

Factors Affecting Running Economy in Trained Distance Runners

Philo U. Saunders,^{1,2} David B. Pyne,¹ Richard D. Telford³ and John A. Hawley²

- 1 Department of Physiology, Australian Institute of Sport, Belconnen, ACT, Australia
- 2 Exercise Metabolism Group, Faculty of Medical Sciences, RMIT University, Bundoora, Victoria, Australia
- 3 School of Physiotherapy and Exercise Science, Griffith University, Gold Coast, Queensland, Australia

Contents

Abstract	465
1. Measurement of Running Economy (RE)	467
1.1 Treadmill RE Compared with Outdoor Running	467
1.2 Reliability of RE	468
1.3 Correcting RE for Body Mass	468
2. RE and Performance	469
3. Physiological Factors Affecting RE	470
4. Biomechanical Factors Affecting RE	471
4.1 Anthropometry	473
4.2 Kinematics and Kinetics	473
4.3 Flexibility	474
4.4 Ground Reaction Forces	475
5. Interventions to Improve RE	477
5.1 Strength Training	477
5.2 Altitude Exposure	478
5.3 Training in the Heat	480
6. Conclusions and Future Directions	480

Abstract

Running economy (RE) is typically defined as the energy demand for a given velocity of submaximal running, and is determined by measuring the steady-state consumption of oxygen ($\dot{V}O_2$) and the respiratory exchange ratio. Taking body mass (BM) into consideration, runners with good RE use less energy and therefore less oxygen than runners with poor RE at the same velocity. There is a strong association between RE and distance running performance, with RE being a better predictor of performance than maximal oxygen uptake ($\dot{V}O_{2max}$) in elite runners who have a similar $\dot{V}O_{2max}$.

RE is traditionally measured by running on a treadmill in standard laboratory conditions, and, although this is not the same as overground running, it gives a good indication of how economical a runner is and how RE changes over time. In order to determine whether changes in RE are real or not, careful standardisation of footwear, time of test and nutritional status are required to limit typical error of measurement. Under controlled conditions, RE is a stable test capable of detecting

relatively small changes elicited by training or other interventions. When tracking RE between or within groups it is important to account for BM. As $\dot{V}O_2$ during submaximal exercise does not, in general, increase linearly with BM, reporting RE with respect to the 0.75 power of BM has been recommended.

A number of physiological and biomechanical factors appear to influence RE in highly trained or elite runners. These include metabolic adaptations within the muscle such as increased mitochondria and oxidative enzymes, the ability of the muscles to store and release elastic energy by increasing the stiffness of the muscles, and more efficient mechanics leading to less energy wasted on braking forces and excessive vertical oscillation.

Interventions to improve RE are constantly sought after by athletes, coaches and sport scientists. Two interventions that have received recent widespread attention are strength training and altitude training. Strength training allows the muscles to utilise more elastic energy and reduce the amount of energy wasted in braking forces. Altitude exposure enhances discrete metabolic aspects of skeletal muscle, which facilitate more efficient use of oxygen.

The importance of RE to successful distance running is well established, and future research should focus on identifying methods to improve RE. Interventions that are easily incorporated into an athlete's training are desirable.

The ability to metabolise energy aerobically is a prerequisite for superior endurance performance.^[1-3] In competitive distance running, successful performance has been correlated to an athlete's maximal oxygen uptake ($\dot{V}O_{2max}$).^[1,3-5] Performance in endurance events is directly influenced by alterations in the availability of oxygen, carbohydrate and fat, and the density of muscle mitochondria.^[6] $\dot{V}O_{2max}$ is influenced by a variety of factors including muscle capillary density, haemoglobin mass, stroke volume, aerobic enzyme activity and muscle fibre type composition.^[6] Although a high $\dot{V}O_{2max}$ is required for distance running, other physiological and performance factors are important in determining endurance capacity.^[4] These factors depend on the race distance and include the percentage of $\dot{V}O_{2max}$ a runner can sustain without accumulating lactic acid, the ability to utilise fat as a fuel at high work rates and thereby 'spare' carbohydrate and running at race pace with relatively low energy expenditure (i.e. good running economy [RE]). The velocity associated with attainment of $\dot{V}O_{2max}$ ($v\dot{V}O_{2max}$) and the velocity at the onset of blood lactate accumulation are good indicators of distance running performance.^[7]

Efficient utilisation of available energy facilitates optimum performance in any endurance running event. Efficiency refers to the ratio of work done to energy expended.^[8] RE is represented by the energy expenditure and expressed as the submaximal $\dot{V}O_2$ at a given running velocity.^[4,9-11] The energy cost of running reflects the sum of both aerobic and anaerobic metabolism, and the aerobic demand (measured by the $\dot{V}O_2$ in L/min) at a given speed does not necessarily account for the total energy cost of running, which is measured in joules or kilojoules of work done.^[8] Runners with good RE use less oxygen than runners with poor RE at the same steady-state speed.^[12] Figure 1 illustrates two international calibre 10km runners measured in our laboratory: both runners had a similar $\dot{V}O_{2max}$, with the more efficient runner (better RE) having a 10km time of 1 minute faster than the less efficient runner. The steady-state condition is verified by the maintenance of blood lactate concentration (La) at baseline levels^[13] and a respiratory exchange ratio (RER) <1 .^[4] RE can vary among runners with a similar $\dot{V}O_{2max}$ by as much as 30%.^[8] In elite or near-elite runners with a similar $\dot{V}O_{2max}$, RE is a better predictor of performance than $\dot{V}O_{2max}$.^[5,14] Accordingly, it

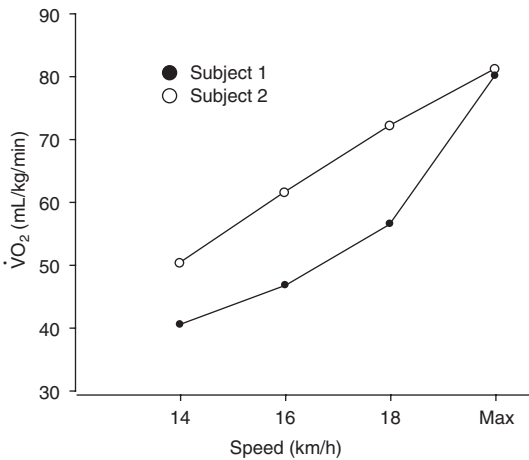


Fig. 1. Comparison of oxygen uptake ($\dot{V}O_2$) [mL/kg/min] in two international calibre 10km runners, one with good economy (subject 1) and the other with poor economy (subject 2) [Saunders et al. unpublished data, 2003]. **Max** = maximum.

follows that substantial improvements in RE could facilitate improved performance in distance runners. In summary, the relationship between RE and performance is well documented, with many independent reports demonstrating a strong relationship between RE and distance running performance.^[1,4,5,10,15,16]

The purposes of this review are to examine the validity and reliability of currently used tests for measuring RE, examine research relating to physiological and biomechanical factors which influence RE, describe interventions that have attempted to improve RE, and discuss potential areas for future research directions in this field.

1. Measurement of Running Economy (RE)

1.1 Treadmill RE Compared with Outdoor Running

Measures of RE have typically been determined in the laboratory by having the athlete run on a motorised treadmill. This practice partially overcomes many of the difficulties in obtaining reliable metabolic data in the field (i.e. during training and competition).^[14] Air and wind resistance are effec-

tively eliminated during indoor running; however, transferring treadmill data to overground running requires caution.^[8,17] Pugh^[18] estimated that 8% of the total energy cost of middle-distance track running (5000m) is expended overcoming air resistance. Another study estimated the amount of energy required to overcome air resistance was 4% for middle-distance runners and 2% for marathon runners.^[19] When a tailwind velocity is equal to running velocity, overground $\dot{V}O_2$ was equivalent to treadmill $\dot{V}O_2$.^[17] Differences between overground running and treadmill running are more likely to be observed as speed increases and the effect of air resistance becomes more pronounced.^[8] Hagerman et al.^[20] reported lower submaximal $\dot{V}O_2$ values at an altitude where the air is less dense than at sea level. Using a 14.5 km/h headwind in order to simulate outdoor conditions, Costill and Fox^[21] reported a 15% difference in submaximal $\dot{V}O_2$ between control conditions (no wind) and a simulated headwind. It is clear that running on the treadmill is not the same as running over ground, where wind resistance affects $\dot{V}O_2$. 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 forces. However, we can be confident that RE measured on a treadmill is highly correlated to RE over ground. It is reasonable, then, to assume that interventions affecting RE on the treadmill will similarly affect RE over ground. From work in our laboratory, we have determined that reliable measures of RE need to be obtained at speeds eliciting $\leq 85\%$ of $\dot{V}O_{2max}$ in highly trained distance runners.

Recent technological advances have allowed measurement of overground RE using portable oxygen analysers. The K4 Cosmed analyser (Rome, Italy) described by Hausswirth et al.^[22] is a lightweight, accurate, telemetric system that enables measurement of energy requirements during both submaximal and maximal exercise in the laboratory or field. The K4 system allows continuous recording of $\dot{V}O_2$ during incremental progressive field tests to accurately determine an athlete's ventilatory characteristics. The validity of the K4 Cosmed telemetric

system was demonstrated against a metabolic measurement cart (CPX, Medical Graphics, Saint-Paul, Minnesota, USA) during both submaximal and maximal exercise, with no difference observed between the two oxygen analysis systems.^[22] Recent research has utilised the K4 portable oxygen analyser to measure $\dot{V}O_2$ in various intervention studies on moderate to highly trained distance runners.^[23-26] It appears that overground RE can be measured in a natural field setting with the K4 Cosmed telemetric system and similar devices, although careful attention must be made to ensure post-testing results are not influenced by changes in environmental conditions.

1.2 Reliability of RE

Consideration of the typical intra-individual variation in RE is essential when investigating the effectiveness of interventions aimed at modifying RE. As has been previously noted,^[14] small sample sizes and omission of the typical error (TE) restricts the degree to which meaningful conclusions on the impact an intervention has on RE can be drawn. In order to interpret the practical significance of various interventions aimed at improving RE, a statement of the test-retest reliability or TE should be provided. In research settings, a rigorous experimental design is necessary to control confounding variables and to permit a valid determination of the impact of interventions on RE. Daniels et al.^[27] observed an 11% variation in the stability of RE in ten trained males running at 16 km/h, even after controlling for variability associated with footwear and test equipment. Well controlled reliability studies measuring RE show intra-individual variations between 1.5–5%,^[28-34] indicating that test-retest intra-individual results are relatively stable.

Factors such as treadmill running experience, footwear, time of day of testing, prior training activity and nutritional status may affect intra-individual variation in RE.^[29] Morgan^[29] investigated 16 male subjects who completed two 10-minute RE tests at the same time of the day within a 4-day period, wearing the same pair of shoes. The intra-individual RE was 1.6%. Another study examined intra-indi-

vidual RE in 17 male runners following 30–60 minutes of treadmill familiarisation at the same time of the day, in the same pair of shoes and in a non-fatigued state.^[32] There was a high day-to-day correlation in RE ($r = 0.95$) with a mean coefficient of variation (CV) of 1.3%. Pereira et al.^[34] reported a CV of 1.5% for RE in five trained male runners by careful control of extrinsic factors such as time of testing, diet, footwear and relative workload.

Pereira and Freedson^[33] note that previous studies investigating intra-individual variation in RE have not compared intra-individual variability between runners differing in training level. These investigators used seven highly trained males ($\dot{V}O_{2max}$; 69.1 mL/kg/min) and eight moderately trained males ($\dot{V}O_{2max}$ 58.3 mL/kg/min) with testing being carried out for 3 weeks at ~88% of the velocity associated with the individual lactate threshold (LT). Time of day, day of the week, diet and footwear were controlled within each subject across the three tests. CVs of 1.8% for the highly trained group and 2.0% for the moderately trained group (average 1.9%) were reported.^[33] After accounting for technical error, biological variation accounted for ~94% of the intra-individual variation in RE. The results suggest that workloads below LT may permit more stable measures of RE to be obtained. Brisswalter and Legros^[28] demonstrated that RE, respiratory measures and stride rate were stable measures for assessing energy cost associated with running in elite middle-distance runners. The authors reported a variation of 4.7% in RE in ten elite 800m runners ($\dot{V}O_{2max}$, 68 mL/kg/min; mean 800m time, 1:49 minutes). In a study of elite French distance runners, subjects were tested three times over a 12-month period to determine the stability of RE. RE was stable over the 12-month period despite an improvement in $\dot{V}O_{2max}$. The authors concluded that in elite distance runners, RE is a difficult parameter to improve.^[35]

1.3 Correcting RE for Body Mass

RE can be expressed as a ratio of a runners' $\dot{V}O_2$ (L/min) divided by their body mass (BM) in kilograms.^[36] However, when comparing individuals or

groups who differ in BM this expression may induce error because submaximal $\dot{V}O_2$ during running does not increase proportionately to BM.^[37] In animals, the oxygen cost of running does not increase proportionately to BM^[38] and in humans, the $\dot{V}O_2$ per kilogram of BM is higher in children than adults.^[8,39-50] Bergh et al.^[37] suggests that, in humans, the higher submaximal $\dot{V}O_2$ observed in children relates to differences in body size and not merely growth and maturation. Sjodin and Svedenhag^[51] concur with this, and suggest that the improved RE measured in relation to BM, observed in adolescent boys during growth, may largely be attributable to its measurement of $\dot{V}O_2$ per kilogram of BM.

Theory associated with elastic components of muscle and connective tissue estimates $\dot{V}O_2$ to be proportional to the 0.75 power of BM.^[52] Bergh et al.^[37] suggested that submaximal $\dot{V}O_2$ and $\dot{V}O_{2max}$ measures during running are better related to $BM^{-0.66}$ or $BM^{-0.75}$ than BM^{-1} . Furthermore, several studies^[40,53,54] have shown an inverse relationship between BM and submaximal $\dot{V}O_2/kg$, providing further support that $\dot{V}O_2$ reported as mL/kg/min may provide misleading comparative results.^[37,51]

Another factor affecting RE is the pattern of distribution of mass in the body. Carrying mass distally increases the aerobic demand of running to a greater extent than carrying mass closer to the centre of mass.^[55-58] Aerobic demand is increased by 1% for every extra kilogram carried on the trunk, however, when the mass was carried in the shoes, aerobic demand increased by 10% for every additional kilogram.^[58] Jones et al.^[56] found an average increase in $\dot{V}O_2$ of 4.5% per kilogram of load carried on the feet when running at 12 km/h. Another study investigated the effect of carrying mass on either the thighs or feet and reported a 7% per kilogram increase in $\dot{V}O_2$ when the mass was carried on the thigh compared with 14% per kilogram increase in $\dot{V}O_2$ when carried on the feet.^[57] The cushioning of shoes also affects RE, with an approximate 2.8% energy saving realised for treadmill running in well cushioned shoes compared with poorly cushioned shoes of similar mass.^[59] The authors attributed this

finding to the extra muscular effort required to provide cushioning if the shoe itself does not provide adequate shock absorption.

2. RE and Performance

The relationship between RE and performance is well documented. Early research comparing elite American distance runners ($\dot{V}O_{2max}$ 79 mL/kg/min) with good distance runners ($\dot{V}O_{2max}$; 69.2 mL/kg/min), indicated that the elite runners had better RE than good runners. When expressed as a percentage of $\dot{V}O_{2max}$ this difference in RE was magnified, with the elite runners working at a lower percentage of their $\dot{V}O_{2max}$.^[16] Di Prampero et al.^[15] stated that a 5% increase in RE induced an approximately 3.8% increase in distance running performance. As an example of the relationship between RE and performance, a case study of American mile record holder Steve Scott, reported that during a 6-month period of training, Scott improved his $\dot{V}O_{2max}$ by 3.8% (74.4 to 77.2 mL/kg/min).^[8] During the same period there was a 6.6% improvement in RE (48.5 to 45.3 mL/kg/min) at a running velocity of 16 km/h. The combined improvement of an increased $\dot{V}O_{2max}$ and a better RE reduced the relative intensity of running at 16 km/h by 10.0% (65.1% to 58.6% of $\dot{V}O_{2max}$) and was associated with improved performance during this period.^[10]

Svedenhag and Sjodin^[60] observed variations in RE and performance in elite distance runners ($\dot{V}O_{2max}$ 75 mL/kg/min) who undertook alternating sessions of slow distance, uphill and interval training over a 22-month period. Athletes significantly reduced their $\dot{V}O_2$ at 15 and 20 km/h accompanied by enhanced performances over 5000m. However, not all studies have demonstrated a significant relationship between RE and performance. Williams and Cavanagh^[54] failed to identify a significant relationship between RE at 13 km/h and 10km performance (~35 minutes) in a group of 16 runners. The percentage of slow-twitch muscle fibres and the runners $\dot{V}O_{2max}$ correlated best with 10km performance. Conley and Krahenbuhl^[4] showed that RE was a good predictor of performance in runners of comparable ability. In that study, 12 highly trained male

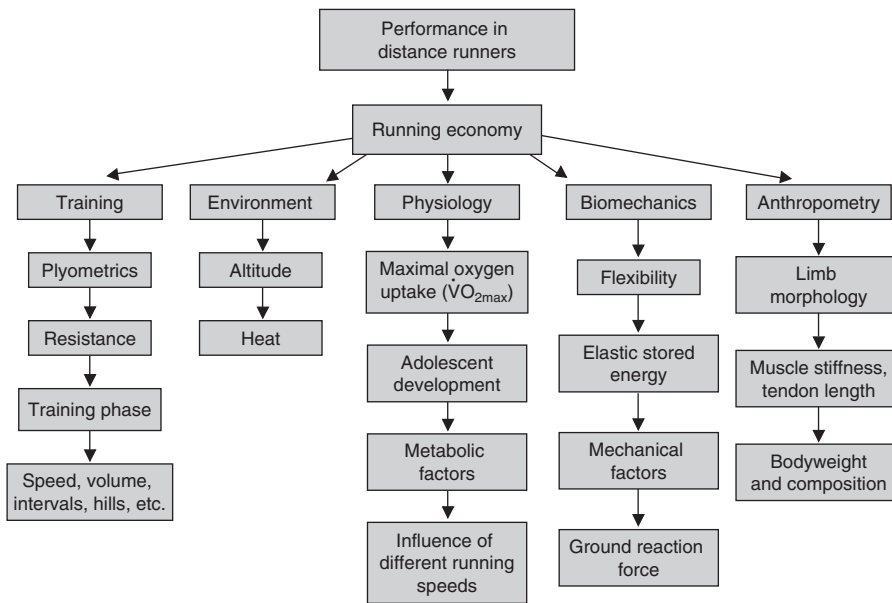


Fig. 2. Factors affecting running economy.

distance runners ($\dot{V}O_{2\max}$ ~ 72 mL/min and 10km performance ~ 32 minutes) were tested 3–6 days after they had competed in a 10km race. There were significant correlations between submaximal $\dot{V}O_2$ and performance at running speeds of 14, 16 and 18 km/h. Some 65% of the variation in race performance could be attributed to differences in RE, with the more economical runners performing the best. The more economical runners were able to run at a lower percentage of their $\dot{V}O_{2\max}$, resulting in lower La at a given speed. The latter factor is closely associated with the pace a runner is able to maintain for races >15 minutes.^[61] These data also provide evidence that RE at slower speeds are useful in predicting performance in races at faster speeds.

Weston et al.^[62] investigated the RE and performance of eight African (Kenyan) and eight Caucasian distance runners. The Kenyan runners had similar 10km race performance to the Caucasian group, despite having a 13% lower $\dot{V}O_{2\max}$. The RE of the Kenyan runners was 5% better than the Caucasian group, and when RE was normalised to $BM^{-0.66}$ the Kenyans had an 8% better RE. The Kenyan runners also completed the 10km at a higher percentage of

their $\dot{V}O_{2\max}$ but with similar La as the Caucasian runners.

These studies indicate that improving athletes RE is related to improvements in distance running performance. RE is likely to be influenced by a number of factors (figure 2) and any intervention (training, altitude, heat) that can reduce the oxygen cost over a range of running velocities will conceivably lead to enhanced performance.

3. Physiological Factors Affecting RE

Fluctuations in physiological factors such as core temperature (C_{Temp}), heart rate (HR), ventilation (V_E) and La, may be associated with changes in RE during competition.^[14,63–65] Thomas et al.^[12] investigated the effect of a simulated 5km race on RE, V_E , C_{Temp} , La and HR. RE was determined using a constant treadmill speed eliciting 80–85% of the athletes $\dot{V}O_{2\max}$. RE decreased significantly and V_E , C_{Temp} , La and HR all increased significantly from the beginning to the end of the 5km run. The increased V_E was the only factor that correlated moderately with the decrease in RE ($r = 0.64$; $p < 0.05$), indicating a greater oxygen cost was associated with the increase in V_E . A higher C_{Temp} increases

$\dot{V}O_2$ at a given speed.^[66-69] Increases in the metabolic cost from augmented circulation, V_E and sweating are the major factors that increase submaximal $\dot{V}O_2$ and decrease RE.^[68] In contrast, Rowell et al.^[70] stated that the mechanical efficiency of muscle increases when C_{Temp} is mildly elevated, reducing $\dot{V}O_2$ by an amount equal to or greater than the increase caused by changes in the cost of circulation, V_E and sweating. The composition of muscle fibres also seems to influence RE. It has been suggested that a higher percentage of slow-twitch muscle fibres is associated with better RE,^[54,71,72] indicating that metabolic activity or actual speed of contraction of the muscle fibres may influence RE. Myocardial $\dot{V}O_2$ also constitutes a significant fraction of whole body $\dot{V}O_2$ during exercise. Reductions in myocardial $\dot{V}O_2$ 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).^[73]

Little consensus exists on the effects of training and RE, largely as a consequence of limitations in existing experimental designs such as small sample sizes, lack of multiple economy measures to account for normal intra-individual variation and failure to control for factors that influence RE (e.g. fatigue level, state of training, treadmill experience and footwear). Some,^[10,74-81] but not all^[5,42,82] studies have reported improvements in RE after various training interventions. The initial level of fitness of the subjects is an important factor when considering whether training alters RE.^[42] Numerous studies indicate that trained subjects are more economical than untrained or less trained subjects^[8,74,79,82-84] and long-distance runners are more economical than middle-distance runners.^[8,16,84] The better RE in long distance runners is largely attributable to a lower vertical displacement of the runner's centre of mass during running probably related to neuromuscular adaptations induced by long, slow distance training.^[85] Endurance training leads to increases in the morphology and functionality of skeletal muscle mitochondria. An increase in the respiratory capacity of skeletal muscle permits trained runners to use less oxygen per mitochondrial respiratory chain for a given submaximal running speed. These responses

invoke improvements in RE, a smaller disturbance in homeostasis and slower utilisation of muscle glycogen in the working musculature.^[86] Daniels and Daniels^[87] found that 800/1500m specialists were more economical than marathon runners at velocities above 19 km/h, yet were less economical than marathon runners at slower speeds. Without a measure of the anaerobic contribution to total metabolism, it is difficult to conclude that the 800/1500m specialists were more economical than the marathon runners at the faster running velocities. Males were more economical than females at common speeds and relative intensities, but there was no difference in RE between males and females at typical race intensities for each sex. Another study was unable to detect significant differences in RE between trained male and female distance runners across four running velocities (12–16 km/h).^[88]

Franch et al.^[78] investigated the effects of three types of intensive running training on RE in 36 male recreational runners ($\dot{V}O_{2max} \sim 55$ mL/kg/min). Subjects were assigned to either continuous-distance training, long-repetition training (4–6 × 4 minutes run with 3 minutes rest) or short-repetition training (30–40 × 15 seconds run with 15 seconds rest) groups, and trained three times a week for 6 weeks.^[78] Runners undertaking continuous-distance training and long-repetition training increased their RE by approximately 3% while short-repetition training had little effect on RE (0.9% change), suggesting that longer training is the best way to improve RE. Thomas et al.^[65] suggests that those training in an effort to improve RE need to concentrate on improving physiological characteristics such as HR, V_E , La and C_{Temp} regulation in order to decrease the energy demand associated with these parameters. Interval training may be beneficial to RE by reducing HR, V_E and La at higher running speeds.^[89]

4. Biomechanical Factors Affecting RE

Running involves the conversion of muscular forces translocated through complex movement patterns that utilise all the major muscle joints in the body. High performance running is reliant on skill

Table I. Biomechanical factors related to better economy in runners^[9]

Factor	Description for better running economy
Height	Average or slightly smaller than average for males and slightly greater than average for females
Ponderal index	High index and ectomorphic or mesomorphic physique
Body fat	Low percentage
Leg morphology	Mass distributed closer to the hip joint
Pelvis	Narrow
Feet	Smaller than average
Shoes	Lightweight but well cushioned shoes
Stride length	Freely chosen over considerable training time
Kinematics	Low vertical oscillation of body centre of mass
	More acute knee angles during swing
	Less range of motion but greater angular velocity of plantar flexion during toe-off
	Arm motion that is not excessive
	Faster rotation of shoulders in the transverse plane
Kinetics	Greater angular excursion of the hips and shoulders about the polar axis in the transverse plane
	Low peak ground reaction forces
Elastic energy	Effective exploitation of stored elastic energy
Training	Comprehensive training background
Running surface	Intermediate compliance

and precise timing in which all movements have purpose and function.^[9] Clearly, changing aspects of running mechanics that result in a runner using less energy at any given speed is advantageous to performance.^[90,91] Biomechanical characteristics associated with improved RE are shown in table I.^[9] The spring-mass model is an important factor associated with RE, where the bounce of the body on the ground is counteracted by the spring behaviour of the support leg. During the eccentric phase of contact, mechanical energy is stored in the muscles, tendons and ligaments acting across joints. Recovery during the concentric phase of the stored elastic energy reduces the energy expenditure. An oscillating system is also characterised by a resonant frequency. The resonant frequency is the frequency at which a system freely vibrates after a mechanical impulse.^[92] RE was significantly correlated with muscle stiffness ($r = 0.80$) and resonant frequency ($r = 0.79$) of the propulsive leg, with stiffer muscles operating at lower resonant frequencies eliciting the best RE.^[92] Several studies that have examined RE and running mechanics after previously fatiguing exercise and have reported little change in running kinematics to explain decreases in RE.^[93-96] In con-

trast, Hausswirth et al.^[97] showed that RE was impaired during the last 45 minutes of a marathon run on a treadmill, which was partly attributed to biomechanical factors such as a greater forward lean and a decrease in stride length. In a similar study, investigating the effects of running a marathon on RE, both submaximal $\dot{V}O_2$ and RER increased during, and 2 hours after, the marathon. The impaired RE observed could not be completely explained by any changes observed in the mechanics, and was attributed to the increasing physiological stresses (e.g. heat accumulation and increased reliance of fat utilisation) associated with running a marathon.^[94] Thomas et al.^[65] investigated the effects of a simulated 5km race on RE and running mechanics of trained female athletes. RE decreased during the 5km race, with athletes metabolising more oxygen at the same intensity. The changes in RE observed in this study were not caused by any alterations in the mechanics of running, indicating that physiological factors are more important in reducing RE. Taken collectively, the weight of evidence from the existing literature suggests that if previously fatiguing exercise is to reduce RE, it is likely to be through physiological rather than biomechanical factors.

4.1 Anthropometry

Anthropometric characteristics such as height, limb dimensions, body fat, as well as BM, have been addressed as potential influences on RE. While leg length contributes to angular inertia and the metabolic cost of moving the legs during running,^[9] there seems little consensus on whether leg length is an important factor in determining RE. In 31 male distance runners with a 10km performance time of ~35 minutes, a large variation in RE was observed in the absence of any differences associated with segmental lengths and masses.^[54] In contrast, there is evidence that leg mass and distribution of mass may influence RE. Williams and Cavanagh^[54] reported a modest inverse relationship between BM and submaximal $\dot{V}O_2/\text{kg}$ ($r = -0.52$) and between maximal thigh circumference and submaximal $\dot{V}O_2/\text{kg}$ ($r = -0.58$), indicating that heavier than average runners use less oxygen per kilogram of BM. Myers and Steudel^[58] hypothesised that a runner with a proportionally smaller amount of BM concentrated in the extremities, particularly the legs, would perform less work moving their body segments during running, assuming that all other factors are unchanged (e.g. speed, BM, running style).

4.2 Kinematics and Kinetics

Early research suggested that well trained runners running at 14 and 16 km/h were most economical at the runner's self-selected stride length, compared with other pre-determined stride lengths.^[98] More recent work has confirmed that the aerobic demand of running at a given speed is lowest at a self-selected stride length.^[90] Submaximal $\dot{V}O_2$ increases curvilinearly as stride length is either lengthened or shortened from that self-selected by the runner.^[90,98-101] Cavanagh and Williams^[90] concluded that there is little need to dictate stride length for well trained athletes since they display near optimal stride length. They postulated two mechanisms for this phenomenon. Firstly, runners naturally acquire an optimal stride length and stride rate over time, based on perceived exertion. Secondly, runners may adapt physiologically through repeated training at a

particular stride length/stride frequency for a given running speed.^[90]

The first studies comparing the biomechanical characteristics of elite and good runners indicated that elite runners had slightly less vertical oscillation, were more symmetrical, and had better RE.^[102] Williams and Cavanagh^[103] found that better RE in elite male distance runners was associated with a more extended lower leg at foot strike, a lower vertical force peak and a longer contact time. More economical runners tend to exhibit less arm movement, as measured by wrist excursion during the stride.^[54,104] Greater maximal plantar flexion velocity and greater horizontal heel velocity at foot contact are also associated with better RE in elite male distance runners.^[103] While these authors demonstrated links with various kinematic parameters and RE, it would appear that further research is warranted to determine if changing a runner's kinematics induces an improvement in RE.

Recent research has comprehensively investigated biomechanical factors affecting RE.^[105] $\dot{V}O_2$ at 12–13 different running speeds was compared with kinematic data and three-dimensional ground reaction forces (GRF) simultaneously with telemetric EMG recordings of selected leg muscles. Joint moments and power were calculated using two-dimensional video analysis and the digitised segment coordinates were transferred to a computer system. The biomechanical parameters examined (angular displacements between the ankle, knee and hip joints; joint angular velocities) were not good predictors of RE. However, force production during ground contact, coupled with the activation of the leg extensors during the pre-activity and braking phases and their coordination with longer-lasting activation of the hamstring muscles were of importance. The authors pointed out that co-activation of the muscles around the knee and ankle joints increases the joint stiffness, which appears to be related to better RE. The action of the hip extensors also becomes beneficial in this respect during ground contact.^[105] Refining mechanical elements such as stride length and frequency or the integration and timing of muscle activity to utilise the storage and release of elastic

energy more effectively may lead to improvements in RE.^[9]

Williams and Cavanagh^[54] provided substantial support for the notion that more economical runners have identifiable kinetic patterns in their running mechanics. They observed that ground-support time and peak medial force correlated with submaximal $\dot{V}O_2$ ($r = 0.49$ and 0.50 , respectively). More economical runners had lower first peaks in the vertical component of the GRF, smaller antero-posterior and vertical peak forces, and a more predominant rear-foot striking pattern.^[54] The authors suggested that these characteristics affect muscular demands both before and during support, with forefoot strikers relying on musculature to assist with cushioning, making them less economical. In contrast, rear foot strikers tend to rely on footwear and skeletal structures to take the load and are more economical.^[54] Well cushioned shoes reduce oxygen cost by up to 2.8% over stiffer shoes of the same weight.^[59,91] However, it appears that there may be an individually optimal degree of cushioning, as shoes with a 'spring rate' that compliments the muscle-tendon units contribute to the exploitation of stored elastic energy.^[9] Elastic energy stored during the eccentric contractions of running substantially contributes to propulsion via release during subsequent contractions.^[106-109]

It has been 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 dissipated in a step while running at moderate speeds.^[110] Cavagna et al.^[111] estimates that $\dot{V}O_2$ during running might be 30–40% higher without contributions from elastic energy storage and return. At higher speeds, elastic recovery of energy prevails over the contractile machinery and accounts for most of the work.^[109,112] Elastic capacitance is influenced by the rate and magnitude of stretch, the level of activation and stiffness of the muscle tendon unit, muscle length at completion of the stretch and the time lag between completion of the stretch and initiation of the succeeding concentric contraction.^[106,107,109] The major role of the muscles during running is to modulate the stiffness of

the springs to maximise the exploitation of elastic energy.^[112-114]

4.3 Flexibility

Several studies contend that trunk and lower limb flexibility affects RE.^[115-117] Godges et al.^[117] observed that moderately trained athletic college students increased their RE at all speeds (40, 60 and 80% $\dot{V}O_{2max}$) with improved hip flexion and extension. Improved hip flexibility, myofascial balance, and pelvic symmetry are thought to enhance neuromuscular balance and contraction, eliciting a lower $\dot{V}O_2$ at submaximal workloads. These findings are compatible with the general belief among runners and coaches that improved flexibility is desirable for increasing RE.^[115]

In contrast, Gleim et al.^[116] found that untrained subjects who exhibited the lowest flexibility were the most economical when running at speeds ranging from 3–11 km/h. This finding was explained by inflexibility in the transverse and frontal planes of the trunk and hip regions of the body, stabilising the pelvis at the time of foot impact with the ground. This has the effect of reducing both excessive range of motion and metabolically expensive stabilising muscular activity.^[116] Elastic energy storage and return could be enhanced by having a tighter musculo-tendinous system.^[118-120] Tightness in the muscles and tendons could increase elastic storage and return of energy and reduce the submaximal $\dot{V}O_2$ demand.

Craib et al.^[115] examined the relationship between RE and selected trunk and lower limb flexibility in well trained male distance runners. Inflexibility in the hip and calf regions was associated with better RE by minimising the need for muscle stabilising activity and increasing the storage and return of elastic energy. Another study found that lower limb and trunk flexibility was negatively related to RE in international standard male distance runners, with a significant relationship between the sit-and-reach test score and submaximal $\dot{V}O_2$ at 16 km/h.^[121] Improved RE may reflect greater stability of the pelvis, a reduced requirement for additional muscular activity at foot strike, and a greater storage

and return of elastic energy due to inflexibility of the lower body.^[121] A short and rapid stretch with a short coupling time and a high force at the end of pre-stretch increases musculo-tendon elasticity.^[105] Kyrolainen et al.^[105] found that stiffer muscles around the ankle and knee joints in the braking phase of running increased force potentiation in the push-off phase. Having stiffer, more inflexible muscles in the legs and lower trunk could enhance RE via increased energy from elastic storage and return, which has no additional oxygen cost.

Taken collectively, the findings from these studies suggest that there is an optimal level of flexibility whereby RE can benefit, although a certain degree of muscle stiffness is also required to maximise elastic energy storage and return in the trunk and legs. Runners should not abandon stretching as part of their training programmes, as a certain amount of flexibility is also required for optimal stride length at high running speeds.

4.4 Ground Reaction Forces

Fresh insight into the inter-individual variations in RE has come from comparative biology. Kram and Taylor^[122] investigated the aerobic demand of running, hopping and trotting in a variety of animal species. They presented a simple inverse relationship between aerobic demand and stance time independent of an animal's size, indicating that the energy cost of running is determined by the cost of supporting an animal's mass and the time course of generating force.^[122] GRF reflect the functional and mechanical requirements during stance. During ground contact, a runner activates muscles for the purpose of stability and maintenance of forward momentum. Excessive changes in momentum in the vertical, antero-posterior and medial-lateral directions are wasteful in terms of metabolic energy requirements. Linear impulse measures the change in momentum and quantifies the time course of the GRF. Quantifying the magnitude of support and forces during ground contact may explain at least in part the variability in RE among individuals of similar fitness.^[123] Figure 3 depicts typical vertical and horizontal GRF for three steps of one subject.

In a well controlled study, Heise and Martin^[123] investigated the support requirements during foot contact of 16 moderately trained male runners ($\dot{V}O_{2\max}$ 62 mL/kg/min). Less economical runners exhibited greater total and net vertical impulse, indicating wasteful vertical motion. Correlations between total vertical impulse and $\dot{V}O_2$, and net vertical impulse and $\dot{V}O_2$ were $r = 0.62$ and 0.60 , respectively. The combined influence of vertical GRF and the time course of the force application explained 38% of the inter-individual variability in RE. Although positive relationships were observed, other GRF characteristics such as twisting, medial-lateral or antero-posterior moments were not significantly correlated with submaximal $\dot{V}O_2$. Kyrolainen et al.^[105] found that GRF and the rate of force production increased with increasing running speed. They suggested that increasing the pre-landing and braking activity of the leg extensor muscles might prevent unnecessary yielding of the runner during the braking phase, helping them tolerate higher impact loads. Pre-activation of these muscles is a preparatory requirement for the enhancement of EMG activity during the braking phase and for the time of muscular action with respect to the ground contact. Centrally programmed pre-landing activity appears to regulate the landing stiffness and compensates for local muscular failure. Pre-activity increases the sensitivity of the muscle spindle via enhanced alpha-gamma co-activation potentiating stretch reflexes, and enhancing musculo-tendon stiffness, with a resulting improvement in RE.^[105]

The requirement to support BM is a major metabolic cost of running.^[124] Vertical GRF is the major determinant of the metabolic cost during running.^[122,123,125] However, horizontal forces can substantially affect the metabolic cost of running, and this is clearly observed when running on a windy day.^[124] Using a wind tunnel to apply a horizontal impeding force, Pugh^[126] showed that the metabolic cost of running increased with the square of headwind velocity. Similarly, a harness to apply impeding forces increased the metabolic cost of running proportionally with an increase in external work.^[127-129] In a recent study, horizontal force was

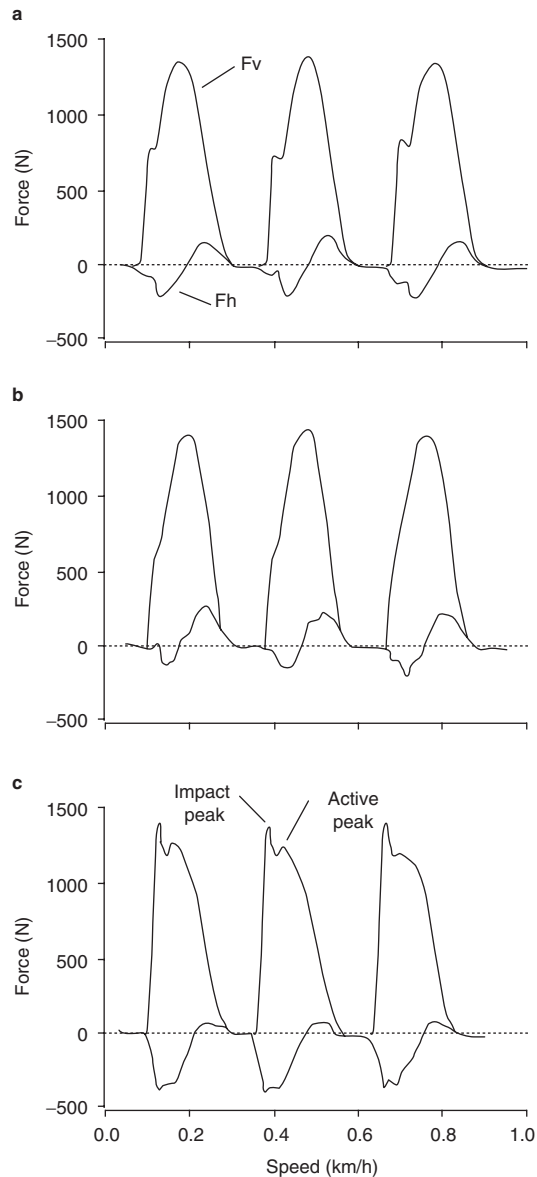


Fig. 3. Typical vertical (F_v) and horizontal (F_h) ground reaction forces for three steps of a single subject: for unloaded, 0% bodyweight applied horizontal force (AHF) control condition (a), with an impeding force of 6% bodyweight AHF (b), and with an aiding force of 15% bodyweight AHF (c) [reproduced from Chang and Kram,^[124] with permission].

altered to both impede and assist runners using a pulley and rubber harness. At the two extreme conditions, a 33% reduction in metabolic cost with a 15% assisting force and a 30% increase in metabolic cost with a 6% impeding force were observed.^[124]

The authors concluded that generating horizontal force is metabolically more expensive per unit of force than horizontal braking force during steady-state running. It appears that the net resultant force generated on the ground affects net muscle moments

at each joint, as well as the force of each muscle crossing the joint. Therefore, it may not be appropriate to consider vertical and horizontal GRF as independent determinants of metabolic cost.^[124]

5. Interventions to Improve RE

RE is influenced by many physiological and biomechanical variables; however, little research exists with regard to improving RE and endurance performance by manipulation of these factors.^[73] Endurance training coupled with various other training methods has been shown to improve RE in untrained and moderately trained subjects, with trained runners having a better RE than their untrained or less trained counterparts.^[8,74,79,82-84] Most studies demonstrating improvements in RE as a result of training have used untrained or moderately trained subjects, and improvement in fitness is a natural adaptation from endurance training. In highly trained runners who already possess a well developed RE through years of endurance training, further improvements in RE are seemingly difficult to obtain. Three areas that have potential to improve RE are strength training, altitude exposure and training in a warm to hot environment.

5.1 Strength Training

Endurance athletes must be able to sustain a high average running velocity for the duration of a race. This emphasises the role of neuromuscular characteristics in voluntary and reflex neural activation, muscle force and elasticity, running mechanics, and the anaerobic capacities in elite endurance runners.^[80,130] The use of strength training is one intervention thought to improve RE. Strength training can improve anaerobic characteristics such as the ability to produce high La and the production of short contact times and fast forces.^[131,132] Heavy resistance training improves the endurance performance of untrained subjects^[133-135] and RE of moderately trained female distance runners without concomitant changes in $\dot{V}O_{2max}$.^[136] Recent work has shown that a combination of heavy-weight training (HWT) and endurance training improved running performance and enhanced RE in well trained

triathletes ($\dot{V}O_{2max}$ 69 mL/kg/min).^[137] In this study, 14 weeks of a HWT intervention elicited in the endurance/strength group a significantly lower (11%) submaximal $\dot{V}O_2$ compared with the endurance-only group, and a marginal enhancement in RE in the endurance/strength group compared with their pre-test.

A specific type of strength training, known as explosive-strength or plyometric training, invokes specific neural adaptations such as an increased activation of the motor units, with less muscle hypertrophy than typical heavy-resistance strength training.^[130,138,139] Plyometric training enhances the muscles' ability to generate power by exaggerating the stretch-shorten cycle, using activities such as bounding, jumping and hopping.^[140] Plyometric training also has the potential to increase the stiffness of the muscle-tendon system, which allows the body to store and utilise elastic energy more effectively.^[141] Both these adaptations from plyometric training could conceivably improve RE by generating more force from the muscles without a proportionate increase in metabolic energy requirement. Paavolainen et al.^[80] indicated that 9 weeks of explosive-strength training improved RE (8%) and 5km performance (3%) with no changes in $\dot{V}O_{2max}$ in moderately trained runners. This group also measured neuromuscular characteristics using a 20m sprint test, the distance covered in five alternate forward leg jumps and the corresponding contact times (shorter times being better), as well as vertical and horizontal forces measured on a force plate during a constant-speed 200m run. The experimental group improved in all of these tests compared with the control group.^[80] These findings indicate that explosive-strength training can improve RE and performance as a consequence of enhanced neuromuscular function. Similarly, recent studies have shown improvements in RE and performance after 6 weeks of plyometric training in moderately trained subjects with no change in $\dot{V}O_{2max}$,^[140,141] with the former study showing a 6% improvement in RE across three running speeds and a 3% increase in 3km run performance. The study by Spurr et al.^[141] demonstrated improvement in muscle-tendon stiff-

ness and rate of force development during a seated calf-raise test, a finding which also supports the theory that improved RE from plyometrics is attributable to increased muscular power, and greater storage and return of elastic energy. To date, there is little research investigating the effects of plyometric training on elite ($\dot{V}O_{2\max} > 70$ mL/kg/min) distance runners.

5.2 Altitude Exposure

The effect of altitude training on endurance performance has been researched extensively.^[142-168] There is a widespread belief in the athletic community that altitude training can enhance sea-level athletic performance.^[149,156,166] The mechanisms for these improvements are not clear, but may include haematological changes (i.e. increased red cell mass)^[148,156] and local muscular adaptations (such as improved skeletal muscle buffer capacity).^[151] The traditional approach to altitude training involves athletes living and training at a moderate (1500–3000m) natural altitude. A more recent approach is for athletes to live/sleep at altitude and train near sea level, the so-called live-high train-low (LHTL) method.^[156] Because the geography of many countries does not readily permit LHTL, a further refinement involves athletes living at simulated altitude under normobaric conditions and training at, or close to, sea level.^[161] In recent years, endurance athletes have utilised several new devices and modalities to complement the LHTL approach. These modalities include: normobaric hypoxia via nitrogen dilution, which allows athletes to undertake LHTL; supplemental oxygen to simulate normoxic or hyperoxic conditions during exercise/sleep at natural altitude; and hypoxic sleeping devices which permit athletes to sleep low and train high (LLTH). Intermittent hypoxic exposure is another method involving brief periods of hypoxic exposure via a hypobaric chamber or inhalation of a hypoxic gas mixture to stimulate erythropoietin production. Data to support these claims are minimal and inconclusive.^[169]

Altitude acclimatisation results in both central and peripheral adaptations that improve oxygen de-

livery and utilisation,^[147,158,168,170] mechanisms that potentially could improve an athlete's RE. However, to date little research has been undertaken on the effects of altitude exposure on RE in highly trained distance runners. Three investigations have reported no change in submaximal $\dot{V}O_2$ after a period of altitude exposure,^[145,156,164] while others have demonstrated improved RE after various stints of hypoxic exposure.^[155,171,172] Similarly, after a period of altitude acclimatisation, sea-level $\dot{V}O_2$ during submaximal cycling is either reduced^[151,153,154,157] or unchanged.^[146,160] A tentative interpretation of these findings is that altitude exposure for runners and cyclists has no detrimental effects on economy and there is good evidence to suggest that it may lead to improvements.

In a study undertaken at sea level, RE of high-altitude residents was compared with that of sea-level residents. $\dot{V}O_2$ was significantly lower in the highlanders, indicating greater economy.^[154] Green et al.^[153] examined the effects of a 21-day expedition to altitude on submaximal cycling economy. Experienced mountain climbers were recruited for this study and were based at 2160m, ascending to heights of 6194m. Three days after the expedition, subjects had a significantly lower $\dot{V}O_2$ during a 40-minute submaximal cycling test (20 minutes at 60% $\dot{V}O_{2\max}$ and 20 minutes at 75% $\dot{V}O_{2\max}$) than before the expedition. With resting $\dot{V}O_2$ unchanged pre- and post-acclimatisation, the authors concluded that the altitude exposure was responsible for the improved economy, indicating net efficiency increased by ~21% post-altitude acclimatisation, independent of the power output. A similar study of mountain climbers showed an ~8% reduction in $\dot{V}O_2$ during steady-state, two-legged kicking exercise, 3 days after a 21-day mountain climbing expedition to 6194m.^[157] These studies involved cycling and two-legged kicking as the mode of exercise to measure economy. Evidence to suggest that altitude exposure improves economy of highly trained athletes was demonstrated by Gore et al.^[151] in a study where six highly trained triathletes ($\dot{V}O_{2\max}$ 73 mL/kg/min) improved cycling efficiency after 23 nights sleeping at a simulated altitude of 3000m, compared

with seven control athletes ($\dot{V}O_{2\max}$ 73 mL/kg/min) who trained the same but slept at normal altitude (~600m). In the LHTL group, overall submaximal cycling efficiency improved significantly by 1%.^[151] Although this group was highly trained and mainly consisted of triathletes who undertook a lot of running training, cycling was still the mode of exercise used to determine improved economy, and further research is required to determine whether altitude training improves RE in highly trained runners.

Currently, three studies have demonstrated improved economy in highly trained runners.^[155,171,172] Katayama and colleagues^[171] have demonstrated on two occasions that intermittent hypoxic exposure improves RE in well trained runners. The first study reported that simulated hypoxic exposure using intermittent hypobaria of 4500m 3 hours per day for 14 consecutive days improved RE and performance in well trained runners ($\dot{V}O_{2\max}$ 68 mL/kg/min). Altitude exposure improved RE by 2.6% (14 km/h) and 3.3% (16 km/h), improved 3000m run time by 1% and time to exhaustion on the treadmill by 2.7%. The improvement in RE accounted for 37% of the improvement observed in the 3000m time trial.^[155] More recently, it was demonstrated that 3 hours per day for 2 weeks of intermittent exposure to normobaric hypoxia (12.3% oxygen) improved RE by 2.6% (14 km/h) and 2.9% (16 km/h) in well trained runners ($\dot{V}O_{2\max}$ 68 mL/kg/min). The improved RE was accompanied by a decreased HR (3.3% and 3.9% at 14 and 16 km/h, respectively) and a trend towards improved 3000m run time (1.3%, $p = 0.06$).^[171] Another recent study demonstrated that 20 days of sleeping at simulated altitude (2000–3100m) and training near sea level (600m) improved (3.3%, $p = 0.005$) RE in elite distance runners ($\dot{V}O_{2\max}$ 73 mL/kg/min) in the absence of any changes in cardiorespiratory measures or red cell mass.^[172]

Mechanisms that have been suggested to improve economy after altitude exposure include: decreased cost of V_E , a shift towards a greater glycolytic involvement of adenosine triphosphate (ATP) regeneration, greater carbohydrate utilisation for oxidative phosphorylation and/or an increased ability

of the excitation and contraction process to perform work at lower energy costs.^[153] Roberts et al.^[160] observed that 4300m altitude acclimatisation for 21 days decreased the reliance on fat as a fuel during rest and cycling at 50% $\dot{V}O_{2\max}$. The authors suggested that the shift towards increased dependence on glucose metabolism and away from reliance on fatty acid consumption under conditions of acute and chronic hypoxia, is advantageous because glucose is a more efficient fuel in terms of generating ATP per mole of oxygen. Another suggested improvement in efficiency is the reduced energy requirement of one or more processes involved in excitation and contraction of the working muscles as a result of metabolic adaptations from altitude acclimatisation.^[153] The reduction in by-product accumulation, such as adenosine diphosphate (ADP), inorganic phosphate and hydrogen that occur after altitude acclimatisation, increases the amount of free energy released from ATP hydrolysis and depresses the need to maintain hydrolysis rates at pre-acclimatised levels.^[153,173]

Saltin et al.^[174] investigated the physiological characteristics of Kenyan and Scandinavian runners. The Kenyan runners lived and trained at altitude while the Scandinavian runners lived and trained at sea level. Kenyan runners did not accumulate La during running until near very high or peak exercise intensities, and had much lower La both at altitude and sea level at high relative exercise intensities. Similarly, Weston et al.^[175] reported Kenyan runners had higher resistance to fatigue when running at the same percentage of peak treadmill velocity than Caucasian runners, despite similar $\dot{V}O_{2\max}$ values in the two groups. Whilst these studies of runners native to high altitude do not necessarily indicate the effect of training at altitude, it has been reported that exercise after altitude training results in reduced La production at submaximal exercise, with lower blood and muscle La being reported.^[146,152,176] On this basis, altitude training allows athletes to maintain a given exercise intensity with lower accumulation of La during post-acclimatised sea-level exercise. One of the mechanisms for lower plasma La accumulation is an increase in skeletal muscle oxi-

ductive enzyme capacity^[177] by shifting metabolism away from anaerobic to aerobic. Weston et al.^[175] showed that Kenyan runners who live and train at altitude have higher oxidative enzyme activities than their Caucasian counterparts of a similar $\dot{V}O_{2max}$.

5.3 Training in the Heat

The mildly elevated C_{Temp} resulting from training in warm to hot conditions may improve RE by increasing the efficiency of the working muscles. A lower C_{Temp} and an increased plasma volume, associated with acute and chronic bouts of exercise in the heat, may attenuate the magnitude of the thermoregulatory response (increased ventilation, circulation and sweating) and reduce the increased energy requirements associated with heat stress.^[178] Heat acclimatisation, accompanied by training, can increase plasma volume by up to 12%. The increase in plasma volume assists in the maintenance of stroke volume, which in turn minimises myocardial work.^[73] It follows that whole blood viscosity is reduced from training in the heat, and a decreased viscosity has positive effects on endurance performance.^[179] Adaptations from training in warm to hot conditions may also allow runners to run at any given speed with a lower HR and C_{Temp} , with both factors associated with improved RE.^[65] These findings support the premise that training in moderate heat may improve RE and performance at normal temperatures, although insufficient data precludes drawing any definitive conclusions.

6. Conclusions and Future Directions

RE has been researched extensively over the last 4–5 decades and is considered a critical factor in the performance of elite distance runners. Factors that influence RE include V_E , C_{Temp} , muscle metabolism, muscle fibre-type, body composition, running technique, GRF, muscle stiffness, and storage and return of elastic energy. Although RE has been researched extensively, there are still relatively few documented interventions that have been shown to improve the RE of elite distance runners. Explosive strength training has been reported to improve RE in

moderately trained distance runners, and some evidence has been reported that HWT tended to improve RE in well trained triathletes. Training at altitude or even sleeping at altitude has demonstrated improved submaximal economy in trained mountain climbers, cyclists and triathletes. Both the use of resistance training and altitude exposure appear to have potential in improving the RE of elite distance runners, but further research into this area is still required. Training in warm to hot conditions is another intervention that has the potential to improve RE in distance runners, but again intervention studies looking at the effect of training in the heat on RE are limited, and further research is needed in this area. Given that well designed resistance training, moderate altitude training and training in warm conditions have other benefits besides the potential to improve RE, it would seem sensible for runners to employ these training methods where possible. An important area of RE is the ability of the muscles to store and release elastic energy, as this energy requires no metabolic cost and could be a critical factor in improving RE. A method to quantify the amount of elastic energy utilised has yet to be developed, and this would provide a useful means of determining the effectiveness of various training interventions. More precision in measuring the contribution of both metabolic and mechanical aspects of RE are required before we are able to gain better insight into how we can improve RE. Current work aimed at developing better overground measurements of metabolic and mechanical work offers potential in improving our understanding of physiological and training factors that affect RE in elite runners.

Acknowledgements

The authors have provided no information on sources of funding or on conflicts of interest directly relevant to the content of this review.

References

1. Costill DL. The relationship between selected physiological variables and distance running performance. *J Sports Med Phys Fitness* 1967; 7 (2): 61-6

2. Hagan RD, Smith MG, Gettman LR. Marathon performance in relation to maximal aerobic power and training indices. *Med Sci Sports Exerc* 1981; 13 (3): 185-9
3. Saltin B, Astrand PO. Maximal oxygen uptake in athletes. *J Appl Physiol* 1967; 23 (3): 353-8
4. Conley DL, Krahenbuhl GS. Running economy and distance running performance of highly trained athletes. *Med Sci Sports Exerc* 1980; 12 (5): 357-60
5. Costill DL, Thomason H, Roberts E. Fractional utilization of the aerobic capacity during distance running. *Med Sci Sports* 1973; 5 (4): 248-52
6. Coyle EF. Physiological determinants of endurance exercise performance. *J Sci Med Sport* 1999; 2 (3): 181-9
7. Billat VL, Flechet B, Petit B, et al. Interval training at VO₂max: effects on aerobic performance and overtraining markers. *Med Sci Sports Exerc* 1999; 31 (1): 156-63
8. Daniels JT. A physiologist's view of running economy. *Med Sci Sports Exerc* 1985; 17 (3): 332-8
9. Anderson T. Biomechanics and running economy. *Sports Med* 1996; 22 (2): 76-89
10. Conley DL, Krahenbuhl GS, Burkett LN, et al. Following Steve Scott: physiological changes accompanying training. *Phys Sportsmed* 1984; 12: 103-6
11. Morgan DW, Craib M. Physiological aspects of running economy. *Med Sci Sports Exerc* 1992; 24 (4): 456-61
12. Thomas DQ, Fernhall B, Grant H. Changes in running economy during a 5km run in trained men and women runners. *J Strength Cond Res* 1999; 13 (2): 162-7
13. MacDougall JD. The anaerobic threshold: its significance for the endurance athlete. *Can J Appl Sports Sci* 1977; 2: 137-40
14. Morgan DW, Baldini FD, Martin PE, et al. Ten kilometer performance and predicted velocity at VO₂max among well-trained male runners. *Med Sci Sports Exerc* 1989; 21 (1): 78-83
15. Di Prampero PE, Capelli C, Pagliaro P, et al. Energetics of best performances in middle-distance running. *J Appl Physiol* 1993; 74 (5): 2318-24
16. Pollock ML. Submaximal and maximal working capacity of elite distance runners. Part I: cardiorespiratory aspects. *Ann N Y Acad Sci* 1977; 301: 310-22
17. Daniels N, Daniels J, Baldwin C, et al. The effect of wind on the aerobic demand of running. National Meeting of the American College of Sports Medicine; 1986 May; Indianapolis
18. Pugh LG. Oxygen intake in track and treadmill running with observations on the effect of air resistance. *J Physiol* 1970; 207 (3): 823-35
19. Davies CT. Effects of wind assistance and resistance on the forward motion of a runner. *J Appl Physiol* 1980; 48 (4): 702-9
20. Hagerman F, Addington WW, Gaensler EA. Severe steady state exercise at sea level and altitude in Olympic oarsmen. *Med Sci Sports* 1975; 7 (4): 275-9
21. Costill DL, Fox EL. Energetics of marathon running. *Med Sci Sports* 1969; 1: 81-6
22. Hausswirth C, Bigard AX, Le Chevalier JM. The Cosmed K4 telemetry system as an accurate device for oxygen uptake measurements during exercise. *Int J Sports Med* 1997; 18 (6): 449-53
23. Billat V, Demarle A, Paiva M, et al. Effect of training on the physiological factors of performance in elite marathon runners (males and females). *Int J Sports Med* 2002; 23 (5): 336-41
24. Slawinski J, Demarle A, Koralsztein JP, et al. Effect of supra-lactate threshold training on the relationship between mechanical stride descriptors and aerobic energy cost in trained runners. *Arch Physiol Biochem* 2001; 109 (2): 110-6
25. Billat VL, Slawinski J, Danel M, et al. Effect of free versus constant pace on performance and oxygen kinetics in running. *Med Sci Sports Exerc* 2001; 33 (12): 2082-8
26. Billat VL, Slawinski J, Bocquet V, et al. Intermittent runs at the velocity associated with maximal oxygen uptake enables subjects to remain at maximal oxygen uptake for a longer time than intense but submaximal runs. *Eur J Appl Physiol* 2000; 81 (3): 188-96
27. Daniels J, Scardina N, Hayes J, et al. Variations in VO₂ submax during treadmill running [abstract]. *Med Sci Sports* 1984; 16: 108
28. 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
29. Morgan DW. Effects of a prolonged maximal run on running economy and running mechanics [dissertation]. Tempe (AZ): Arizona State University, 1988
30. Morgan DW, Baldini FD, Martin PE. Day-to-day stability in running economy and step length among well-trained male runners [abstract]. *Int J Sports Med* 1987; 8: 242
31. Morgan DW, Craib MW, Krahenbuhl GS, et al. Daily variability in running economy among well-trained male and female distance runners. *Res Q Exerc Sport* 1994; 65 (1): 72-7
32. Morgan DW, Martin PE, Krahenbuhl GS, et al. Variability in running economy and mechanics among trained male runners. *Med Sci Sports Exerc* 1991; 23 (3): 378-83
33. 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
34. Pereira MA, Freedson PS, Maliszewski AF. Intra-individual variation during inclined steady rate treadmill running. *Res Q Exerc Sport* 1994; 65: 184-8
35. Brisswalter J, Legros P. Variability in energy cost of running during one training season in high level runners. *J Sports Med Phys Fitness* 1994; 34 (2): 135-40
36. Davies MJ, Mahar MT, Cunningham LN. Running economy: comparison of body mass adjustment methods. *Res Q Exerc Sport* 1997; 68 (2): 177-81
37. Bergh U, Sjodin B, Forsberg A, et al. The relationship between body mass and oxygen uptake during running in humans. *Med Sci Sports Exerc* 1991; 23 (2): 205-11
38. Taylor CR, Heglund NC, Maloiy 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
39. Astrand PO. Experimental studies of physical working capacity in relation to sex and age. Copenhagen: Ejnar Munksgaard, 1952
40. Bourdin M, Pastene J, Germain M, et al. Influence of training, sex, age and body mass on the energy cost of running. *Eur J Appl Physiol Occup Physiol* 1993; 66 (5): 439-44
41. Daniels J, Oldridge N. Changes in oxygen consumption of young boys during growth and running training. *Med Sci Sports* 1971; 3 (4): 161-5
42. Daniels J, Oldridge N, Nagle F, et al. Differences and changes in VO₂ among young runners 10 to 18 years of age. *Med Sci Sports* 1978; 10 (3): 200-3
43. Krahenbuhl GS, Morgan DW, Pangrazi RP. Longitudinal changes in distance-running performance of young males. *Int J Sports Med* 1989; 10 (2): 92-6

44. Krahenbuhl GS, Skinner JS, Kohrt WM. Developmental aspects of maximal aerobic power in children. *Exerc Sport Sci Rev* 1985; 13: 503-38
45. Leger L, Mercier D. Gross energy cost of horizontal treadmill and track running. *Sports Med* 1984; 1 (4): 270-7
46. MacDougall JD, Roche PD, Bar-Or O, et al. Maximal aerobic capacity of Canadian schoolchildren: prediction based on age-related oxygen cost of running. *Int J Sports Med* 1983; 4 (3): 194-8
47. Morgan DW, Martin PE, Krahenbuhl GS. Factors affecting running economy. *Sports Med* 1989; 7 (5): 310-30
48. Rowland TW. Oxygen uptake and endurance fitness in children: a developmental perspective. *Pediatr Exerc Sci* 1989; 1: 313-28
49. Rowland TW, Green GM. Physiological responses to treadmill exercise in females: adult-child differences. *Med Sci Sports Exerc* 1988; 20 (5): 474-8
50. Unnithan VB, Eston RG. Stride frequency and submaximal treadmill running economy in adults and children. *Pediatr Exerc Sci* 1990; 2: 149-55
51. Sjodin B, Svedenhag J. Oxygen uptake during running as related to body mass in circumpubertal boys: a longitudinal study. *Eur J Appl Physiol Occup Physiol* 1992; 65 (2): 150-7
52. Svedenhag J, Sjodin 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
53. Pate RR, Macera CA, Bailey SP, et al. Physiological, anthropometric, and training correlates of running economy. *Med Sci Sports Exerc* 1992; 24 (10): 1128-33
54. Williams KR, Cavanagh PR. Relationship between distance running mechanics, running economy, and performance. *J Appl Physiol* 1987; 63 (3): 1236-45
55. Catlin ME, Dressendorfer RH. Effect of shoe weight on the energy cost of running [abstract]. *Med Sci Sports* 1979; 11: 80
56. Jones BH, Knapik JJ, Daniels WL, et al. The energy cost of women walking and running in shoes and boots. *Ergonomics* 1986; 29 (3): 439-43
57. Martin PE. Mechanical and physiological responses to lower extremity loading during running. *Med Sci Sports Exerc* 1985; 17 (4): 427-33
58. Myers MJ, Steudel K. Effect of limb mass and its distribution on the energetic cost of running. *J Exp Biol* 1985; 116: 363-73
59. Fredrick EC, Clarke TE, Larsen JL, et al. The effects of shoe cushioning on the oxygen demands of running. In: Nigg BM, Kerr BA, editors. *Biomechanical aspects of sport shoes and playing surfaces*. Calgary: University of Calgary, 1983; 107-14
60. Svedenhag J, Sjodin B. Physiological characteristics of elite male runners in and off-season. *Can J Appl Sport Sci* 1985; 10 (3): 127-33
61. Farrell PA, Wilmore JH, Coyle EF, et al. Plasma lactate accumulation and distance running performance. 1979. *Med Sci Sports Exerc* 1993; 25 (10): 1091-7
62. Weston AR, Mbambo Z, Myburgh KH. Running economy of African and Caucasian distance runners. *Med Sci Sports Exerc* 2000; 32 (6): 1130-4
63. Adams WC, Bernauer EM. The effect of selected pace variations on the oxygen requirement of running a 4:37 mile. *Res Q* 1968; 39 (4): 837-46
64. Armstrong LE, Gehlsen G. Running mechanics of national class distance runners during a marathon. *Track Field Q Rev* 1985; 85: 37-9
65. Thomas DQ, Fernhall B, Blanpied P, et al. Changes in running economy and mechanics during a 5 km run. *J Strength Cond Res* 1995; 9: 170-5
66. Brooks GA, Hittelman KJ, Faulkner JA, et al. Temperature, skeletal muscle mitochondrial functions, and oxygen debt. *Am J Physiol* 1971; 220 (4): 1053-9
67. Brooks GA, Hittelman KJ, Faulkner JA, et al. Temperature, liver mitochondrial respiratory functions, and oxygen debt. *Med Sci Sports* 1971; 3 (2): 72-4
68. MacDougall JD, Reddan WG, Layton CR, et al. Effects of metabolic hyperthermia on performance during heavy prolonged exercise. *J Appl Physiol* 1974; 36 (5): 538-44
69. Saltin B, Stenberg J. Circulatory response to prolonged severe exercise. *J Appl Physiol* 1964; 19: 833-8
70. Rowell LB, Brengelmann GL, Murray JA, et al. Human metabolic responses to hyperthermia during mild to maximal exercise. *J Appl Physiol* 1969; 26 (4): 395-402
71. Bosco C, Montanari G, Ribacchi R, et al. Relationship between the efficiency of muscular work during jumping and the energetics of running. *Eur J Appl Physiol Occup Physiol* 1987; 56 (2): 138-43
72. Kaneko M. Mechanics and energetics in running with special reference to efficiency. *J Biomech* 1990; 23 Suppl. 1: 57-63
73. Bailey SP, Pate RR. Feasibility of improving running economy. *Sports Med* 1991; 12 (4): 228-36
74. Bransford DR, Howley ET. Oxygen cost of running in trained and untrained men and women. *Med Sci Sports* 1977; 9 (1): 41-4
75. Daniels J. Physiological characteristics of champion male athletes. *Res Q* 1974; 45 (4): 342-8
76. Ekblom B, Astrand PO, Saltin B, et al. Effect of training on circulatory response to exercise. *J Appl Physiol* 1968; 24 (4): 518-28
77. Conley DL, Krahenbuhl GS, Burkett LN, et al. Physiological correlates of female road racing performance. *Res Q Exerc Sport* 1981; 52 (4): 441-8
78. Franch J, Madsen K, Djurhuus MS, et al. Improved running economy following intensified training correlates with reduced ventilatory demands. *Med Sci Sports Exerc* 1998; 30 (8): 1250-6
79. Mayers N, Gutin B. Physiological characteristics of elite prepubertal cross-country runners. *Med Sci Sports* 1979; 11 (2): 172-6
80. Paavolainen L, Hakkinen K, Hamalainen I, et al. Explosive-strength training improves 5-km running time by improving running economy and muscle power. *J Appl Physiol* 1999; 86 (5): 1527-33
81. Sjodin B, Jacobs I, Svedenhag J. Changes in onset of blood lactate accumulation (OBLA) and muscle enzymes after training at OBLA. *Eur J Appl Physiol Occup Physiol* 1982; 49 (1): 45-57
82. Dolgener F. Oxygen cost of walking and running in untrained, sprint trained, and endurance trained females. *J Sports Med Phys Fitness* 1982; 22 (1): 60-5
83. Krahenbuhl GS, Pangrazi RP. Characteristics associated with running performance in young boys. *Med Sci Sports Exerc* 1983; 15 (6): 486-90
84. Pollock ML, Jackson AS, Pate RR. Discriminant analysis of physiological differences between good and elite distance runners. *Res Q Exerc Sport* 1980; 51 (3): 521-32
85. 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

86. Holloszy JO, Rennie MJ, Hickson RC, et al. Physiological consequences of the biochemical adaptations to endurance exercise. *Ann N Y Acad Sci* 1977; 301: 440-50
87. Daniels J, Daniels N. Running economy of elite male and elite female runners. *Med Sci Sports Exerc* 1992; 24 (4): 483-9
88. Daniels J, Krahenbuhl G, Foster C, et al. Aerobic responses of female distance runners to submaximal and maximal exercise. *Ann N Y Acad Sci* 1977; 301: 726-33
89. Costill DL. Muscle metabolism and electrolyte balance during heat acclimation. *Acta Physiol Scand Suppl* 1986; 556: 111-8
90. 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
91. Fredrick EC. Measuring the effects of shoes and surfaces on the economy of locomotion. In: Nigg BM, Kerr BA, editors. *Biomechanical aspects of sport shoes and playing surfaces*. Calgary: University of Calgary, 1983: 93-106
92. Dalleau G, Belli A, Bourdin M, et al. The spring-mass model and the energy cost of treadmill running. *Eur J Appl Physiol Occup Physiol* 1998; 77 (3): 257-63
93. Collins MH, Pearsall DJ, Zavorsky GS, et al. Acute effects of intense interval training on running mechanics. *J Sports Sci* 2000; 18 (2): 83-90
94. Kyrolainen H, Pullinen T, Candau R, et al. Effects of marathon running on running economy and kinematics. *Eur J Appl Physiol* 2000; 82 (4): 297-304
95. Morgan DW, Martin PE, Baldini FD, et al. Effects of a prolonged maximal run on running economy and running mechanics. *Med Sci Sports Exerc* 1990; 22 (6): 834-40
96. Nichol C, Komi PV, Marconnet P. Effects of marathon fatigue on running kinematics and economy. *Scand J Med Sci Sports* 1991; 1: 195-204
97. Hausswirth C, Bigard AX, Guezennec CY. Relationships between running mechanics and energy cost of running at the end of a triathlon and a marathon. *Int J Sports Med* 1997; 18 (5): 330-9
98. Hogberg P. How do stride length and stride frequency influence the energy output during running. *Arbeitsphysiologie* 1952; 14: 437-41
99. Kaneko M, Matsumoto M, Ito A, et al. Optimum step frequency in constant speed running. In: Jonsson B, editor. *Biomechanics X-B*. Champaign (IL): Human Kinetics, 1987: 803-7
100. 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
101. Powers SK, Hopkins P, Ragsdale MR. Oxygen uptake and ventilatory responses to various stride lengths in trained women. *Am Correct Ther J* 1982; 36 (1): 5-8
102. Cavanagh PR, Pollock ML, Landa J. A biomechanical comparison of elite and good distance runners. *Ann N Y Acad Sci* 1977; 301: 328-45
103. Williams KR, Cavanagh PR. Biomechanical correlates with running economy in elite distance runners. *Proceedings of the North American Congress on Biomechanics*; Montreal; 1986 Aug, 287-8
104. Anderson T, Tseh W. Running economy, anthropometric dimensions and kinematic variables [abstract]. *Med Sci Sports Exerc* 1994; 26 (5 Suppl.): S170
105. Kyrolainen H, Belli A, Komi PV. Biomechanical factors affecting running economy. *Med Sci Sports Exerc* 2001; 33 (8): 1330-7
106. Aruin AS, Prilutskii BI. Relationship of the biomechanical properties of muscles to their ability to utilize elastic deformation energy. *Hum Physiol* 1985; 11 (1): 8-12
107. Aruin AS, Prilutskii BI, Raitsin LM, et al. Biomechanical properties of muscles and efficiency of movement. *Hum Physiol* 1979; 5 (4): 426-34
108. 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 Occup Physiol* 1986; 55 (1): 37-43
109. Cavagna GA, Kaneko M. Mechanical work and efficiency in level walking and running. *J Physiol* 1977; 268 (2): 647-81
110. Ker RF, Bennett MB, Bibby SR, et al. The spring in the arch of the human foot. *Nature* 1987; 325 (7000): 147-9
111. Cavagna GA, Saibene FP, Margaria R. Mechanical work in running. *J Appl Physiol* 1964; 18: 1-9
112. Taylor CR. Relating mechanics and energetics during exercise. *Adv Vet Sci Comp Med* 1994; 38A: 181-215
113. Alexander RM. Energy-saving mechanisms in walking and running. *J Exp Biol* 1991; 160: 55-69
114. Cavagna GA, Franzetti P, Heglund NC, et al. The determinants of the step frequency in running, trotting and hopping in man and other vertebrates. *J Physiol* 1988; 399: 81-92
115. Craib MW, Mitchell VA, Fields KB, et al. The association between flexibility and running economy in sub-elite male distance runners. *Med Sci Sports Exerc* 1996; 28 (6): 737-43
116. Gleim GW, Stachenfeld NS, Nicholas JA. The influence of flexibility on the economy of walking and jogging. *J Orthop Res* 1990; 8 (6): 814-23
117. Godges JJ, Macrae H, Longdon C, et al. The effects of two stretching procedures on hip range of motion and gait economy. *J Orthop Sports Phys Ther* 1989; 7: 350-7
118. 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
119. Dawson TJ, Taylor CR. Energetic cost of locomotion in kangaroos. *Nature* 1973; 246: 313-4
120. Ker RF. Dynamic tensile properties of the plantaris tendon of sheep (*Ovis aries*). *J Exp Biol* 1981; 93: 283-302
121. Jones AM. Running economy is negatively related to sit-and-reach test performance in international-standard distance runners. *Int J Sports Med* 2002; 23 (1): 40-3
122. Kram R, Taylor CR. Energetics of running: a new perspective. *Nature* 1990; 346 (6281): 265-7
123. 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
124. Chang YH, Kram R. Metabolic cost of generating horizontal forces during human running. *J Appl Physiol* 1999; 86 (5): 1657-62
125. Farley CT, McMahon TA. Energetics of walking and running: insights from simulated reduced-gravity experiments. *J Appl Physiol* 1992; 73 (6): 2709-12
126. Pugh LG. The influence of wind resistance in running and walking and the mechanical efficiency of work against horizontal or vertical forces. *J Physiol* 1971; 213 (2): 255-76
127. Cooke CB, McDonagh MJ, Nevill AM, et al. Effects of load on oxygen intake in trained boys and men during treadmill running. *J Appl Physiol* 1991; 71 (4): 1237-44
128. Lloyd BB, Zacks RM. The mechanical efficiency of treadmill running against a horizontal impeding force. *J Physiol* 1972; 223 (2): 355-63

129. Zacks RM. The mechanical efficiencies of running and bicycling against a horizontal impeding force. *Int Z Angew Physiol* 1973; 31 (4): 249-58
130. Hakkinen K. Neuromuscular adaptation during strength-training, aging, detraining, and immobilization. *Crit Rev Phys Rehab Med* 1994; 6: 161-98
131. Bulbulian R, Wilcox AR, Darabos BL. Anaerobic contribution to distance running performance of trained cross-country athletes. *Med Sci Sports Exerc* 1986; 18 (1): 107-13
132. Houmard JA, Costill DL, Mitchell JB, et al. The role of anaerobic ability in middle distance running performance. *Eur J Appl Physiol Occup Physiol* 1991; 62 (1): 40-3
133. Hickson RC, Dvorak BA, Gorostiaga EM, et al. Potential for strength and endurance training to amplify endurance performance. *J Appl Physiol* 1988; 65 (5): 2285-90
134. Marciniak EJ, Potts J, Schlabach G, et al. Effects of strength training on lactate threshold and endurance performance. *Med Sci Sports Exerc* 1991; 23 (6): 739-43
135. McCarthy JP, Agre JC, Graf BK, et al. Compatibility of adaptive responses with combining strength and endurance training. *Med Sci Sports Exerc* 1995; 27 (3): 429-36
136. Johnston RE, Quinn TJ, Kertzer R, et al. Strength training in female distance runners: impact on running economy. *J Strength Cond Res* 1997; 11: 224-9
137. Millet GP, Jaouen B, Borrani F, et al. Effects of concurrent endurance and strength training on running economy and VO (2) kinetics. *Med Sci Sports Exerc* 2002; 34 (8): 1351-9
138. Hakkinen K, Komi PV, Alen M. Effect of explosive type strength training on isometric force- and relaxation-time, electromyographic and muscle fibre characteristics of leg extensor muscles. *Acta Physiol Scand* 1985; 125 (4): 587-600
139. Sale D. Neural adaptation to strength training. In: Komi PV, editor. *The encyclopedia of sports medicine*. Oxford: Blackwell, 1991: 249-65
140. Turner AM, Owings M, Schwane JA. Improvement in running economy after 6 weeks of plyometric training. *J Strength Cond Res* 2003; 17 (1): 60-7
141. Spurrs RW, Murphy AJ, Watsford ML. The effect of plyometric training on distance running performance. *Eur J Appl Physiol* 2003; 89 (1): 1-7
142. Ashenden MJ, Gore CJ, Dobson GP, et al. Simulated moderate altitude elevates serum erythropoietin but does not increase reticulocyte production in well-trained runners. *Eur J Appl Physiol* 2000; 81 (5): 428-35
143. Ashenden MJ, Gore CJ, Dobson GP, et al. "Live high, train low" does not change the total haemoglobin mass of male endurance athletes sleeping at a simulated altitude of 3000m for 23 nights. *Eur J Appl Physiol Occup Physiol* 1999; 80 (5): 479-84
144. Ashenden MJ, Gore CJ, Martin DT, et al. Effects of a 12-day 'live high, train low' camp on reticulocyte production and haemoglobin mass in elite female road cyclists. *Eur J Appl Physiol Occup Physiol* 1999; 80 (5): 472-8
145. Bailey DM, Davies B, Romer L, et al. Implications of moderate altitude training for sea-level endurance in elite distance runners. *Eur J Appl Physiol Occup Physiol* 1998; 78 (4): 360-8
146. Brooks GA, Butterfield GE, Wolfe RR, et al. Increased dependence on blood glucose after acclimatization to 4300m. *J Appl Physiol* 1991; 70 (2): 919-27
147. Brooks GA, Wolfel EE, Groves BM, et al. Muscle accounts for glucose disposal but not blood lactate appearance during exercise after acclimatization to 4300m. *J Appl Physiol* 1992; 72 (6): 2435-45
148. Burtscher M, Nachbauer W, Baumgartl P, et al. Benefits of training at moderate altitude versus sea level training in amateur runners. *Eur J Appl Physiol Occup Physiol* 1996; 74 (6): 558-63
149. Dick FW. Training at altitude in practice. *Int J Sports Med* 1992; 13 Suppl. 1: S203-6
150. Gore CJ, Hahn A, Rice A, et al. Altitude training at 2690m does not increase total haemoglobin mass or sea level VO2max in world champion track cyclists. *J Sci Med Sport* 1998; 1 (3): 156-70
151. Gore CJ, Hahn AG, Aughey RJ, et al. Live high: train low increases muscle buffer capacity and submaximal cycling efficiency. *Acta Physiol Scand* 2001; 173 (3): 275-86
152. Grassi B, Marzorati M, Kayser B, et al. Peak blood lactate and blood lactate vs. workload during acclimatization to 5050m and in deacclimatization. *J Appl Physiol* 1996; 80 (2): 685-92
153. Green HJ, Roy B, Grant S, et al. Increases in submaximal cycling efficiency mediated by altitude acclimatization. *J Appl Physiol* 2000; 89 (3): 1189-97
154. Hochachka PW, Stanley C, Matheson GO, et al. Metabolic and work efficiencies during exercise in Andean natives. *J Appl Physiol* 1991; 70 (4): 1720-30
155. Katayama K, Matsuo M, Ishida K, et al. Intermittent hypoxia improves endurance performance and submaximal efficiency. *High Alt Med Biol* 2003; 4 (3): 291-304
156. Levine BD, Stray-Gundersen J. 'Living high-training low': effect of moderate-altitude acclimatization with low-altitude training on performance. *J Appl Physiol* 1997; 83 (1): 102-12
157. MacDonald MJ, Green HJ, Naylor HL, et al. Reduced oxygen uptake during steady state exercise after 21-day mountain climbing expedition to 6,194 m. *Can J Appl Physiol* 2001; 26 (2): 143-56
158. Mairbaurl H, Schobersberger W, Humpeler E, et al. Beneficial effects of exercising at moderate altitude on red cell oxygen transport and on exercise performance. *Pflugers Arch* 1986; 406 (6): 594-9
159. Piehl Aulin K, Svedenhag J, Wide L, et al. Short-term intermittent normobaric hypoxia: haematological, physiological and mental effects. *Scand J Med Sci Sports* 1998; 8 (3): 132-7
160. Roberts AC, Butterfield GE, Cymerman A, et al. Acclimatization to 4300m altitude decreases reliance on fat as a substrate. *J Appl Physiol* 1996; 81 (4): 1762-71
161. Rusko HR. New aspects of altitude training. *Am J Sports Med* 1996; 24 (6 Suppl.): S48-52
162. Schmidt W, Heinicke K, Rojas J, et al. Blood volume and hemoglobin mass in endurance athletes from moderate altitude. *Med Sci Sports Exerc* 2002; 34 (12): 1934-40
163. Stray-Gundersen J, Chapman RF, Levine BD. 'Living high-training low' altitude training improves sea level performance in male and female elite runners. *J Appl Physiol* 2001; 91 (3): 1113-20
164. Telford RD, Graham KS, Sutton JR, et al. Medium altitude training and sea level performance [abstract]. *Med Sci Sports Exerc* 1996; 28 (5 Suppl.): S124
165. van Hall G, Calbet JA, Sondergaard H, et al. The re-establishment of the normal blood lactate response to exercise in humans after prolonged acclimatization to altitude. *J Physiol* 2001; 536 (Pt 3): 963-75
166. Wilber R. Altitude training for the enhancement of sea level endurance performance. *Olympic Coach* 1995; 5: 6-10
167. Wolfel EE, Groves BM, Brooks GA, et al. Oxygen transport during steady-state submaximal exercise in chronic hypoxia. *J Appl Physiol* 1991; 70 (3): 1129-36

168. Young AJ, Evans WJ, Cymerman A, et al. Sparing effect of chronic high-altitude exposure on muscle glycogen utilization. *J Appl Physiol* 1982; 52 (4): 857-62
169. Wilber RL. Current trends in altitude training. *Sports Med* 2001; 31 (4): 249-65
170. Sutton JR, Reeves JT, Wagner PD, et al. Operation Everest II: oxygen transport during exercise at extreme simulated altitude. *J Appl Physiol* 1988; 64 (4): 1309-21
171. Katayama K, Sato K, Matsuo H, et al. Effect of intermittent hypoxia on oxygen uptake during submaximal exercise in endurance athletes. *Eur J Appl Physiol*. Epub 2004 Feb 26
172. Saunders PU, Telford RD, Pyne DB, et al. Improved running economy in elite runners after 20 days of simulated moderate-altitude exposure. *J Appl Physiol* 2004; 96 (3): 931-7
173. Newsholme EA, Leech AR. *Biochemistry for the medical sciences*. New York: Wiley, 1983: 357-79
174. Saltin B, Larsen H, Terrados N, 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
175. Weston AR, Karamizrak O, Smith A, et al. African runners exhibit greater fatigue resistance, lower lactate accumulation, and higher oxidative enzyme activity. *J Appl Physiol* 1999; 86 (3): 915-23
176. Green HJ, Sutton JR, Wolfel EE, et al. Altitude acclimatization and energy metabolic adaptations in skeletal muscle during exercise. *J Appl Physiol* 1992; 73 (6): 2701-8
177. Gollnick PD, Saltin B. Significance of skeletal muscle oxidative enzyme enhancement with endurance training. *Clin Physiol* 1982; 2 (1): 1-12
178. Svedenhag J. Running economy. In: Bangsbo J, Larsen H, editors. *Running and science*. Copenhagen: Munksgaard, 2000: 85-105
179. Telford RD, Kovacic JC, Skinner SL, et al. Resting whole blood viscosity of elite rowers is related to performance. *Eur J Appl Physiol Occup Physiol* 1994; 68 (6): 470-6

Correspondence and offprints: *Philo U. Saunders*, Department of Physiology, Australian Institute of Sport, PO Box 176, Belconnen, ACT 2616, Australia.
E-mail: Philo.Saunders@ausport.gov.au