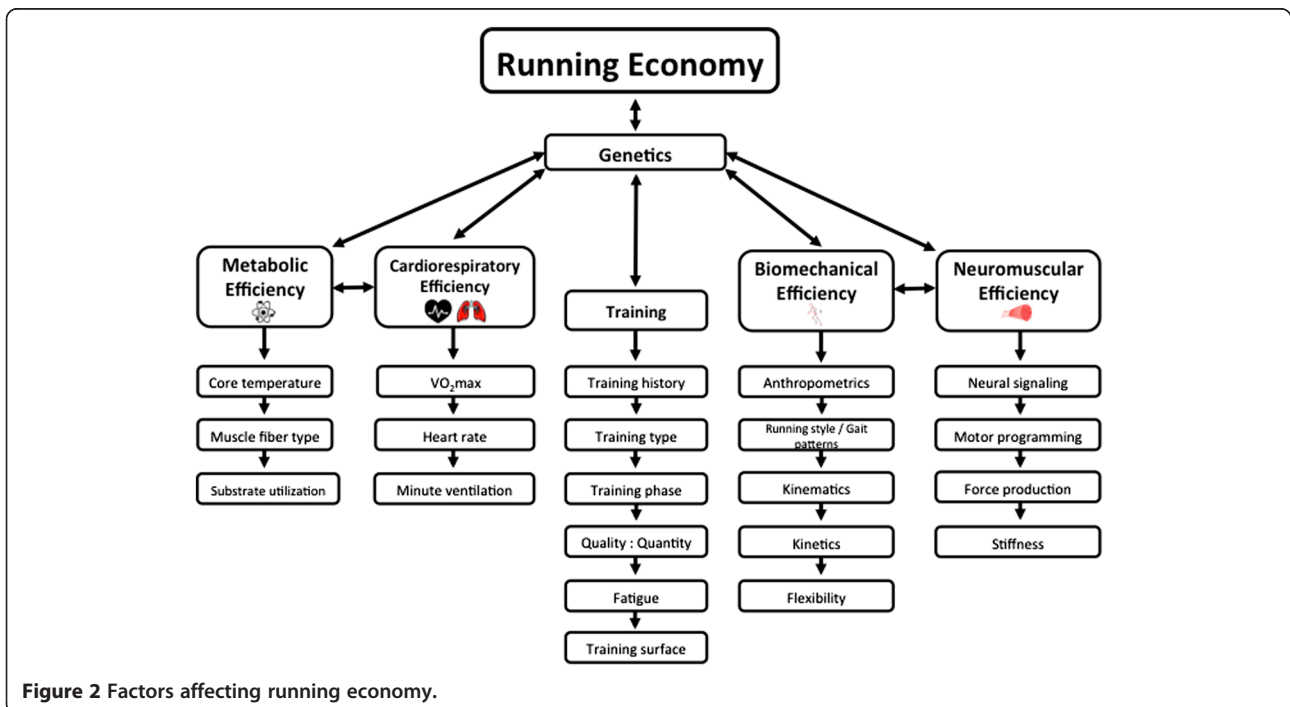
¹Sports Performance Research Institute New Zealand, AUT University, Auckland, New Zealand

²Department of Movement Science, Grand Valley State University, Allendale, Michigan, USA



ability to convert power output into translocation and therefore performance [5]. The multifaceted concept of RE, with multiple types of efficiency (that is, accounting for the work done and energy lost) may be intuitively understood by scientists, practitioners and coaches, nonetheless it has yet to be defined or discussed in great detail in the literature. The heritability of genetic traits is no doubt the prevailing factor affecting RE (Figure 2),

however at the moment, there is limited research examining specific genotypes related to better economy [11,12]. Furthermore, many of these factors are modifiable through various training modalities (Figure 2). Therefore RE is an important measure for coaches, athletes and practitioners to understand, quantify and attempt to enhance. The purpose of this review is to 1) examine and review how RE is defined and measured and 2)



consider the metabolic, cardiorespiratory, biomechanical, and neuromuscular components that determine RE.

Defining and measuring running economy

Defining running economy

Work economy for a given task has emerged as a measurement which is both conceptually clear and practically useful for the evaluation of endurance activities and has become almost universally accepted as the physiological criterion for 'efficient' performance [13]. Despite this, there is a discrepancy over the term RE and its definition. Conley and Krahenbuhl (1980) define economy as submaximal oxygen consumption ($VO_{2\text{submax}}$) [1]. Williams (1985) refers to $VO_{2\text{submax}}$ for a given task as the "physiological efficiency" and Goldspink (1977) claims that economy usually refers to muscle efficiency [7,14]. According to Taylor [15] muscles produce economic force rather than efficient work during running. Efficiency refers to the ratio of work done to energy expended, and thus the terms "efficient" and "efficiency" should *not* be used to relate the energy demands of running to velocity of running because running velocity represent only part of the work being performed by the body while it is transported from one point to another [2]. Other terms such as "cost," "oxygen cost," "energy cost," and "requirement" have all found their way into the literature as ways of describing the relationship between oxygen consumption (VO_2) and running velocity [2]. The energy cost of running reflects the sum of both aerobic and anaerobic metabolism, and the aerobic demand, measured by the VO_2 in $L\cdot\text{min}^{-1}$ at a given speed does not necessarily account for the energy cost of running, which is measured in joules, kilojoules, calories or kilocalories of work done [2,3,16].

Running economy is represented by the energy demand for a given velocity of submaximal running and expressed as the submaximal VO_2 at a given running velocity [1-3]. This value reflects gross or total economy; a measurement that represents the metabolic, cardiorespiratory, biomechanical and neuromuscular components of running without consideration for what portion of that VO_2 is a function of good or bad mechanics as opposed to being related to differences in metabolism or force production which may exist in different athletes or under different conditions [2,5,10]. Accordingly, the measure of RE may be flawed as it is determined by multiple variables that may or may not be based on oxygen consumption alone, nevertheless, having an understanding of the underlying idea of RE provides insight into the complexity of this measurement. Still being able to describe the VO_2 related to a particular velocity of running provides a useful way of comparing individuals, or any individual with him or herself under various conditions, and this VO_2 gives a measure of *running economy*.

2.2 Measuring and expressing running economy

The standard approach to quantifying RE involves measuring VO_2 while running on a treadmill at various constant speeds for a duration long enough to achieve physiological steady-state. Typically, durations of 3 to 15 min have been used in studies if the speed is below the ventilatory/lactate threshold [8], since above this intensity, a slow component of VO_2 is evident [17]. Often, the steady-state condition is verified by considering other physiological parameters such as verifying that blood lactate concentration are similar to baseline levels [18] and the respiratory exchange ratio (RER) is <1 [1]. Comparisons between individuals RE are traditionally made by interpolating the VO_2 to a common running velocity and expressing RE relative to body mass per minute ($\text{ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) or by the total volume of oxygen needed to run one kilometer relative to body mass ($\text{ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) [19]. The most commonly used reference velocity is $16\text{ km}\cdot\text{hr}^{-1}$ ($268\text{ m}\cdot\text{min}^{-1} = 4.47\text{ m}\cdot\text{s}^{-1}$), which represents 6 minutes per mile, or 3 min 44 sec per km, however, velocities from 12 to $21\text{ km}\cdot\text{hr}^{-1}$ appear in the literature [1,3,6,20-32]. In running, however, allometric scaling to the power of 0.67 or 0.75 (e.g. $\text{ml}\cdot\text{kg}^{-0.67}\cdot\text{min}^{-1}$ or $\text{ml}\cdot\text{kg}^{-0.75}\cdot\text{min}^{-1}$) has also been reported in order to compare RE between individuals and animals with varying body mass [22,33-47]. However, assessing RE by simply measuring VO_2 does not take into account differences in substrate use at any given running speed, therefore some studies have expressed RE as the caloric unit cost ($\text{kcal}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) [16,48-51].

Normative data

From studies to date it is difficult to accurately ascertain what is good, average, and poor RE due to variation in protocols, gas-analysis equipment, data averaging techniques and differences in maximal aerobic capacity. However, acknowledging these potential limitations, representative VO_2 values for different caliber of runners from the existing literature are presented in Table 1. The lowest reported value for VO_2 at $16\text{ km}\cdot\text{hr}^{-1}$ is $39.0\text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ in an individual East African runner, capable of running 1500 m in 3:35 with a $VO_{2\text{max}}$ of only $63\text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ [19]. However, the current Men's Half Marathon World Record holder's (Tadese Zerisenay, 58 min 23 s; $VO_{2\text{max}} = 83.0\text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) RE was measured at $150\text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ at $19\text{ km}\cdot\text{hr}^{-1}$ ($317\text{ m}\cdot\text{min}^{-1}$) which is equivalent to $40.0\text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ at $16\text{ km}\cdot\text{hr}^{-1}$ or 48.2% relative intensity of effort compared to 61.9% of the aforementioned athletes $VO_{2\text{max}}$ [26]. The concept of relative intensity is an important one because trained runners all perform at near equal percentages of their respective $VO_{2\text{max}}$ depending on the distance of the event in question (Figure 3) [22,52]. Other examples of exceptional RE include Paula Radcliffe (Women's Marathon World Record holder, 2 hr 15 min 25 s; $VO_{2\text{max}} = 75.0\text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$)

Table 1 Normative running economy data for male and female runners of varying ability levels

Runner classification	Speed (km·hr ⁻¹)	Male mean (range)		Female mean (range)	
		Running economy (ml·kg ⁻¹ ·min ⁻¹)	VO ₂ max (ml·kg ⁻¹ ·min ⁻¹)	Running economy (ml·kg ⁻¹ ·min ⁻¹)	VO ₂ max (ml·kg ⁻¹ ·min ⁻¹)
Recreational [19,77,202,220-223]	10	36.7 (35.4-38.8)	54.2 (51.0-57.8)	37.7 (32.8-42.6)	49.7 (45.2-54.1)
	12	42.2 (40.4-45.3)		43.2 (38.5-48.1)	
	14	47.4 (46.0-49.5)		47.3 (40.1-51.9)	
Moderatelytrained [94,224-229]	12	40.7 (37.4-48.1)	62.2 (56.6-69.1)	41.9 (28.9-41.7)	55.8 (50.5-59.4)
	14	46.8 (42.0-55.5)		47.9 (41.3-53.5)	
	16	51.4 (51.6-62.3)		52.9 (45.7-61.0)	
Highly trained [1,21,23,27,31,230,231]	12	n/a	70.8 (65.3-80.2)	41.3 (33.3-50.2)	61.7 (56.2-72.3)
	14	45.0 (32.4-56.5)		48.3 (39.0-56.7)	
	16	50.6 (40.5-66.8)		54.5 (46.2-61.9)	
	18	58.1 (48.0-72.0)		58.6 (54.4-67.1))	
	20	66.5 (65.7-71.6)		n/a	
Elite [21,22,29,31,58,232]	14	39.9 (36.1-44.5)	75.4 (68.2-84.1)	41.9 (38.7-46.9)	66.2 (61.1-74.2)
	16	47.9 (43.2-53.4)		48.9 (45.1-55.8)	
	18	55.9 (50.5-62.3)		56.1 (51.8-63.8)	
	20	63.91 (57.5-71.2)		n/a	

n/a = not applicable.

44.0 ml·kg⁻¹·min⁻¹ at 16 km·hr⁻¹ [53]; Frank Shorter (Men’s Olympic Marathon Gold [1976] and Silver [1980] medalist; VO₂max = 71.3 ml·kg⁻¹·min⁻¹) 57.0 ml·kg⁻¹·min⁻¹ at 19.3 km·hr⁻¹ [29]; and Jim Ryun (former Men’s 880 yd, 1 min 44.9 s; 1500 m, 3 min 33.1 s; 1 mile, 3 min 51.1 s World Record holder; VO₂max = 78.3 ml·kg⁻¹·min⁻¹) 48.3 ml·kg⁻¹·min⁻¹ at 16 km·hr⁻¹ [54].

Treadmill and overground running

Due to the difficulty of obtaining metabolic data during overground running in the field (i.e. during training and competitions), measurements of RE have typically been made in the laboratory on motorized treadmills during which pulmonary gas-exchange is determined during bouts of constant-speed running and analyzed using various forms of manual (i.e. Douglas bag method) [55] or

automated (i.e. breath-by-breath analyzers) gas-analysis systems [56-58]. However, since air and wind resistance are not factors during laboratory testing, transferring treadmill data to overground running requires caution [2,3,8]. Specifically, differences between overground and treadmill running are likely to be found since as speed increases the effects of air and wind resistance become more pronounced (more on air and wind resistance in Kinetics / Ground Reaction Forces section below) [2,59]. Furthermore, the technique of running on a treadmill is different to running over ground where the hamstrings are used to a greater extent to produce propulsive horizontal and vertical forces [60]. For these reasons, data collected during laboratory treadmill testing sessions are typically under-estimations of the true energy demands during over ground running, although a slight incline on the treadmill gradient (~1%) can be used to increase the energy demand in compensation for the lack of air resistance experienced during overground running [60]. In recent years, however, lightweight, accurate, portable telemetric metabolic measuring systems have been designed that enable researchers and practitioners to obtain measurements during running outside of a laboratory environment. However, Saunders et al. [3] caution that careful attention must be made to ensure post- or repeated-measure results are not influenced by changes in environmental conditions.

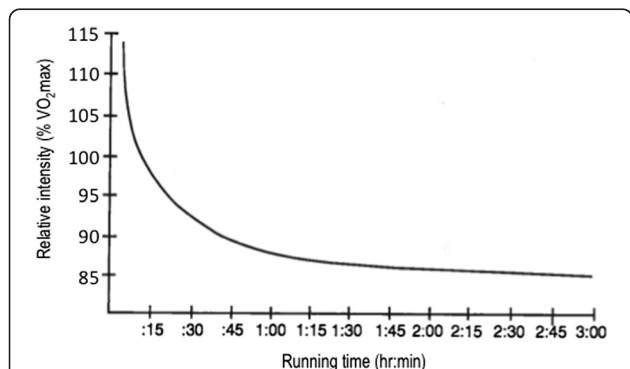


Figure 3 Relationship between race duration and relative intensity.

Reliability of running economy

In order to evaluate the effectiveness of running training throughout the season or the effect of specific interventions

aimed at improving RE, the intraindividual variation (typical error) of RE should be considered. Factors such as treadmill running experience [61], training level [62], footwear [31,61-64], time of day of testing [31,61-64], prior training activity [61,64], nutritional status [62,64], testing equipment [31] and laboratory environment [31] may affect the test-retest reliability of RE measures. Well-controlled studies using moderately trained to elite caliber subjects report intraindividual variation in RE between 1.3% and 5% at speeds between 12 and 18 km·hr⁻¹ [20,27,31,32,57,61-64], indicating that within-subject results are relatively stable. While no patterns emerge between the training status or gender of the athlete and reliability of RE, it does appear that the typical error is less at running velocities at which the athletes typically train [31,61,62]. While durations of up to 15 min have been used in the assessment of RE [62], multiple ~4 min stages at progressively faster running speeds (e.g. 12, 14, 16, 18 km·hr⁻¹) have been used in moderate to highly trained runners familiar with treadmill running because steady-state VO₂ can be reached within 2–3 min at each running speed [31].

Additionally, Hopkins [65] has proposed the concept of the smallest worthwhile change (SWC) to determine the practical significance of interventions. The SWC identifies the magnitude of change required to elicit a meaningful or significant improvement in RE. The SWC, calculated as a proportion of the effect size, represents the magnitude of improvement in a variable as a function of the between-athlete standard deviation of the particular cohort [66,67]. Saunders et al. [31] estimated a SWC of 2.6%, 2.4%, and 2.2% for RE at 14, 16, and 18 km·h⁻¹ respectively in 70 highly trained distance runners. Therefore, a distance runner must improve their RE by ~2.2-2.6% before a coach or practitioner can be reasonably confident that a real change (improvement) has occurred. However, the data reported by Saunders et al. [31] is for VO₂ at a given absolute speed across all subjects. The SWC may be considerably less than this if RE is assessed at the same relative speed and expressed as either an oxygen required to cover a given distance or energy demand (in relation to substrate utilization using RER) to run a given distance [16,68].

Metabolic and cardiorespiratory efficiency and running economy

In the context of improving RE, metabolic and cardiorespiratory efficiency refers to processes that result in better use of oxygen (increased energy production) relative to a given work output. Fluctuations in cardiorespiratory measures [heart rate (HR), minute ventilation (V_E)], thermoregulation [core temperature (C_{Temp})], and substrate metabolism [muscle contractile efficiency, mitochondrial efficiency] have been associated with changes in RE [3,69-73].

Cardiorespiratory measures

Bailey and Pate [69] and Pate et al. [74] have suggested that changes in cardiorespiratory measures (HR and V_E) are partly responsible for changes in RE during submaximal and maximal exercise. Thomas et al. [75] found a correlation of $r = 0.79$ ($p < 0.05$) between changes in V_E and changes in oxygen demand during a 5-km race in trained female runners. The increased oxygen demand was postulated to be caused by the increased O₂ demand of breathing [76]. Franch et al. [77] also reported a correlation ($r = 0.77$; $p < 0.0001$) between improvements in RE and reductions in pulmonary ventilation which may account for 25-70% of the decrease in aerobic demand after an intense run training program in recreational runners. Another study attempted to determine the impact of a simulated 5-km race on RE, V_E, HR, and C_{Temp} [4]. Consistent with other findings [69,75], RE decreased significantly and V_E, HR, and C_{Temp} all increased significantly from the beginning to the end of the 5-km run. Similar to previous studies [75,77], the increase in V_E was the only measure related to the increased RE ($r = 0.64$; $p < 0.05$). The fact that the two variables were correlated in several studies does not in itself imply cause and effect; however, quantitative estimates of the reduced cost of breathing with the training-induced decrement in V_E suggest that ventilatory adaptation may indeed play a role in improving RE [77].

Interindividual variation in RE has been linked to differences in HR and V_E. In a report by Pate et al. [74] involving 167 habitual runners, both HR and V_E were significantly and positively correlated with VO₂, indicating that better RE was associated with lower HR and V_E. Myocardial VO₂ also constitutes a fraction (1-2%) of whole body VO₂ during exercise [78]. Reductions in myocardial VO₂ would result in improved RE from a more efficient combination of HR and stroke volume (i.e. a reduction in HR and increase in stroke volume) [74]. However, according to Bailey and Pate [69] it is unlikely changes in HR make a significant contribution to changes in RE. A 20-bpm change in HR only increased VO₂ by 8 ml·min⁻¹, which increased RE from 41.8 to 41.9 ml·kg⁻¹·min⁻¹. Whereas, voluntary hyperpnoea at rest, which increased V_E from 70 to 100 ml·min⁻¹, has been found to increase VO₂ by 122 ml·min⁻¹ [79]. If training is able to decrease the work of breathing at a specific running velocity, this could contribute to an improved RE [69]. Using recent cost estimates of exercise V_E, the cost of V_E increased O₂ consumption by 31–50 ml (0.4-0.6 ml·kg⁻¹·min⁻¹) in men and 19–31 ml (0.3-0.5 ml·kg⁻¹·min⁻¹) in women. This explains 12-19% of the increase in VO₂ in men and 16-26% for the women [80,81]. Other estimates have found the work of ventilation to constitute up to 6-7% of the total oxygen cost of exercise [82]. Thus variables other than V_E are also responsible for the changes in RE.

Body temperature

There is conflicting evidence regarding the relationship between C_{Temp} and RE [63,69]. In some studies, a higher C_{Temp} has resulted in an increase in VO_2 at a given speed under hyperthermic conditions [83,84], likely due to increases in metabolic demand from augmented circulation, sweating, V_E , and a decrease in efficiency of oxidative phosphorylation [84-86]. In this regard, Grimby [87] found that a 1.3 ° C increase in C_{Temp} increased VO_2 by 5.5% and Thomas [4] found a slightly greater change in VO_2 (6.2%) after a 1.0 ° C increase in C_{Temp} . In contrast, results from other studies [88,89] indicate no change or a reduction in VO_2 occurred during hyperthermic exercise, suggesting a higher C_{Temp} enhanced mechanical efficiency of muscle to a degree equal to or greater than the increase caused by changes in circulation, sweating, and V_E .

Muscle fiber type

It is now accepted that a range of muscle fiber types exist in humans [90,91] and that each exhibit their own metabolic characteristics [71]. Indeed, the structure and composition of muscle fibers seems to influence RE [71,92,93]. Type IIA fibers are more oxidative than type IIX fibers and have functional characteristics more similar to type I fibers [94]. Type-II specific myosin ATPase isoforms require 1.6- to 2.1-fold more ATP per unit force production than type I and therefore require a proportionately higher oxidative phosphorylation [95]. Therefore an increase in type IIA fibers should increase the oxidative capacity of muscle and should contribute to improved RE. Although no research has examined the genetic link between muscle fiber type and RE, athletes may be predisposed to better or worse economy based on their composition of type I and type II muscle fibers [96]. Current results suggest there are mixed findings between muscle fiber type and RE [90-93,97].

Biomechanics and running economy

Running involves the conversion of muscular forces translocated through complex movement patterns that utilize all the major muscles and joints in the body [5]. Current evidence suggests that a variety of biomechanical characteristics are likely to contribute to RE; these include a variety of anthropometric dimensions [73,91,98-103], select gait patterns [104-111], and kinematic and kinetic factors [46,91,103,111-117] that have been shown to affect biomechanical efficiency and relate to better RE.

Anthropometric characteristics

Body mass and mass distribution

A variety of anthropometric characteristics such as height, body mass, physique, and segmental mass distribution may help explain interindividual and group differences as well as potential influences on RE. It is well-known that the oxygen demand of running does not increase proportional to body

mass [15,101], and the VO_2 per kilogram of body mass is higher in children than adults [2,8,118-128]. Indeed, in running events ranging from 800-m to the marathon, it's not uncommon to see individuals range by as much as 25 kg and/or 30 cm in the same race, even at the elite level. Several studies [129,130] have shown lightweight men to be no more or less economical than their heavier counterparts. Other research has demonstrated that when body mass is artificially increased by adding weight to the trunk during running, VO_2 per kilogram of body mass decreases both in children [128,131,132] and adults [128,131,133]. Consequently, several authors have suggested that the lower submaximal VO_2 in adults compared with children is a function of differences in body mass and not merely growth and maturation [39,134]. In support, several studies [73,91,102,103] have shown small to moderate inverse relationship between body mass and RE. Arellano and Kram [45] suggest body weight support and forward propulsion comprises ~80% of the net metabolic demand of running, while the task of leg-swing comprises ~7%, maintaining lateral balance ~2% and arm-swing actually reduces the demand by ~3%, indicating a net metabolic benefit.

The relationship between body mass and RE has been proposed to be a result of individual differences in mass distribution within the body, particularly in the limb segments [98]. For example, subtle differences in physique, particularly a low body mass index and long slender legs where the majority of mass is distributed higher on the thigh, have been suggested to be the primary reason for the extraordinary RE of African runners [19,25,135,136]. Although it is difficult to obtain a direct measure of the relationship between segmental mass distribution and RE, indirect support comes from experimental studies in which mass has been added to the lower limb segments of runners [137-143]. In general, the results from these studies indicate that the aerobic demand of carrying an extra load becomes more significant when the mass is located more distally. Myers [141] found that the aerobic demand of carrying an extra kilogram on the trunk is increased by 1% whereas when an equal mass is carried in the shoes, aerobic demand is increased by 10%. Other studies have found an increased VO_2 of 4.5% [144] and 14% [140] per kilogram carried on the feet and 7% increase when carried on the thigh [140]. Given the distal location of the feet, foot size or foot size relative to body size would also suggest it influences RE [5]. If one considers that a typical standard shoe weighs about 350 g, about 200 g more than most minimal shoes, and that the aerobic demand for every 100 g added to the trunk increases by about 0.1% and added to the foot increases by 1% [141,145], then the results from Perl et al. [146] suggest the net savings to minimal-shoe running is between 4.4% and 6.8%. These results support previous studies [142,143,147-153] reporting running barefoot or in minimal shoes to be more economical than running in

standard shoes. However, cushioning and other features of shoe design besides weight have been shown to have significant effect on RE [145]. For example, the aerobic demand during treadmill running was about 2.8% less when running in well cushioned shoes compared with poorly cushioned shoes of similar mass [145].

Limb length

While lower limb mass distribution has been shown to affect RE, there is no consensus on whether leg length is a factor in determining RE. Humans and animals of different sizes use approximately same amount of energy to run [Roberts, 1998 #1329; Roberts, 1998 #820]. Running involves little work against the environment; work is done by muscles and tendons to lift and accelerate the body and limbs. Some of the work is recovered from muscle-tendon springs without metabolic cost, however, regardless of the amount of work muscles do, the limbs must be activated and develop force to support the weight of the body [Kram, 1990 #821]. Leg length contributes to angular inertia and the metabolic cost of moving legs during running [5,154], and while there has been some research focusing on the relationship between leg length and stride length [99,155], the influence of leg length on economy has only been investigated indirectly. Research examining the physiques of male and female sprinters, middle-distance and long-distance runners have characterized sprinters as short-legged and middle- and long-distance runners and long-legged [156]. In general middle- and long-distance runners have been found to exhibit better economy than sprinters [22,29,92,102], however the influence of leg length on these differences is unknown. Myers and Steudel [141] suggest that for a given body mass, speed and gait pattern, runners that are smaller and have proportionately greater amount of body mass distributed proximally in the legs perform less work to accelerate and decelerate the limbs. However, despite Williams and Cavanagh [91] finding a large variation in RE among 31 male distance runners, there were no differences associated with segmental leg lengths and masses.

Achilles tendon moment arm

The amount of energy stored in a tendon depends on the mechanical properties of the tendon and on the forces that stretch the tendon, such as foot length. Kinetic and potential energy removed from the body in the first half of the stance phase is stored briefly as elastic strain energy and then returned in the second half by elastic recoil [157]. Thus, for a given kinematic pattern, and hence kinetic pattern, tendon force is inversely related to the moment arm of the Achilles tendon [100]. Since it is generally accepted that storage and reutilization of elastic energy in tendons substantially reduces energy demands in running [158] previous research has been able to

establish a moderate [159], large [100] and extremely large [Barnes, 2014 #1278] (Figure 4) relationship between the variation in RE and the moment arm of the Achilles tendon, albeit in small sample sizes of 8 to 63 [Barnes, 2014 #1278; Raichlen, 2011 #606; Scholz, 2008 #605]. Shorter Achilles tendon moment arm length and less flexible lower limb joints are associated with improved RE [100,160,161].

Other anthropometric characteristics throughout the body have also been investigated. Foot length has been found to be negatively correlated with RE in elite male runners [103]. Pelvic and shoulder width could theoretically have an influence on RE [5] but have been studied very little with available evidence suggesting either no relationship [91,112], or a moderate negative correlation between pelvic width and RE [103]. The only postural characteristic that has been investigated relative to RE is trunk angle or degree of forward lean while running. When comparing distance runners grouped by RE, Williams and Cavanagh [91] found that the most economical group displayed a slightly greater forward lean (5.9°) compared with the middle (3.3°) and least (2.4°) economical groups.

Running style / gait patterns

There is a belief amongst practitioners that, over time, runners adopt their most economical running style [162,163]. Accordingly, high training volumes and the number of years of running experience have been suggested to be important for improved RE [164]. Indeed, a number of studies show that individuals tend to freely choose their most economical gait pattern

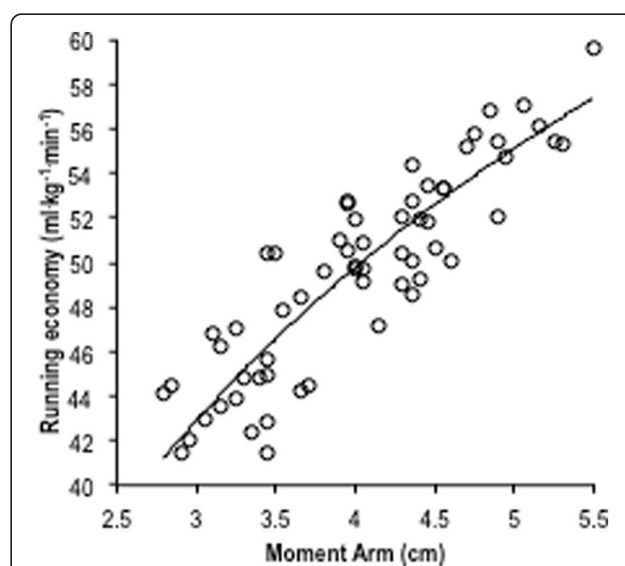


Figure 4 Relationship between moment arm length and running economy at 16 km·hr⁻¹ and moment arm ($r = 0.90$). Reproduced from Barnes et al. [Barnes, 2014 #1278] with permission.

[13,104,165-167]. While studies have identified small to moderate relationships between biomechanical characteristics and RE [91,104,111,166,168-170], stride length is one of the few gait variables that has been shown by direct experimental evidence to affect economy [104-106,171].

Stride length and stride rate

Results from a number of studies [104,166,167,171,172] have indicated that submaximal VO_2 increases curvilinearly as stride length is either lengthened or shortened from that self-selected by the runner. This basic curvilinear relationship between stride length and economy has also been shown for walking [173] and racewalking [106]. The basic assumption behind this research appears to be that strides which are too long will require considerable power during propulsion, excessive vertical oscillation of the center of mass, produce a foot strike position which creates large braking forces and require joint ranges of motion which invoke increased internal friction and stiffness [5]. Conversely, strides that are too short would increase internal work of contracting muscles through increased frequency and reciprocal movements, resulting in increased energy expenditure and decrease in RE [5].

Previous research has shown that VO_2 was lowest at stride lengths close to the self-selected condition [104,171]. Based on these results, Cavanagh and Williams [104] concluded that there is little need to dictate stride length for most runners since they already tend to display near optimal stride lengths. They proposed two mechanisms for this phenomenon. First, runners naturally acquire an optimal stride length and stride rate over time, based on perceived exertion [91], which supports the premises put forth previously [91,162,164]. Second, runners may adapt physiologically through repeated training at a particular stride length/stride rate for a given running speed [104].

Kaneko et al. [166] suggested that the link between stride rate and economy may be associated with muscle fiber recruitment. At slower stride rates (and longer stride lengths), the muscles need to develop relatively high external power during propulsion to overcome large braking forces. Conversely at fast strides rates (short stride lengths), the mechanical power associated with moving the limbs increases due to increased frequency of reciprocal movements. They indicated that these extreme conditions may require a greater reliance on less economical Type II fibers than more intermediate stride rate/stride length combinations [166]. Consequently, efforts to improve RE via stride rate manipulation would be ineffective, unless the runner's freely chosen stride rate is not economically optimal [69]. Kram and Taylor [Kram, 1990 #821] suggest differences in oxygen demand are proportional to stride rate at equivalent speeds, suggesting that the time available for developing force is important in determining RE.

Vertical oscillation

Studies comparing the biomechanical characteristics of elite and good runners, found that elite distance runners have slightly less vertical oscillation and had better RE than good runners [107,110,111,114]. Similarly, Williams and Cavanagh [91] showed a trend, although nonsignificant, towards less vertical oscillation and better RE. The intuitive perception is that vertical oscillation is adversely related to economy; however, Cavagna et al. [107] reported that less vertical oscillation results in high stride frequency and higher internal work to accelerate lower limb segments, thus increasing oxygen demand and reducing RE. Conversely, Halvorsen et al. [174] showed that reducing vertical oscillation has a positive effect on RE.

Footstrike patterns

It continues to be argued that a forefoot strike pattern during running is more economical than a rearfoot pattern; however, previous studies using one habitual footstrike group have found no difference in RE between footstrike patterns [103,108,109]. In fact, Gruber et al. [175] found no differences in VO_2 between 19 habitual forefoot runners and 18 habitual rearfoot runners. However, when subjects ran with the alternative footstrike pattern, VO_2 increased significantly (5.5%, $p < 0.001$) with the forefoot pattern but not the rearfoot pattern. Contrary to popular belief, these results suggest that the forefoot pattern is not more economical than the rearfoot pattern.

Kinematics and kinetics

While stride length, stride rate and other gait related characteristics have been associated with RE, other kinematic and kinetic factors such as angular velocities of limb segments and joints [91,103,111-114] and ground reaction forces [46,115-117] have also demonstrated a relationship with RE.

Lower body kinematics

Comparisons of elite and good distance runners indicate that better economy in elite runners was associated with greater maximal angle of the thigh during hip extension, more extended lower leg at foot strike, more acute knee angles during swing and toe-off and that good runners plantar flexed an average of 10° more during toe-off than elite runners [103,113,114]. Whereas running with experimentally increased knee flexion ('Groucho running') has been shown to increase the oxygen demand of running by as much as 50% [176]. Results from a number of studies indicate relationships between economy and joint angles and velocities were trivial to moderate in strength [91,103,113,114,177,178], suggesting optimal kinematic patterns may be specific to the individual.

Upper body kinematics

Most investigations of RE and running mechanics have focused on the kinematics of lower limbs with only a few studies [103,111,112] considering the upper body limbs. Anderson and Tseh [112] found no relationship between RE and shoulder width, hip width, or ratio of shoulder:hip width. Whereas Williams and Cavanagh [103] found a moderate negative correlation between shoulder:pelvic width and RE in elite male runners, indicating that the moments and forces generated by counter-rotations of the shoulders and hips and movements of the arms may effect RE [179-181]. Accordingly, a positive correlation between economy and angular velocity of shoulder rotation and angular displacement of the hips and shoulders about the polar axis of the trunk [112] as well as a negative correlation between economy and angular displacement of the shoulder in the sagittal plane has previously been described [112]. However, Tartaruga et al. [111] found no relationship between velocity changes of the wrists and shoulders or rotation of the hips and shoulders relative to the polar axis of the trunk and economy. Some results have shown less arm movement, as measured by wrist excursion during the gait cycle, tended to reduce total upper body excursion from the body center of mass both laterally and horizontally and be associated with better RE [91,111,112,181].

Kinetics / ground reaction forces

Investigations related to kinetics and RE are limited and most work has focused on vertical ground reaction forces. Kram and Taylor [46] presented a simple inverse relationship between the aerobic demand during running and the time the foot applies force to the ground during each stride, independent of body mass, indicating that the energy demand during running is determined by the cost of supporting one's body mass and the time course of generating force. Williams and Cavanagh [91] surmised that more economical runners have identifiable kinetic patterns in their running style, which are recognizable by less wasteful vertical motion [117]. However, data collected from elite male and female distance runners showed relatively low correlations between ground reaction forces and RE [103,113] suggesting that ground reaction forces are not likely to be the determining factor that makes one runner more economical than another, and that in fact some elite runners are economical despite low ground reaction forces.

While vertical ground reaction forces have been shown to affect the metabolic demand during running in recreational and moderately trained runners due to the requirement to support body mass [46,115-117], horizontal forces can also substantially affect RE. For example, in 25 well-trained endurance athletes, Nuumela et al. [168] reported mass-specific horizontal forces were substantially related to RE at five different running speeds. Similarly, Storen et al.

[182] found that the sum of horizontal and vertical peak forces were inversely correlated with RE ($r = 0.66$).

Neuromuscular characteristics and running economy

In addition to metabolic, cardiorespiratory, and biomechanical factors, neuromuscular characteristics are also important aspects of RE. The interaction between the neural and muscle systems (i.e. neuromuscular system) is fundamental to all movement, and effectively translates cardiorespiratory capacity into efficient mechanics and therefore into performance. It is becoming more evident that aerobic factors are not the only variables that affect endurance performance [10]. In fact, Green and Patla [183] suggest that any failure of the contractile machinery could prevent full utilization of available oxygen, suggesting that in some cases, the ability to use available oxygen might not be the limiting factor in endurance performance. Essentially neuromuscular efficiency can be divided into two categories: 1) factors that improve the neural signaling and motor programming of the running motion and 2) those that improve the muscle force production itself.

Neural signaling and motor programing

High performance running is a skill, much like hitting a golf ball or shooting a basketball, that requires precise timing of nearly all the major muscles and joints in the body to convert muscular force in translocation [5]. Similar to those skills, practice is needed to improve the efficiency at the activity. Motor learning studies have shown that continued practice of a task results in more skilled control of movement, characterized by decreased amplitude and duration of muscle activity, decreased muscle co-activation and less variability of movement [97,184,185]. Recent evidence has shown that recreational runners ($3.4 \pm 2.8 \text{ km}\cdot\text{wk}^{-1}$) exhibited greater individual variance (i.e. variability between strides), greater population variance (i.e. variability of muscle recruitment between athletes), more extensive and more variable muscle co-activation and longer durations of muscle activity than moderately trained runners (6.6 ± 1.4 years of running experience, who ran $61.4 \pm 8.8 \text{ km}\cdot\text{wk}^{-1}$) [186]. These findings are consistent with previous short-term training studies of arm, hand and leg (pedaling) movements [185,187-189], suggesting that ongoing neuromuscular adaptations occur as a result of continued training. It is apparent within the literature that run training can induce positive changes in RE [118,190,191]. Running appears to induce adaptations in motor programing and recruitment that are critical for superior RE [5,184,185]. If neuromuscular adaptations are responsible for the changes in RE then it would be reasonable to suggest that there would be alterations in neural signaling during running following training. Bonacci et al. [10] advocate that adaptations to motor recruitment as a result of

training represent a learning effect. Positive adaptations infer that an individual learns to produce specific patterns of muscle recruitment that are associated with improved efficiency of the task (e.g. improved biomechanical and neuromuscular efficiency) resulting in enhanced performance [10].

Muscle force production and stiffness

There are two muscle contraction-related issues that potentially influence energy demand and RE; velocity of contraction and balance between concentric and eccentric contractions. With regards to velocity of contraction, Taylor [15] has observed that it is less costly for muscles to generate force at low velocities, that force is highest and metabolic rate lowest during isometric contraction, and that the energy cost of generating force increases dramatically with great shorting velocity. The proposed mechanism for this is that muscle contractions are primarily isometric, adjusting the stiffness of the muscle-tendon unit during the eccentric phase to produce simultaneous deceleration and elastic stretch, then producing a nearly isometric impulse that initiates ballistic concentric acceleration. This proposed mechanism would promote optimization by exploitation 'free' elastic energy, and minimizing metabolic requirements. Such optimization would obviously demand precise timing, and integration and refinement of the temporal, kinetic and kinematic patterns, which would require considerable practice and training.

Muscle power

It has been suggested that endurance performance may be limited not only by aerobic power but also by 'muscle power' factors related to the force and velocity characteristics of the neuromuscular system [192]. Indeed, performance during a 5-km and 10-km run has been shown to be partially determined by neuromuscular characteristics and muscle power, suggesting the skeletal muscle contractility differs between fast and slow runners [192-194]. Similarly, in a homogenous group of highly trained endurance runners with similar VO_2max values, those athletes with faster 10-km and 5-km run times displayed higher relative muscle pre-activation (prior to touchdown), accompanied with lower relative integrated electromyographic (iEMG) activity during the propulsion phase, along with shorter stance phase contact times than those athletes with slower run times [194,195]. Furthermore, there was a significant correlation between RE and mean stance phase contact times during constant velocity running, suggesting muscle power characteristics play an important role in determining distance running performance in highly trained runners [194].

Lower-leg stiffness

It is possible that shorter stance phase contact times and greater muscle pre-activation may represent enhanced leg

muscle stiffness, leading to faster transition from the braking to propulsive phase of ground contact [195,196]. Dalleau et al. [197] highlighted the importance of neuromuscular factors by demonstrating that RE was related to the stiffness of the propulsive leg, with greater stiffness eliciting the best RE. Arampatzis et al. [198] corroborate this finding such that in a group of 28 long-distance runners separated into three groups by economy, the most economical runners had highest tendon stiffness. Leg stiffness is modulated by neuromuscular activation, and changes in stiffness have been shown to occur as a result of neuromuscular adaptation to training [199]. In support of the association between motor recruitment and leg stiffness, a reduction in EMG pre-activation was shown to be significantly related to a decrease in post-landing leg stiffness following fatiguing exercise [200]. Greater duration of muscle co-activation of bi-articular leg muscles during stance has also been significantly associated with better RE [201]. Muscle co-activation modulates leg stiffness during running and may alter RE through utilization of stored elastic energy, which has no additional metabolic cost. Albracht and Arampatzis [202] indicated that increased tendon stiffness is indicative of greater energy storage and return and a redistribution of muscular output within the lower extremities while running, which might result in improved RE. Running economy and stiffness have been shown to change together with training [48,203]. It has also been shown that stiffness of the muscle-tendon unit increases with running speed [105,158,204].

Stretch shortening cycle

Kyrolainen et al. [177] found that as running speed increased so did EMG preactivation and ground reaction forces, along with their rate of force production. Preparatory muscle function is an important function of the stretch shortening cycle (SSC). The SSC is a combination of a high velocity eccentric contraction followed immediately with a concentric contraction. Stretch shortening cycle muscle function enhances performance during the final phase (concentric action) [205], and the increase in preparatory muscle activity with higher running speeds was suggested to be a mechanism to tolerate higher impact loads, regulate landing stiffness [206] and improve RE [177]. A recent study showed that a greater ratio of eccentric to concentric vastus lateralis muscle activity was associated with a lower metabolic demand during running (i.e. better RE) [207].

Elastic energy storage

The balance between eccentric and concentric contractions could potentially influence RE, since the eccentric contractions during which elastic energy is stored are less costly than the concentric contractions in which the energy is released [14]. There is clear evidence that the

mechanical efficiency of running exceeds the efficiency of conversion of chemical energy to kinetic energy by muscles [13,14,158]. Elastic energy stored during the eccentric contractions of running makes a substantial contribution to propulsion as it is released during subsequent concentric contractions [158,208]. Unfortunately, there currently are no data available from which to quantify the relative energy cost of the two types of contractions nor has there been a method devised to differentiate true eccentric contractions from tendon stretching or to quantify the storage and release of elastic energy [13,14,209–212]. There is however, consensus that this phenomenon contributes to both efficiency and economy of movement.

Both actomyosin cross-bridges and tendons have been implicated as important sites of energy storage [157,213]. Ker et al. [157] have estimated that the Achilles tendon and tendons in the arch of the foot can store 35% and 17%, respectively, of the kinetic and potential energy gained and lost in a step while running at moderate speed. Alexander [214] has shown that in a 70 kg human running at $\sim 16 \text{ km hr}^{-1}$, more than half of the elastic energy can be stored in just two springs, the Achilles tendon and the arch of the foot. Cavagna et al. [215] have estimated that VO_2 during running might be 30 to 40% higher without contributions from elastic storage and return of energy. At higher running speeds, elastic recovery of energy prevails over the contractile machinery and accounts for most of the work [15,158]. The available evidence indicates that there may be substantial interindividual differences in ability to store and release elastic energy [216–218] and it has been suggested that fiber composition, gender and maturity are likely contributors to these differences [219].

Conclusions

Running economy is a complex, multifactorial concept that represents the sum of metabolic, cardiorespiratory, biomechanical and neuromuscular efficiency during running. It is possible to obtain reliable measures of RE in the laboratory, and a range of values from varying standards of runners is retrievable from current literature. Metabolic and cardiorespiratory factors that affect RE include HR, V_E , C_{Temp} , and muscle fiber type. While, there does not appear to be any easily identifiable or universally applicable biomechanical pattern of 'efficient' movement that will apply to all runners, it does appear that runners with a variety of anthropometric characteristics such as a mass distribution closer to the torso and shorter Achilles moment arms tend to have better RE. Neuromuscular efficiency may play an important role in determining RE, especially in athletes with similar physiological attributes. Specifically, the timing and amplitude of muscle activity prior to and in the initial phase of ground contact affect economy by augmenting leg stiffness and the exploitation of stored elastic energy. It is likely that adjusting a given

determining factor may result in an economy enhancement in one athlete but the same adjustment in another might be uneconomical because of differences in other physiological or biomechanical characteristics. Perhaps a more promising avenue of research may be to concentrate on the individual runner in an effort to best identify how that athlete's structure and functional abilities influence RE, subsequent performance as well as injury susceptibility.

Competing interests

The authors declare that they have no competing interests.

Authors' contribution

KB and AK reviewed the literature and participated in the drafting and writing of this manuscript. Both authors read and approved the final manuscript.

Acknowledgements

No sources of funding were used to assist in the preparation of this review.

Received: 28 May 2014 Accepted: 16 December 2014

Published online: 27 March 2015

References

- Conley DL, Krahenbuhl GS. Running economy and distance running performance of highly trained athletes. *Med Sci Sports Exerc.* 1980;12(5):357–60.
- Daniels JT. A physiologist's view of running economy. *Med Sci Sports Exerc.* 1985;17(3):332–8.
- Saunders PU, Pyne DB, Telford RD, Hawley JA. Factors affecting running economy in trained distance runners. *Sports Med.* 2004;34(7):465–85.
- Thomas DQ, Fernhall B, Granat H. Changes in running economy during a 5-km run in trained men and women runners. *J Strength Cond Res.* 1999;13(2):162–7.
- Anderson T. Biomechanics and running economy. *Sports Med.* 1996;22(2):76–89.
- Costill DL, Thomason H, Roberts E. Fractional utilization of the aerobic capacity during distance running. *Med Sci Sports.* 1973;5(4):248–52.
- Goldspink G. Muscle energetics in animal locomotion. In: Alexander RM, Goldspink G, editors. *Mechanics and Energetics of Animal Locomotion*. London: Chapman and Hall, Ltd.; 1977.
- Morgan DW, Martin PE, Krahenbuhl GS. Factors affecting running economy. *Sports Med.* 1989;7(5):310–30.
- Morgan DW, Baldini FD, Martin PE, Kohrt WM. Ten kilometer performance and predicted velocity at VO_2max among well-trained male runners. *Med Sci Sports Exerc.* 1989;21(1):78–83.
- Bonacci J, Chapman A, Blanch P, Vicenzino B. Neuromuscular adaptations to training, injury and passive interventions: implications for running economy. *Sports Med.* 2009;39(11):903–21.
- He Z, Hu Y, Feng L, Lu Y, Liu G, Xi Y, et al. NRF2 genotype improves endurance capacity in response to training. *Int J Sports Med.* 2007;28(9):717–21.
- Rodas G, Calvo M, Estruch A, Garrido E, Ercilla G, Arcas A, et al. Heritability of running economy: a study made on twin brothers. *Eur J Appl Physiol.* 1998;77(6):511–6.
- Cavanagh PR, Kram R. The efficiency of human movement—a statement of the problem. *Med Sci Sports Exerc.* 1985;17(3):304–8.
- Williams KR. The relationship between mechanical and physiological energy estimates. *Med Sci Sports Exerc.* 1985;17(3):317–25.
- Taylor CR. Relating mechanics and energetics during exercise. *Adv Vet Sci Comp Med.* 1994;38A:181–215.
- Fletcher JR, Esau SP, Macintosh BR. Economy of running: beyond the measurement of oxygen uptake. *J Appl Physiol.* 2009;107(6):1918–22.
- Jones AM, Koppo K, Burnley M. Effects of prior exercise on metabolic and gas exchange responses to exercise. *Sports Med.* 2003;33(13):949–71.
- MacDougall J. The anaerobic threshold: its significance for the endurance athlete. *Can J Appl Sport Sci.* 1977;2:137–40.
- Foster C, Lucia A. Running economy: the forgotten factor in elite performance. *Sports Med.* 2007;37(4–5):316–9.
- Brisswalter J, Legros P. Daily stability in energy cost of running, respiratory parameters and stride rate among well-trained middle distance runners. *Int J Sports Med.* 1994;15(5):238–41.
- Daniels JT, Scardina N, Hayes J, Foley P. Elite and subelite female middle- and long-distance runners. In: Landers DM, editor. *The 1984 Olympic*

- Scientific Conference Proceedings. Champaign, IL: Human Kinetics; 1986. p. 57–72.
22. Daniels JT, Daniels N. Running economy of elite male and elite female runners. *Med Sci Sports Exerc.* 1992;24(4):483–9.
 23. Daniels JT, Krahenbuhl G, Foster C, Gilbert J, Daniels S. Aerobic responses of female distance runners to submaximal and maximal exercise. *Ann N Y Acad Sci.* 1977;301:726–33.
 24. Joyner MJ. Modeling: optimal marathon performance on the basis of physiological factors. *J Appl Physiol.* 1991;70(2):683–7.
 25. Lucia A, Esteve-Lanao J, Oliven J, Gomez-Gallego F, San Juan AF, Santiago C, et al. Physiological characteristics of the best Eritrean runners-exceptional running economy. *Appl Physiol Nutr Metab.* 2006;31(5):530–40.
 26. Lucia A, Oliven J, Bravo J, Gonzalez-Freire M, Foster C. The key to top-level endurance running performance: a unique example. *Br J Sports Med.* 2008;42(3):172–4. discussion 4.
 27. Morgan DW, Craib MW, Krahenbuhl GS, Woodall K, Jordan S, Filarski K, et al. Daily variability in running economy among well-trained male and female distance runners. *Res Q Exerc Sport.* 1994;65(1):72–7.
 28. Morgan DW, Daniels JT. Relationship between VO₂max and the aerobic demand of running in elite distance runners. *Int J Sports Med.* 1994;15(7):426–9.
 29. Pollock ML. Submaximal and maximal working capacity of elite distance runners. Part I: Cardiorespiratory aspects. *Ann N Y Acad Sci.* 1977;301:310–22.
 30. Saltin B, Larsen H, Terrados N, Bangsbo J, Bak T, Kim CK, et al. 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(4):209–21.
 31. Saunders PU, Pyne DB, Telford RD, Hawley JA. Reliability and variability of running economy in elite distance runners. *Med Sci Sports Exerc.* 2004;36(11):1972–6.
 32. Williams TJ, Krahenbuhl GS, Morgan DW. Daily variation in running economy of moderately trained male runners. *Med Sci Sports Exerc.* 1991;23(8):944–8.
 33. Helgerud J. Maximal oxygen uptake, anaerobic threshold and running economy in women and men with similar performances level in marathons. *Eur J Appl Physiol.* 1994;68(2):155–61.
 34. Helgerud J, Ingjer F, Stromme SB. Sex differences in performance-matched marathon runners. *Eur J Appl Physiol.* 1990;61(5–6):433–9.
 35. Helgerud J, Storen O, Hoff J. Are there differences in running economy at different velocities for well-trained distance runners? *Eur J Appl Physiol.* 2010;108(6):1099–105.
 36. Sunde A, Storen O, Bjerkaas M, Larsen MH, Hoff J, Helgerud J. Maximal strength training improves cycling economy in competitive cyclists. *J Strength Cond Res.* 2010;24(8):2157–65.
 37. Svedenhag J. Maximal and submaximal oxygen uptake during running: how should body mass be accounted for? *Scand J Med Sci Sports.* 1995;5(4):175–80.
 38. Åstrand P-O. *Textbook of work physiology : physiological bases of exercise.* 4th ed. Champaign, IL: Human Kinetics; 2003.
 39. Bergh U, Sjödin B, Forsberg A, Svedenhag J. The relationship between body mass and oxygen uptake during running in humans. *Med Sci Sports Exerc.* 1991;23(2):205–11.
 40. Heil DP. Body mass scaling of peak oxygen uptake in 20- to 79-yr-old adults. *Med Sci Sports Exerc.* 1997;29(12):1602–8.
 41. Welsman JR, Armstrong N, Nevill AM, Winter EM, Kirby BJ. Scaling peak VO₂ for differences in body size. *Med Sci Sports Exerc.* 1996;28(2):259–65.
 42. Rogers DM, Olson BL, Wilmore JH. Scaling for the VO₂-to-body size relationship among children and adults. *J Appl Physiol.* 1995;79(3):958–67.
 43. Svedenhag J, Sjödin B. Body-mass-modified running economy and step length in elite male middle- and long-distance runners. *Int J Sports Med.* 1994;15(6):305–10.
 44. Taylor C, Heglund N, McMahon T, Looney T. Energetic cost of generating muscular force during running—a comparison of large and small animals. *J Exp Biol.* 1980;86:9–18.
 45. Arellano CJ, Kram R. Partitioning the metabolic cost of human running: a task-by-task approach. *Integr Comp Biol.* 2014;54(16):1084–98.
 46. Kram R, Taylor CR. Energetics of running: a new perspective. *Nature.* 1990;346(6281):265–7.
 47. Roberts TJ, Kram R, Weyand PG, Taylor CR. Energetics of bipedal running. I. metabolic cost of generating force. *J Exp Biol.* 1998;201(Pt 19):2745–51.
 48. Fletcher JR, Esau SP, Macintosh BR. Changes in tendon stiffness and running economy in highly trained distance runners. *Eur J Appl Physiol.* 2010;110(5):1037–46.
 49. Fletcher JR, Pfister TR, Macintosh BR. Energy cost of running and Achilles tendon stiffness in man and woman trained runners. *Physiol Rep.* 2013;1(7):e00178.
 50. Margaria R, Cerretelli P, Aghemo P, Sassi G. Energy cost of running. *J Appl Physiol.* 1963;18:367–70.
 51. Pialoux V, Proust O, Mounier R. Energy expenditure of submaximal running does not increase after cycle-run transition. *J Sports Med Phys Fitness.* 2008;48(2):143–8.
 52. Daniels JT, Gilbert J. *Oxygen Power: Performance Tables for Distance Runners.* Tempe, AZ: Daniels and Gilbert, POB 26287; 1979.
 53. Jones AM. The physiology of the women's world record holder for the women's marathon. *Int J Sports Sci Coach.* 2006;1(2):101–15.
 54. Daniels JT. Running with Jim Ryun: a five-year study. *PhysicianSportsmed.* 1974;2(September):62–7.
 55. Truijens MJ, Rodriguez 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(2):328–37.
 56. Barnes KR, Hopkins WG, McGuigan MR, Kilding AE. Effects of different uphill interval-training programs on running economy and performance. *Int J Sports Physiol Perform.* 2013;8(6):639–47.
 57. Barnes KR, Hopkins WG, McGuigan MR, Northuis ME, Kilding AE. Effects of resistance training on running economy and cross-country performance. *Med Sci Sports Exerc.* in press May 21.
 58. Saunders PU, Telford RD, Pyne DB, Peltola EM, Cunningham RB, Gore CJ, et al. Short-term plyometric training improves running economy in highly trained middle and long distance runners. *J Strength Cond Res.* 2006;20(4):947–54.
 59. Daniels JT, Foster C, Daniels S, Krahenbuhl G. Altitude and human performance with special consideration of the aerobic demands of running. Orlando, Florida: Proceedings of the NCEAM/NAPECW National Conference; 1977. p. 61–7.
 60. Jones AM, Doust JH. A 1% treadmill grade most accurately reflects the energetic cost of outdoor running. *J Sports Sci.* 1996;14(4):321–7.
 61. Morgan DW, Martin PE, Krahenbuhl GS, Baldini FD. Variability in running economy and mechanics among trained male runners. *Med Sci Sports Exerc.* 1991;23(3):378–83.
 62. Pereira MA, Freedson PS. Intraindividual variation of running economy in highly trained and moderately trained males. *Int J Sports Med.* 1997;18(2):118–24.
 63. Morgan DW, Martin PE, Baldini FD, Krahenbuhl GS. Effects of a prolonged maximal run on running economy and running mechanics. *Med Sci Sports Exerc.* 1990;22(6):834–40.
 64. Pereira MA, Freedson PS, Maliszewski AF. Intraindividual variation during inclined steady-rate treadmill running. *Res Q Exerc Sport.* 1994;65(2):184–8.
 65. Hopkins WG. Measures of reliability in sports medicine and science. *Sports Med.* 2000;30(1):1–15.
 66. Hopkins WG, Marshall SW, Batterham AM, Hanin J. Progressive statistics for studies in sports medicine and exercise science. *Med Sci Sports Exerc.* 2009;41(1):3–13.
 67. Hopkins WG, Schabert EJ, Hawley JA. Reliability of power in physical performance tests. *Sports Med.* 2001;31(3):211–34.
 68. Shaw AJ, Ingham SA, Fudge BW, Folland JP. The reliability of running economy expressed as oxygen cost and energy cost in trained distance runners. *Appl Physiol Nutr Metab.* 2013;38(12):1268–72.
 69. Bailey SP, Pate RR. Feasibility of improving running economy. *Sports Med.* 1991;12(4):228–36.
 70. Jones AM. Dietary nitrate: the new magic bullet? *Sports Sci Exch.* 2013;26(110):1–5.
 71. Morgan DW, Craib M. Physiological aspects of running economy. *Med Sci Sports Exerc.* 1992;24(4):456–61.
 72. Svedenhag J. *Running Economy.* In: Bangsbo J, Larsen H, editors. *Running and Science.* Copenhagen: Munksgaard; 2000. p. 85–105.
 73. Pate RR, Macera CA, Bailey SP, Bartoli WP, Powell KE. Physiological, anthropometric, and training correlates of running economy. *Med Sci Sports Exerc.* 1992;24(10):1128–33.
 74. Pate RR. Physiological and anatomical correlates of running economy in habitual runners. *Med Sci Sports Exerc.* 1989;21 Suppl 2:S26.
 75. Thomas D, Fernhall B, Blanpied P. Changes in running economy and mechanics during a 5 km run. *J Strength Cond Res.* 1995;9:170–5.
 76. Hagberg JM, Mullin JP, Nagle FJ. Oxygen consumption during constant-load exercise. *J Appl Physiol.* 1978;45(3):381–4.

77. Franch J, Madsen K, Djurhuus MS, Pedersen PK. Improved running economy following intensified training correlates with reduced ventilatory demands. *Med Sci Sports Exerc.* 1998;30(8):1250–6.
78. Kitamura K, Jorgensen CR, Gobel FL, Taylor HL, Wang Y. Hemodynamic correlates of myocardial oxygen consumption during upright exercise. *J Appl Physiol.* 1972;32(4):516–22.
79. Coast JR, Krause KM. Relationship of oxygen consumption and cardiac output to work of breathing. *Med Sci Sports Exerc.* 1993;25(3):335–40.
80. Poole DC. Role of exercising muscle in slow component of VO₂. *Med Sci Sports Exerc.* 1994;26(11):1335–40.
81. Aaron EA, Seow KC, Johnson BD, Dempsey JA. Oxygen cost of exercise hyperpnea: implications for performance. *J Appl Physiol.* 1992;72(5):1818–25.
82. Milic-Emili G, Petit JM, Deroanne R. Mechanical work of breathing during exercise in trained and untrained subjects. *J Appl Physiol.* 1962;17:43–6.
83. Saltin B. Circulatory Response to Submaximal and Maximal Exercise after Thermal Dehydration. *J Appl Physiol.* 1964;19:1125–32.
84. MacDougall JD, Reddan WG, Layton CR, Dempsey JA. Effects of metabolic hyperthermia on performance during heavy prolonged exercise. *J Appl Physiol.* 1974;36(5):538–44.
85. Brooks GA, Hittelman KJ, Faulkner JA, Beyer RE. Temperature, skeletal muscle mitochondrial functions, and oxygen debt. *Am J Physiol.* 1971;220(4):1053–9.
86. Brooks GA, Hittelman KJ, Faulkner JA, Beyer RE. Temperature, liver mitochondrial respiratory functions, and oxygen debt. *Med Sci Sports.* 1971;3(2):72–4.
87. Grimby G. Exercise in man during pyrogen-induced fever. *Scand J Clin Lab Invest.* 1962;14 Suppl 67:1–112.
88. Rowell LB, Brengelmann GL, Murray JA, Kraning 2nd KK, Kusumi F. Human metabolic responses to hyperthermia during mild to maximal exercise. *J Appl Physiol.* 1969;26(4):395–402.
89. Maron MB, Horvath SM, Wilkerson JE, Gliner JA. Oxygen uptake measurements during competitive marathon running. *J Appl Physiol.* 1976;40(5):836–8.
90. Bosco C, Montanari G, Ribacchi R, Giovenali P, Latteri F, Iachelli G, et al. Relationship between the efficiency of muscular work during jumping and the energetics of running. *Eur J Appl Physiol.* 1987;56(2):138–43.
91. Williams KR, Cavanagh PR. Relationship between distance running mechanics, running economy, and performance. *J Appl Physiol.* 1987;63(3):1236–45.
92. Kaneko M. Mechanics and energetics in running with special reference to efficiency. *J Biomech.* 1990;23 Suppl 1:57–63.
93. Kyrolainen H, Kivela R, Koskinen S, McBride J, Andersen JL, Takala T, et al. Interrelationships between muscle structure, muscle strength, and running economy. *Med Sci Sports Exerc.* 2003;35(1):45–9.
94. Johnston R, Quinn T, Kertzer R, Vroman N. Strength training in female distance runners: impact on running economy. *J Strength Cond Res.* 1997;11(4):224–9.
95. Reggiani C, Bottinelli R, Stienen GJ. Sarcomeric myosin isoforms: fine tuning of a molecular motor. *Physiology.* 2000;15(1):26–33.
96. Tucker R, Santos-Concejeiro J, Collins M. The genetic basis for elite running performance. *Br J Sports Med.* 2013;47(9):545–9.
97. Wang K, McCarter R, Wright J, Beverly J, Ramirez-Mitchell R. Viscoelasticity of the sarcomere matrix of skeletal muscles. The titin-myosin composite filament is a dual-stage molecular spring. *Biophys J.* 1993;64(4):1161–77.
98. Cavanagh PR, Kram R. Mechanical and muscular factors affecting the efficiency of human movement. *Med Sci Sports Exerc.* 1985;17(3):326–31.
99. Cavanagh PR, Kram R. Stride length in distance running: velocity, body dimensions and added mass effects. *Champaign: Human Kinetics; 1989.*
100. Scholz MN, Bobbert MF, van Soest AJ, Clark JR, van Heerden J. Running biomechanics: shorter heels, better economy. *J Exp Biol.* 2008;211(Pt 20):3266–71.
101. Taylor CR, Heglund NC, Maloij GM. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J Exp Biol.* 1982;97:1–21.
102. Bourdin M, Pastene J, Germain M, Lacour JR. Influence of training, sex, age and body mass on the energy cost of running. *Eur J Appl Physiol.* 1993;66(5):439–44.
103. Williams K, Cavanagh PR. Biomechanical correlates with running economy in elite distance runners. *Montreal: Proceedings of the North American Congress on Biomechanics; 1986. p. 287–8.*
104. Cavanagh PR, Williams KR. The effect of stride length variation on oxygen uptake during distance running. *Med Sci Sports Exerc.* 1982;14(1):30–5.
105. Morgan D, Martin P, Craib M, Caruso C, Clifton R, Hopewell R. Effect of step length optimization on the aerobic demand of running. *J Appl Physiol.* 1994;77(1):245–51.
106. Morgan DW, Martin PE. Effects of stride length alteration on racewalking economy. *Can J Appl Sport Sci.* 1986;11(4):211–7.
107. Cavagna GA, Heglund NC, Willems PA. Effect of an increase in gravity on the power output and the rebound of the body in human running. *J Exp Biol.* 2005;208(Pt 12):2333–46.
108. Di Michele R, Merni F. The concurrent effects of strike pattern and ground-contact time on running economy. *J Sci Med Sport.* 2013;17(4):414–8.
109. Nilsson J, Thorstensson A. Adaptability in frequency and amplitude of leg movements during human locomotion at different speeds. *Acta Physiol Scand.* 1987;129(1):107–14.
110. Svedenhag J, Sjodin B. Maximal and submaximal oxygen uptakes and blood lactate levels in elite male middle- and long-distance runners. *Int J Sports Med.* 1984;5(5):255–61.
111. Tartaruga MP, Brisswalter J, Peyre-Tartaruga LA, Avila AO, Alberton CL, Coertjens M, et al. The relationship between running economy and biomechanical variables in distance runners. *Res Q Exerc Sport.* 2012;83(3):367–75.
112. Anderson T, Tseh W. Running economy, anthropometric dimensions and kinematic variables [abstract]. *Med Sci Sports Exerc.* 1994;26(5 Suppl):S170.
113. Williams KR, Cavanagh PR, Ziff JL. Biomechanical studies of elite female distance runners. *Int J Sports Med.* 1987;8 Suppl 2:107–18.
114. Cavanagh PR, Pollock ML, Landa J. A biomechanical comparison of elite and good distance runners. *Ann N Y Acad Sci.* 1977;301:328–45.
115. Chang YH, Kram R. Metabolic cost of generating horizontal forces during human running. *J Appl Physiol.* 1999;86(5):1657–62.
116. Farley CT, McMahon TA. Energetics of walking and running: insights from simulated reduced-gravity experiments. *J Appl Physiol.* 1992;73(6):2709–12.
117. Heise GD, Martin PE. Are variations in running economy in humans associated with ground reaction force characteristics? *Eur J Appl Physiol.* 2001;84(5):438–42.
118. Daniels JT, Oldridge N. Changes in oxygen consumption of young boys during growth and running training. *Med Sci Sports.* 1971;3(4):161–5.
119. Daniels JT, Oldridge N, Nagle F, White B. Differences and changes in VO₂ among young runners 10 to 18 years of age. *Med Sci Sports.* 1978;10(3):200–3.
120. Rowland T, Cunningham L, Martel L, Vanderburgh P, Manos T, Charkoudian N. Gender effects on submaximal energy expenditure in children. *Int J Sports Med.* 1997;18(6):420–5.
121. Rowland TW, Auchinachie JA, Keenan TJ, Green GM. Submaximal aerobic running economy and treadmill performance in prepubertal boys. *Int J Sports Med.* 1988;9(3):201–4.
122. Unnithan VB, Timmons JA, Brogan RT, Paton JY, Rowland TW. Submaximal running economy in run-trained pre-pubertal boys. *J Sports Med Phys Fitness.* 1996;36(1):16–23.
123. Rowland TW, Auchinachie JA, Keenan TJ, Green GM. Physiologic responses to treadmill running in adult and prepubertal males. *Int J Sports Med.* 1987;8(4):292–7.
124. Krahenbuhl GS, Pangrazi RP. Characteristics associated with running performance in young boys. *Med Sci Sports Exerc.* 1983;15(6):486–90.
125. Krahenbuhl GS, Pangrazi RP, Chomokos EA. Aerobic responses of young boys to submaximal running. *Res Q.* 1979;50(3):413–21.
126. MacDougall JD, Roche PD, Bar-Or O, Moroz JR. Maximal aerobic capacity of Canadian schoolchildren: prediction based on age-related oxygen cost of running. *Int J Sports Med.* 1983;4(3):194–8.
127. Silverman M, Anderson SD. Metabolic cost of treadmill exercise in children. *J Appl Physiol.* 1972;33(5):696–8.
128. Thorstensson A. Effects of moderate external loading on the aerobic demand of submaximal running in men and 10 year-old boys. *Eur J Appl Physiol.* 1986;55(6):569–74.
129. Davies CT, Thompson MW. Aerobic performance of female marathon and male ultramarathon athletes. *Eur J Appl Physiol.* 1979;41(4):233–45.
130. Skinner JS, Hutsler R, Bergsteinova V, Buskirk ER. Perception of effort during different types of exercise and under different environmental conditions. *Med Sci Sports.* 1973;5(2):110–5.
131. Cooke CB, McDonagh MJ, Nevill AM, Davies CT. Effects of load on oxygen intake in trained boys and men during treadmill running. *J Appl Physiol.* 1991;71(4):1237–44.

132. Davies CT. Metabolic cost of exercise and physical performance in children with some observations on external loading. *Eur J Appl Physiol.* 1980;45(2-3):95-102.
133. Abe D, Fukuoka Y, Muraki S, Yasukouchi A, Sakaguchi Y, Niihata S. Effects of load and gradient on energy cost of running. *J Physiol Anthropol.* 2011;30(4):153-60.
134. Sjodin B, Svendenhag J. Oxygen uptake during running as related to body mass in circumpubertal boys: a longitudinal study. *Eur J Appl Physiol.* 1992;65(2):150-7.
135. Larsen HB. Kenyan dominance in distance running. *Comp Biochem Physiol A Mol Integr Physiol.* 2003;136(1):161-70.
136. Wilber RL, Pitsiladis YP. Kenyan and Ethiopian distance runners: what makes them so good? *Int J Sports Physiol Perform.* 2012;7(2):92-102.
137. Cureton KJ, Sparling PB, Evans BW, Johnson SM, Kong UD, Purvis JW. Effect of experimental alterations in excess weight on aerobic capacity and distance running performance. *Med Sci Sports.* 1978;10(3):194-9.
138. Jones BH, Toner MM, Daniels WL, Knapik JJ. The energy cost and heart-rate response of trained and untrained subjects walking and running in shoes and boots. *Ergonomics.* 1984;27(8):895-902.
139. Keren G, Epstein Y, Magazaniq A, Sohar E. The energy cost of walking and running with and without a backpack load. *Eur J Appl Physiol.* 1981;46(3):317-24.
140. Martin PE. Mechanical and physiological responses to lower extremity loading during running. *Med Sci Sports Exerc.* 1985;17(4):427-33.
141. Myers MJ, Steudel K. Effect of limb mass and its distribution on the energetic cost of running. *J Exp Biology.* 1985;116:363-73.
142. Catlin M. Effect of shoe weight on energy cost of running [abstract]. *Med Sci Sports Exerc.* 1979;11:80.
143. Soule RG, Goldman RF. Energy cost of loads carried on the head, hands, or feet. *J Appl Physiol.* 1969;27(5):687-90.
144. Jones BH, Knapik JJ, Daniels WL, Toner MM. The energy cost of women walking and running in shoes and boots. *Ergonomics.* 1986;29(3):439-43.
145. Frederick EC. Physiological and ergonomics factors in running shoe design. *Appl Ergon.* 1984;15(4):281-7.
146. Perl DP, Daoud AI, Lieberman DE. Effects of footwear and strike type on running economy. *Med Sci Sports Exerc.* 2012;44(7):1335-43.
147. Burkett LN, Kohrt WM, Buchbinder R. Effects of shoes and foot orthotics on VO₂ and selected frontal plane knee kinematics. *Med Sci Sports Exerc.* 1985;17(1):158-63.
148. Divert C, Mornieux G, Freychat P, Baly L, Mayer F, Belli A. Barefoot-shod running differences: shoe or mass effect? *Int J Sports Med.* 2008;29(6):512-8.
149. Hanson NJ, Berg K, Deka P, Meendering JR, Ryan C. Oxygen cost of running barefoot vs running shod. *Int J Sports Med.* 2011;32(6):401-6.
150. Squadrone R, Gallozzi C. Biomechanical and physiological comparison of barefoot and two shod conditions in experienced barefoot runners. *J Sports Med Phys Fitness.* 2009;49(1):6-13.
151. Lussiana T, Fabre N, Hebert-Losier K, Mourou L. Effect of slope and footwear on running economy and kinematics. *Scand J Med Sci Sports.* 2013;23(4):e246-53.
152. Sobhani S, Bredeweg S, Dekker R, Kluitenberg B, van den Heuvel E, Hijmans J, et al. Rocker shoe, minimalist shoe, and standard running shoe: A comparison of running economy. *J Sci Med Sport.* 2013;17(3):212-6.
153. Warne JP, Warrington GD. Four-week habituation to simulated barefoot running improves running economy when compared with shod running. *Scand J Med Sci Sports.* 2012;24(3):563-8.
154. Roberts TJ, Chen MS, Taylor CR. Energetics of bipedal running. II Limb design and running mechanics. *J Exp Biol.* 1998;201(Pt 19):2753-62.
155. Elliott BC, Blanksby BA. Optimal stride length considerations for male and female recreational runners. *Br J Sports Med.* 1979;13(1):15-8.
156. Malina RM, Harper AB, Avent HH, Campbell DE. Physique of female track and field athletes. *Med Sci Sports.* 1971;3(1):32-8.
157. Ker RF, Bennett MB, Bibby SR, Kester RC, Alexander RM. The spring in the arch of the human foot. *Nature.* 1987;325(7000):147-9.
158. Cavagna GA, Kaneko M. Mechanical work and efficiency in level walking and running. *J Physiol.* 1977;268(2):467-81.
159. Raichlen DA, Armstrong H, Lieberman DE. Calcaneus length determines running economy: implications for endurance running performance in modern humans and Neandertals. *J Hum Evol.* 2011;60(3):299-308.
160. Hunter GR, Katsoulis K, McCarthy JP, Ogard WK, Bamman MM, Wood DS, et al. Tendon length and joint flexibility are related to running economy. *Med Sci Sports Exerc.* 2011;43(8):1492-9.
161. Barnes KR, McGuigan MR, Kilding AE. Lower-body determinants of running economy in male and female distance runners. *J Strength Cond Res.* 2014;28(5):1289-97.
162. Nelson RC, Gregor RJ. Biomechanics of distance running: a longitudinal study. *Res Q.* 1976;47(3):417-28.
163. Moore IS, Jones AM, Dixon SJ. Mechanisms for improved running economy in beginner runners. *Med Sci Sports Exerc.* 2012;44(9):1756-63.
164. Morgan DW, Bransford DR, Costill DL, Daniels JT, Howley ET, Krahenbuhl GS. Variation in the aerobic demand of running among trained and untrained subjects. *Med Sci Sports Exerc.* 1995;27(3):404-9.
165. Cavagna GA, Willems PA, Franzetti P, Detrembleur C. The two power limits conditioning step frequency in human running. *J Physiol.* 1991;437:95-108.
166. Kaneko M, Matsumoto M, Ito A, Fuchimoto T. Optimum step frequency in constant speed running. *Human Kinetics: Champaign;* 1987.
167. Knuttgen HG. Oxygen uptake and pulse rate while running with undetermined and determined stride lengths at different speeds. *Acta Physiol Scand.* 1961;52:366-71.
168. Nummela A, Keranen T, Mikkelsen LO. Factors related to top running speed and economy. *Int J Sports Med.* 2007;28(8):655-61.
169. Nummela A, Rusko H, Mero A. EMG activities and ground reaction forces during fatigued and nonfatigued sprinting. *Med Sci Sports Exerc.* 1994;26(5):605-9.
170. McCann DJ, Higginson BK. Training to maximize economy of motion in running gait. *Curr Sports Med Rep.* 2008;7(3):158-62.
171. Hogberg P. How do stride length and stride frequency influence the energy-output during running? *Arbeitsphysiologie.* 1952;14(6):437-41.
172. Powers SK, Hopkins P, Ragsdale MR. Oxygen uptake and ventilatory responses to various stride lengths in trained women. *Am J Physiol.* 1982;36(1):5-8.
173. Dicharry J. Kinematics and kinetics of gait: from lab to clinic. *Clin Sports Med.* 2010;29(3):347-64.
174. Halvorsen K, Eriksson M, Gullstrand L. Acute effects of reducing vertical displacement and step frequency on running economy. *J Strength Cond Res.* 2012;26(8):2065-70.
175. Gruber AH, Umberger BR, Braun B, Hamill J. Economy and rate of carbohydrate oxidation during running with rearfoot and forefoot strike patterns. *J Appl Physiol.* 2013;115(2):194-201.
176. McMahon TA, Valiant G, Frederick EC. Groucho running. *J Appl Physiol.* 1987;62(6):2326-37.
177. Kyrolainen H, Belli A, Komi PV. Biomechanical factors affecting running economy. *Med Sci Sports Exerc.* 2001;33(8):1330-7.
178. Paulson S, Braun WA. Prophylactic ankle taping: Influence on treadmill running kinematics and running economy. *J Strength Cond Res.* 2013 Jul 8.
179. Cappelzozzo A. The forces and couples in the human trunk during level walking. *J Biomech.* 1983;16(4):265-77.
180. Cappelzozzo A. Force actions in the human trunk during running. *J Sports Med Phys Fit.* 1983;23(1):14-22.
181. Hinrichs R. Upper extremity function in distance running. *Biomechanics of distance running.* Champaign (IL): Human Kinetics; 1990. p. 107-34.
182. Storen O, Helgerud J, Hoff J. Running stride peak forces inversely determine running economy in elite runners. *J Strength Cond Res.* 2011;25(1):117-23.
183. Green HJ, Patla AE. Maximal aerobic power: neuromuscular and metabolic considerations. *Med Sci Sports Exerc.* 1992;24(1):38-46.
184. Throughoutman KA, Shadmehr R. Electromyographic correlates of learning an internal model of reaching movements. *J Neurosci.* 1999;19(19):8573-88.
185. Osu R, Franklin DW, Kato H, Gomi H, Domen K, Yoshioka T, et al. Short- and long-term changes in joint co-contraction associated with motor learning as revealed from surface EMG. *J Neurophysiol.* 2002;88(2):991-1004.
186. Chapman AR, Vicenzino B, Blanch P, Hodges PW. Is running less skilled in triathletes than runners matched for running training history? *Med Sci Sports Exerc.* 2008;40(3):557-65.
187. Chapman A, Vicenzino B, Blanch P, Hodges P. Do differences in muscle recruitment between novice and elite cyclists reflect different movement patterns or less skilled muscle recruitment? *J Sci Med Sport.* 2009;12(1):31-4.
188. Chapman AR, Vicenzino B, Blanch P, Hodges PW. Patterns of leg muscle recruitment vary between novice and highly trained cyclists. *J Electromyogr Kinesiol.* 2008;18(3):359-71.
189. Chapman AR, Vicenzino B, Blanch P, Hodges PW. Leg muscle recruitment during cycling is less developed in triathletes than cyclists despite matched cycling training loads. *Exp Brain Res.* 2007;181(3):503-18.
190. Bransford DR, Howley ET. Oxygen cost of running in trained and untrained men and women. *Med Sci Sports.* 1977;9(1):41-4.

191. Dolgener F. Oxygen cost of walking and running in untrained, sprint trained, and endurance trained females. *J Sports Med Phys Fit.* 1982;22(1):60–5.
192. Noakes TD. Implications of exercise testing for prediction of athletic performance: a contemporary perspective. *Med Sci Sports Exerc.* 1988;20(4):319–30.
193. Paavolainen LM, Hakkinen K, Hamalainen I, Nummela A, Rusko H. Explosive-strength training improves 5-km running time by improving running economy and muscle power. *J Appl Physiol.* 1999;86(5):1527–33.
194. Paavolainen LM, Nummela AT, Rusko HK. Neuromuscular characteristics and muscle power as determinants of 5-km running performance. *Med Sci Sports Exerc.* 1999;31(1):124–30.
195. Paavolainen LM, Nummela A, Rusko H, Hakkinen K. Neuromuscular characteristics and fatigue during 10 km running. *Int J Sports Med.* 1999;20(8):516–21.
196. Nummela AT, Heath KA, Paavolainen LM, Lambert MI, St Clair Gibson A, Rusko HK, et al. Fatigue during a 5-km running time trial. *Int J Sports Med.* 2008;29(9):738–45.
197. Dalleau G, Belli A, Bourdin M, Lacour JR. The spring-mass model and the energy cost of treadmill running. *Eur J Appl Physiol.* 1998;77(3):257–63.
198. Arampatzis A, De Monte G, Karamanidis K, Morey-Klapsing G, Stafiliadis S, Bruggemann GP. Influence of the muscle-tendon unit's mechanical and morphological properties on running economy. *J Exp Biol.* 2006;209(Pt 17):3345–57.
199. Franklin DW, Burdet E, Osu R, Kawato M, Milner TE. Functional significance of stiffness in adaptation of multijoint arm movements to stable and unstable dynamics. *Exp Brain Res.* 2003;151(2):145–57.
200. Avela J, Komi PV. Reduced stretch reflex sensitivity and muscle stiffness after long-lasting stretch-shortening cycle exercise in humans. *Eur J Appl Physiol.* 1998;78(5):403–10.
201. Heise G, Shinohara M, Binks L. Biarticular leg muscles and links to running economy. *Int J Sports Med.* 2008;29(8):688–91.
202. Albracht K, Arampatzis A. Exercise-induced changes in triceps surae tendon stiffness and muscle strength affect running economy in humans. *Eur J Appl Physiol.* 2013;113(6):1605–15.
203. Kubo K, Tabata T, Ikebukuro T, Igarashi K, Tsunoda N. A longitudinal assessment of running economy and tendon properties in long-distance runners. *J Strength Cond Res.* 2010;24(7):1724–31.
204. Saibene F. The mechanisms for minimizing energy expenditure in human locomotion. *Eur J Clin Nutr.* 1990;44 Suppl 1:65–71.
205. Nicol C, Avela J, Komi PV. The stretch-shortening cycle : a model to study naturally occurring neuromuscular fatigue. *Sports Med.* 2006;36(11):977–99.
206. Gollhofer A, Kyrolainen H. Neuromuscular control of the human leg extensor muscles in jump exercises under various stretch-load conditions. *Int J Sports Med.* 1991;12(1):34–40.
207. Abe D, Muraki S, Yanagawa K, Fukuoka Y, Niihata S. Changes in EMG characteristics and metabolic energy cost during 90-min prolonged running. *Gait Posture.* 2007;26(4):607–10.
208. Aruin AS, Prilutskii BI, Raitsin LM, Savel'ev IA. Biomechanical properties of muscles and efficiency of movement. *Hum Physiol.* 1979;5(4):426–34.
209. Asmussen E, Bonde-Petersen F. Apparent efficiency and storage of elastic energy in human muscles during exercise. *Acta Physiol Scand.* 1974;92(4):537–45.
210. Luhtanen P, Komi PV. Mechanical energy states during running. *Eur J Appl Physiol.* 1978;38(1):41–8.
211. Leger L, Mercier D. Gross energy cost of horizontal treadmill and track running. *Sports Med.* 1984;1(4):270–7.
212. Winter DA. Calculation and interpretation of mechanical energy of movement. *Exerc Sport Sci Rev.* 1978;6:183–201.
213. Cavagna GA, Citterio G. Effect of stretching on the elastic characteristics and the contractile component of frog striated muscle. *J Physiol.* 1974;239(1):1–14.
214. Alexander R. Elastic mechanisms in animal movement. Cambridge: University Press; 1988.
215. Cavagna GA, Saibene FP, Margaria R. Mechanical work in running. *J Appl Physiol.* 1964;19:249–56.
216. Williams KR, Cavanagh PR. A model for the calculation of mechanical power during distance running. *J Biomech.* 1983;16(2):115–28.
217. Ito A, Komi PV, Sjodin B, Bosco C, Karlsson J. Mechanical efficiency of positive work in running at different speeds. *Med Sci Sports Exerc.* 1983;15(4):299–308.
218. Aura O, Komi PV. The mechanical efficiency of locomotion in men and women with special emphasis on stretch-shortening cycle exercises. *Eur J Appl Physiol.* 1986;55(1):37–43.
219. Aura O, Komi PV. Mechanical efficiency of pure positive and pure negative work with special reference to the work intensity. *Int J Sports Med.* 1986;7(1):44–9.
220. Cheng CF, Cheng KH, Lee YM, Huang HW, Kuo YH, Lee HJ. Improvement in running economy after 8 weeks of whole-body vibration training. *J Strength Cond Res.* 2012;26(12):3349–57.
221. Ferrauti A, Bergemann M, Fernandez-Fernandez J. Effects of a concurrent strength and endurance training on running performance and running economy in recreational marathon runners. *J Strength Cond Res.* 2010;24(10):2770–8.
222. Taipale RS, Mikkola J, Nummela A, Vesterinen V, Capostagno B, Walker S, et al. Strength training in endurance runners. *Int J Sports Med.* 2009;31(7):486–76.
223. Taipale RS, Mikkola J, Vesterinen V, Nummela A, Hakkinen K. Neuromuscular adaptations during combined strength and endurance training in endurance runners: maximal versus explosive strength training or a mix of both. *Eur J Appl Physiol.* 2013;113(2):325–35.
224. Berryman N, Maurel D, Bosquet L. Effect of plyometric vs dynamic weight training on the energy cost of running. *J Strength Cond Res.* 2010;24(7):1818–25.
225. Denadai BS, Ortiz MJ, Greco CC, de Mello MT. Interval training at 95% and 100% of the velocity at VO₂ max: effects on aerobic physiological indexes and running performance. *Appl Physiol Nutr Metab.* 2006;31(6):737–43.
226. Guglielmo LG, Greco CC, Denadai BS. Effects of strength training on running economy. *Int J Sports Med.* 2009;30(1):27–32.
227. Mikkola J, Vesterinen V, Taipale R, Capostagno B, Hakkinen K, Nummela A. Effect of resistance training regimens on treadmill running and neuromuscular performance in recreational endurance runners. *J Sports Sci.* 2011;29(13):1359–71.
228. Spurr RW, Murphy AJ, Watsford ML. The effect of plyometric training on distance running performance. *Eur J Appl Physiol.* 2003;89(1):1–7.
229. Storen O, Helgerud J, Stoa EM, Hoff J. Maximal strength training improves running economy in distance runners. *Med Sci Sports Exerc.* 2008;40(6):1087–92.
230. Saunders PU, Green DJ. Runners and Walkers. In: Tanner R, Gore CJ, editors. *Physiological Tests for Elite Athletes.* Champaign: Human Kinetics; 2013. p. 404.
231. Daniels JT, Scardina N, Foley P. VO₂max during five modes of exercise. In: Bachl N, Prokop L, Suckert R, editors. *Proceedings of the World Congress on Sports Medicine.* Vienna: Urban & Schwarzenberg; 1984. p. 604–15.
232. Daniels JT. Physiological characteristics of champion male athletes. *Res Q.* 1974;45(4):342–8.

Submit your manuscript to a SpringerOpen[®] journal and benefit from:

- Convenient online submission
- Rigorous peer review
- Immediate publication on acceptance
- Open access: articles freely available online
- High visibility within the field
- Retaining the copyright to your article

Submit your next manuscript at ► springeropen.com