

The interplay of footwear and exercise-induced fatigue on substrate partitioning and energy cost of running during steady-state running exercise

by

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ABSTRACT

The purpose of this study was to assess the interplay of footwear and exercise-induced fatigue (EIF) on substrate partitioning and energy cost of running during steady-state running exercise.

Ten trained male distance runners partook first in an incremental test 7 days prior to the experimental session. Participants performed three 8 min treadmill runs in randomized order in minimalist and shod footwear prior to and immediately after an EIF protocol. Cardiorespiratory parameters, substrate partitioning, RPE and blood lactate were measured throughout the experimental sessions.

No significant difference was observed pre- to post-EIF on $\dot{V}O_2$ during Cr, although $\dot{V}CO_2$ production showed a trend towards significance ($p = 0.063$). Furthermore, there was no significant effect of footwear but there was significant main effect of time (pre- vs. post-EIF) on CHO ($p = 0.003$) and lipid ($p = 0.004$) oxidation. The caloric cost of running showed no significant difference from pre- to post-EIF (0.98 ± 0.14 , 1.00 ± 0.14). Ultimately alteration in substrate contribution to energy production plausibly stems from muscle glycogen depletion. Although not measured muscle glycogen has certainly greatly contributed to maintain running performance during EIF. This is supported by indirect markers of fatigue such as lactate production, RPE score and peak HR.

Keywords: Exercise induced fatigue, Substrate partitioning, Energy cost of running

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List of Abbreviations

BF: Barefoot

Bf: Breathing frequency

BLa: Blood lactate

BPM: Beat per minute

CHO_{ox}: Carbohydrate oxidation

CO₂: Carbon dioxide

C_R: Energy cost of running

EIF: Exercise induced fatigue

EP: Energy Production

EQO₂: Oxygen equivalent

EQCO₂: Carbon dioxide equivalent

FAT_{ox}: Lipid oxidation

HIIT: High intensity interval training

HR: Heart Rate

HRR: Heart rate recovery

IT: Interval training

MAS: Maximal aerobic speed

MIN: Minimalist footwear

MI: Minimalist Index

O₂: Oxygen

PROT_{ox}: Protein oxidation

RE: Running economy

RER: Respiratory exchange ratio

RPE: Rate of perceived Exertion

TM: Treadmill running

$\dot{V}CO_2$: Volume carbon dioxide uptake

$\dot{V}E$: Ventilation (Volume of air expired/min)

$\dot{V}O_2$: Volume oxygen uptake

V_T: Tidal Volume

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1. Introduction

1.1 Background of study

Measurements of energy expenditure and substrate oxidation have been of interest since the late 1800s. Indirect calorimetry is a method used to estimate in vivo rates of substrate oxidation, a technique based on the quantification on volume of oxygen uptake ($\dot{V}O_2$) and volume of carbon dioxide ($\dot{V}CO_2$) output (Jeukendrup and Wallis, 2005)

In fasting and resting states as well as during low intensity exercise, skeletal muscle mostly oxidizes free fatty acid (FFA) (Jeukendrup, 2002). Indeed, low-intensity exercise brings about an increase by several- fold in metabolism compared to resting conditions, and FFA oxidation increases accordingly (Jeukendrup, 2002). Moderate- and high-intensity exercises are known to elevate contraction-induced muscle glycogenolysis and glycolysis, altering the contribution of substrate to energy production (Brooks, 1998). Jeukendrup and Wallis, (2005) cited Christensen and Hansen (1939) who first described a shift from lipid to carbohydrate oxidation as a function of exercise intensity [from moderate to high intensity exercise] using indirect calorimetry. The authors measured $\dot{V}O_2$, $\dot{V}CO_2$, and determined respiratory exchange ratio (RER) to ascertain the effect of exercise intensity on the fuel mix during exercise. Since this seminal work, many studies have shown that carbohydrate metabolism increases as a function of exercise intensity and the contribution of lipid reduces at high exercise intensities (Jeukendrup, 2002). As a consequence of the change in substrate oxidation during high intensity exercise, high reliance on lipid oxidation is chiefly responsible for the reduction in energy cost of running following high intensity or prolonged exercise (Collins et al., 2000).

In addition, the changes in substrate contribution to energy production following high intensity or prolonged exercise, which is revealed by a lower RER, would correspond to a lower energy yield per litre of oxygen uptake (Morgan et al., 1990). In fact, Xu and Montgomery (1995) reported significant elevation in submaximal oxygen uptake in trained male distance runners throughout 90 min of running at 65% and 80% $\dot{V}O_{2max}$. Later, Sproule (1998) also documented increases in submaximal oxygen uptake following 60 min running at 70% and 80% of maximum oxygen uptake. Elevation in oxygen uptake may be explained by increased lipid utilization following exercise-induced fatigue, and this should be reflected in energy cost of running. As reported by Fletcher, Esau and MacIntosh (2009) energy cost of running must be altered by the change in contribution of substrate partitioning and should, then, be a better indicator of running efficiency and performance. However, to the best of our knowledge no studies have considered substrate partitioning during sub-maximal run following exercise-induced fatigue to confirm alteration of energy cost of running. In addition, no study has addressed the potential impact of footwear on these variables.

1.2 Purpose of the study

The purpose of this study was to assess the interplay of footwear and exercise-induced fatigue (EIF) on substrate partitioning and energy cost of running during steady-state running exercise.

1.3 Significance of the study

This study examined substrate partitioning and the energy cost of running following exercise-induced fatigue and how footwear choice potentially moderates these effects. In fact, debate remains as to whether footwear characteristics have an impact on running performance in trained individuals. Meanwhile, different approaches have been developed to determine running efficiency, and discrepancies are reported between studies using different calculation of running efficiency, that is, running economy, energy cost of running and caloric unit of cost, to name the main approaches. The important of this study was to outline the impact of exercise-induced fatigue on energy cost of running, using indirect calorimetry as a technique for the determination of substrate partitioning which is a more sensitive calculation of running efficiency.

2. Review of Literature

2.1 Definition of Energy cost of running and running economy

Several studies such as Cavanagh and Kram, 1985; Daniels, 1985; Morgan, Martin, and Krahenbuhl, 1989; Daniels and Daniels, 1992; Caird, McKenzie, and Sleivert, 1999; Jones and Carter, 2000; Saunders et al., 2004, Noakes, 2001 defined running economy as correlation between oxygen uptake and the velocity of running, also known as the aerobic demand of running (Cavanagh and Kram, 1985; Daniels, 1985; Morgan, Martin, and Krahenbuhl, 1989; Daniels and Daniels, 1992; Caird, McKenzie, and Sleivert, 1999; Jones and Carter, 2000; Saunders et al., 2004) and denoted as the volume of oxygen up taken ($\dot{V}O_2$), per distance, per unit of mass ($\text{mlO}_2 \text{ km}^{-1} \text{ kg}^{-1}$). Burgess and Lambert (2010) also define running economy as the energy cost of running at a submaximal velocity. Although, metabolic rate of exercise remains the gold standard to estimate the efficacy of mechanical work, and a reliable tool to predict endurance performance in running, metabolic demand can also be expressed as the energy spent per unit distance (energy cost of running, Cr) (Lacour and Bourdin, 2015). Di Prampero and colleagues (1986) identified energy cost of running as one of the factors that influence aerobic performance along with maximal oxygen uptake ($\dot{V}O_{2\text{max}}$), and the fraction of $\dot{V}O_{2\text{max}}$ that can be sustained over a given distance (ventilatory threshold). When energy expenditure is used relative to distance covered, it makes the cost dimensionless, because time is not accounted for. Therefore, Cr differs from running economy. However, the energy yielded per litre of oxygen depends on substrate partitioning, which indicates the contribution of CHO and lipid to energy production. It, therefore, represents the caloric cost of running that appears to be a more suitable way to express running efficiency (Fletcher, Esau and MacIntosh, 2009) and refers as energy cost of running. For sake of simplicity metabolic demand of exercise at a given speed will be

referred in this thesis as energy cost of running (Cr). How running speed, exercise-induced fatigue and shoe types affect the energy cost of running is described in the next section.

Energy cost of running is an essential indicator of endurance running performance (Burgess and Lambert, 2010). The Cr can differ among runners with identical maximal oxygen uptake ($\dot{V}O_{2max}$) by as much as 30% (Saunders et al., 2004; Daniels, 1985) and within-group variations of 2-11% have been reported (Morgan, Martin and Krahenbuhl, 1989). However, comparisons of Cr between individuals are only valid amongst homologous populations (Burgess and Lambert, 2010; Daniels et al., 1978; Daniels and Daniels, 1992; Daniels, 1985; Morgan and Craib, 1992; Morgan, 1992). In a homogeneous group of runners, Cr predicts distance running performance, with better runners having lower cost of running at a set submaximal running speed (Saunders et al., 2004; Noakes, 2001; Daniels, 1985; Conley and Krahenbuhl, 1980; Bernard et al., 1998; Krahenbuhl and Morgan 1989, Morgan et al., 1990). In addition, athletes with good Cr are more efficient at utilizing lipids as a fuel source at an increased work rate, delaying the accumulation of metabolites and sparing carbohydrates while running at a race pace (Saunders et.al., 2004). A good Cr will permit a runner to spare skeletal muscle glycogen at the expand of oxygen uptake at a fixed submaximal workload compared to a runner that has “poor” Cr (Burgess and Lambert, 2010). Therefore, any change in Cr is based on the change in $\dot{V}O_2$ and $\dot{V}CO_2$ during submaximal running whereby an increase in respiratory exchange ratio (RER) indicates a decrease in Cr and vice versa. Although, maximal aerobic power of an athlete has been linked to performance during distance running (Conley and Krahenbuhl, 1980; Saunders et al., 2004), Cr is a reliable measure for predicting endurance performance (Pinnington and Dawson, 2001; Tartaruga et al., 2012). According to Di Prampero and colleagues (1993), a 5% increase in Cr results in an approximate 3.8% increase in performance during a distance running

event; a finding replicated by Hanson et al. (2011). Therefore, it is of great advantage to conserve energy (optimal energy production) during competition. Energy cost of running could be improved at the level of elite athletes (Cavanagh and Kram, 1985). Indeed, a significant drop in oxygen uptake affects performance of endurance events. Moreover, numerous authors (Conley and Krahenbuhl, 1980; 1984; Daniels, 1985; Daniels and Daniels, 1992; Krahenbuhl et al., 1989; Morgan, 1992) have successfully shown that interval training can be used to improve running performance and therefore, energy cost of running.

2.2 Effect of speed on energy cost of running

Margaria et al. (1963) was the first group to report no increase in Cr between 8 and 20 km h⁻¹; an outcome later supported by di Prampero et al. (1986), and Saibene and Minetti (2003). On contrary, many studies have reported a minimal increase in Cr as a function of running speed in male or female runners (Costill et al., 1971; Bransford and Howley, 1977; Daniels et al., 1977, 1986; Davies and Thompson, 1986; Conley and Krahenbuhl, 1980; Svedenhag and Sjödin, 1994) while several investigators considered Cr to be independent of running speed (Fletcher, Esau and MacIntosh, 2009; Shaw, Ingham and Folland, 2014). Such a discrepancy in research findings demands further examination. Higher metabolic rate causes a progressive shift of substrates toward glucose oxidation that should be associated with an elevation in O₂. As reported by Fletcher, Esau and MacIntosh (2009, 2010) and Shaw, Ingham, and Folland (2014), Cr was constant through a range of running speed, but oxygen uptake increased as a function of speed. If one includes the contribution of substrate level phosphorylation (fast glycolytic energy production) calculated from blood lactate concentration to total energy cost of running, it results in an increase equivalent of 3 ml O₂ kg⁻¹ per mmol L⁻¹ (Di Prampero and Ferretti 1999). In fact, Kyröläinen et al. (2001, 2003) observed an increase in gross energy expenditure as a function of

speed up to $\dot{V}O_{2 \max}$ when the energy equivalent of blood lactate concentration was added. In addition to the above-mentioned factors, fatigue occurrence might influence Cr.

2.3 Effect of fatigue on oxygen uptake and energy cost of running.

Most studies that investigated the relationship between energy cost of running and fatigue propose that Cr decreases during prolonged exercise and that there is a positive relationship between the magnitude of the decline in energy cost of running, exercise intensity and duration (Sproule, 1998; Xu and Montgomery, 1995; Hausswirth, Bigard, and Guezennec, 1997; Cavanagh et al., 1985; Hausswirth et al., 1996; Woledge, 1998). Xu and Montgomery (1995) showed significant increases in submaximal oxygen uptake in trained male distance runners during 90 min of running at 65% and 80% of maximal oxygen uptake. Similarly, Sproule (1998), reported increases in submaximal oxygen uptake shortly after 60 min of running at 70% and 80% of maximal oxygen uptake. Both studies also showed elevation in submaximal oxygen uptake at higher exercise intensities (Sproule, 1998; Xu and Montegomary 1995). Furthermore, Nicol, Komi and Marconnet (1991) examined the fatigue effects of a paced marathon run on submaximal oxygen uptake in experienced endurance runners. Oxygen uptake was assessed four days before the marathon, at 20-km during the marathon, and immediately after the marathon. Oxygen uptake was determined during a 6 min run at 75%, 100%, and 125% of the individual's marathon speed. It was noticed that oxygen uptake was significantly elevated immediately after the marathon at 75% and 100% of the individual marathon speed compared to pre-marathon values. Kryöläinen, Pullinen, and Candau (2000) also studied the effects of a paced marathon run on submaximal oxygen uptake in seven experienced triathletes. Submaximal oxygen uptake was assessed, in a 5 min submaximal run, one week prior to marathon, at 0-km, 13-km, 26-km and 42-km respectively during the marathon, two hours after the marathon, and at two, four, and six days after the marathon. The study revealed that submaximal oxygen uptake was significantly

elevated at the end of the marathon (42-km), and two hours after the marathon. No other significant differences in submaximal oxygen uptake were noticed during the marathon run (Kryöläinen, Pullinen, and Candau, 2000). Brueckner et al. (1991) noticed a similar finding, where pronounced elevations in the energy cost of running were only noticed after 32-km and 42-km of running at a constant speed on an indoor track. Further, Hauswirth, Bigard and Guezennec (1997) noticed an increase in submaximal oxygen uptake during and at the end of simulated triathlon and marathon runs, when compared to values gathered during an isolated 45 min run. However, Davies and Thompson (1986) showed gradual increases in submaximal oxygen uptake during a four-hour run on a treadmill. In this study, the increase in submaximal oxygen uptake became more apparent after 110 min of running. It was hypothesized that both central (cardiorespiratory system) and peripheral (tissue extraction of oxygen) factors may have contributed to the deterioration in energy cost of running associated with prolonged exercise (Davis and Thompson, 1986). Elevation in submaximal oxygen uptake during fatiguing exercise may be associated with increases in pulmonary ventilation (Bailey and Pate, 1991) and heart rate (Sproule, 1998; Xu and Montgomery, 1995), increases in energy expenditure associated with the dissipation of heat generated during exercise (Sproule, 1998), increases in blood catecholamine and growth hormone concentrations (Braun and Dutton, 2003; Kaciuba-Uscilko et al., 1992), and increases in lipids metabolism (Xu and Montgomery, 1995). Further, raise in submaximal oxygen uptake may also be associated with skeletal muscle damage and weakness that may occur during prolonged exercise, and may therefore reveal an increase in muscle fibre recruitment (Burgess, 2010 cited Xu and Montgomery 1995; Calbert, Chavarren, and Dorado, 2001; Davis and Thompson, 1986; Perry et al, 2001; Kryöläinen, Takala and Komi, 1998; Dick and Cavanagh, 1987). However, little is known regarding the cumulative effect of prolonged

periods of vigorous training and frequent competitive distance racing on energy cost of running (Morgan and Craib, 1992; Morgan et al, 1990).

Using a more aggressive approach, Morgan et al., (1990), studied the effects of a 30 min maximal run at 89% of maximal oxygen uptake on energy cost of running and running mechanics in male runners. The study showed no changes in energy cost of running on day one, two, and four after the maximal run, signifying that there were no lasting effects of fatigue from the high intensity protocol on submaximal oxygen uptake. Dressendorfer (1991) studied steady-state exercise in trained male runners during a controlled bout of submaximal exercise, and following a paced outdoor 21.1-km run. There were no differences in submaximal oxygen uptake following the 21.1-km run, compared to the control values. While the association between Cr and fatigue appears to be relatively linear, it is important to note that fatigue during running has a multi-faceted response that impacts many physiological and biomechanical variables. It is also imperative to note that fatigue response may be different between individuals. Thus, it has been hypothesized that variations in physiological and biomechanical variables may mask the measure of Cr or, otherwise, be the underlying cause of a decrease observed with fatigue (Candau et al., 1998; Hunter and Smith, 2007). For example, alterations in gait characteristics (Candau et al., 1998; Hanley and Mohan, 2014; Hauswirth, Bigard, Guezennec, 1997; Kyrolainen et al., 2000; Nicol, Komi and Marconnet, 1991; Williams, McClay, Manal, 2000), elevation in respiratory muscle effort (Candau et al., 1998; Davies and Thompson, 1986; Nicol, Komi and Marconnet, 1991), and elevation in activation of the lower limb musculature (Davies and Thompson, 1986; Nicol, Komi and Marconnet, 1991; Williams, McClay, Manal, 2000) due to fatigue have been suggested to influence Cr.

2.4 Effect of fatigue on substrate partitioning and energy cost of running.

Measuring human energy expenditure and substrate oxidation have been of interest since the late 1800s. The method of indirect calorimetry was used to measure substrate oxidation, a technique based on the measurement of oxygen uptake and amount of carbon dioxide expired. At first, such measurements were made under resting conditions, while measurements during exercise were already being made in the early 20th century (Frayn, 1983). Indirect calorimetry is still the most reliable and valid technique to study acute and chronic metabolic responses both at rest and during exercise.

It was also recognized, however, that these measurements could determine the contribution of carbohydrate and lipids to energy production. In this regard, as early as 1920, measurements of pulmonary gas exchange were performed at rest and during exercise (Krogh and Lindhardt, 1920). Using handcrafted equipment Krogh and Lindhardt, (1920) showed that the fuel mix oxidized during exercise was affected by several factors including exercise intensity, exercise duration, and dietary intake in the days before the measurement. Furthermore, in the 1930s more refined indirect calorimetry measurements confirmed that changes in substrate utilization during exercise can occur with changes in exercise intensity and duration (Christensen, 1932; Christensen and Hansen, 1939; Edward and Margaria, 1934). Information on the relative use of fuel energy substrates (carbohydrates, lipids, proteins) helped to develop a model on energy-substrate partitioning in which the effects of exercise intensity, gender, endurance training and nutrition are coordinated and regulated (Brooks, 1998).

At rest and during exercise, skeletal muscle is the main site of oxidation of free fatty acid (FFA) (Jeukendrup, 2002). In resting conditions and especially after fasting, FFAs are the predominant fuel contributing to energy production (Jeukendrup, 2002). During low-intensity

exercise, metabolism elevates several-fold compared to resting conditions, and lipid oxidation increases (Jeukendrup, 2002). In addition, genotypic response to training allows high aerobic capacity. Phenotypic regulations from endurance training induces muscular, biochemical and endocrine adjustments that spare glycogen, match glycolysis to tri-carboxylic acid (TCA) cycle turnover and improve lipid oxidation to given submaximal exercise stresses (Bouchard et al, 1988). Moderate and high intensity exercises are considered to increase contraction-induced muscle glycogenolysis and glycolysis, changing the pattern of fibre type recruitment to include fast-glycolytic fibres with elevation of sympathetic nervous system (SNS) activity, thus increasing carbohydrate catabolism, a phenomenon known as crossover concept (Brook, 1998). However, Jeukendrup (2002) claimed that when exercise intensity increases, lipid oxidation increases further, up to 65% $\dot{V}O_{2max}$; after a decline occurs. Christensen and Hansen (1939) reported a shift from CHO towards lipid oxidation as a function of intensity (moderate to high intensity exercise). In contrast to carbohydrate metabolism, which increases as a function of the aerobic work rate, the relative contribution of lipid to energy production reduces at the high exercise intensities (Jeukendrup, 2002). Although distance running performance requires high $\dot{V}O_{2max}$, other physiological factors contribute to determining endurance capacity. Their contribution varies according to race distance and includes the ventilatory threshold [the percentage of $\dot{V}O_{2max}$ a runner can maintain while minimizing metabolites accumulation]. The latter associates with the capability of oxidizing lipid at high work rates thereby sparing carbohydrate (i.e. good energy cost of running) (Saunders, 2004). The change in substrate utilization with high dependency on lipid oxidation is chiefly responsible for increased time-to-exhaustion (Collins et al., 2000).

In addition, the changes in substrate utilization, as shown by the reduced respiratory exchange ratio, would correspond to a lower energy yield per litre of oxygen uptake (19.61 J per litre for RER=0.7 to 21.6 J per litre for RER=1.0). Morgan et al. (1990) replicated Martin et al.'s (1987) study and found participants' metabolic response mirrors that obtained by Martin et al. (1987) in eight elite runners. Their result showed that economy remains unchanged one day following a hard training run despite their lower RER and increased blood [FFA]. Morgan et al. (1990) replicated the latter study with special attention to the influence of circadian variation and footwear on energy cost of running by ensuring that subjects performed all submaximal testing at the same time of the day and in the same pair of shoes. Subjects were also required to refrain from road race participation during the testing period, and reduced the intensity and duration of their running workout prior to testing. The outcomes revealed that Cr and heart rate remained unchanged following prolonged maximal run, followed by similar decrease in RER (Morgan et al., 1990). More recently, Sproule (1998) showed that 60 min of running at 70% and 80% of $\dot{V}O_{2max}$ provoked a decline in energy cost of running by 6.7% and 9.5% respectively. This elevation in oxygen uptake may be explained by an increase in lipid utilization. Effectively, for similar number of carbons, lipid oxidation requires more O₂ than carbohydrate to produce the same quantity of ATP. Theoretically, this biochemical modification causes a decrease in the RER (Astrand, 1986).

2.5 Effect of exercise-induced fatigue on skeletal muscle substrate contents

One must separate the effect of speed from the effect of fatigue. It has been known since quite a long time that running at a steady-state pace for extended duration leads to an increase in oxygen demand, the so-called cardiovascular drift, a phenomenon that has lately been associated with dehydration and elevated body core temperature (Coyle and Gonzalez-Alonzo, 2001). In addition to the cardiovascular response to prolonged exercise, other metabolic processes were

targeted as potential factors that induced fatigue. The term prolonged exercise mostly describes cyclical exercise of 30 to 180 min of duration. As shown by Peronnet et al (2006), exercise beyond 70% of $\dot{V}O_{2max}$ is mainly sustained by muscle glycogen during the first 30-40 min. After about an hour, a progressive increase in FFA oxidation due to the action of catecholamines, glucagon, and cortisol as well as an increase in blood glucose uptake is observed. However, ATP production becomes compromised with the depletion of muscle and liver glycogen as the low rate of ATP re-synthesis from lipid oxidation cannot compensate the ATP deficit. It ensues a decrement in running performance. A large body of evidence exists supporting a correlation between the depletion of intramuscular glycogen store and the onset of fatigue. However, the evidence also shows that other factors are acting in conjunction with glycogen depletion to produce local muscle fatigue (Fitts et al, 1982). Glycogen, a complex glucose polymer found in most species in the animal kingdom, functions as a storage form for glucose found in a variety of tissues, mainly in skeletal muscles and the liver. The wide occurrence of glycogen in skeletal muscles shows its importance in providing substrate by which ATP can quickly be produced in muscle cells, and display a high and quick fluctuating energy turnover (Ørtenblad, Westerblad, and Nielsen, 2013). The reduction of muscle glycogen store during prolonged, strenuous exercise lead to performance decrement and fatiguing state as observed for decades (Hermansen, Hultman and Saltin, 1967). In addition, a depletion of stored glycogen compromises muscle functions, even in an abundance of other fuel sources (Bergstrom et al., 1967). There exists a close correlation between muscle glycogen content and fatigue resistance, both during prolonged (more than 1 h) and during high-intensity intermittent exercise (Pernow and Saltin, 1971; Gollnick et al. 1972). The most recognized theory to explain the glycogen content and muscle alteration relationship during exercise stems from a decrease in the rate of ATP regeneration

resulting from glycogen depleted store (Ørtenblad, Westerblad, and Nielsen, 2013). As a result, the muscle cannot sustain an adequate energy supply to one or more of the processes involved in excitation and contraction, causing inability to translate the motor drive into an expected force, i.e., fatigue develops (Ørtenblad, Westerblad, and Nielsen, 2013).

In the absence of glucose supplementation (e.g. by carbohydrate ingestion), a progressive reduction in blood glucose levels during prolonged exercise occurs, as liver glycogen levels become depleted (Hargreaves, 2005). Reduction in blood glucose availability mirrors the reduced rate of carbohydrate oxidation and the occurrence of fatigue. In fact, increased exogenous glucose by carbohydrate ingestion increases carbohydrate oxidation and improves endurance performance (Hargreaves, 2005). This may be partly due to enhanced glucose uptake by muscles (McConnell et al., 1994) and improved muscle energy balance (Spencer et al., 1991), but apparently not to reduction of muscle glycogen utilization (Hargreaves, 2005 cited Coyle et al., 1986). Because the brain takes up glucose as the key substrate, hypoglycaemia may also reduce brain glucose uptake and thereby contribute to central fatigue (Nybo and Secher, 2004). Thus, carbohydrate ingestion during prolonged strenuous exercise enhances cerebral energy balance and the maintenance of central neural drive (Nybo and Secher, 2004). Recent studies have also showed improved physical and mental function with carbohydrate ingestion during intermittent exercise of the type used in team sports (Welsh et al., 2002; Winnick et al., 2005).

Brisk breakdown of muscle glycogen and glucose during vigorous exercise causes a large increase in lactic acid production. At physiological *pH*, the pyruvic acid produced at the end of the fast-glycolytic pathway flows into two metabolic pathways according to glucose catabolic rate (flux). It enters into the Krebs cycle via the formation of Acetyl-CoA and, when overflows, breaks down into lactate and H^+ (Fitt, 1994). Lactate was considered as a dead-end metabolite

accumulated during exercise that gives rise to fatigue and oxygen debt. However, lactate represents a metabolic intermediate between carbohydrate storage forms and metabolic end products (CO_2 , and H_2O). The advantage of lactate as metabolic intermediate lies in its rapid switch between tissue compartments. Lactate, a low molecular weight ion, does not require insulin for transport, and moves across cell membrane barriers by facilitated transport (Fitt, 1994). Lactate ion appears to have no major negative effects on the capacity of skeletal muscle to generate force, although conflicting data exist in the literature (Hargreaves, 2005). In humans exercising at different work intensities, lactate levels do not relate well with muscle fatigue (Fortier, 2004). A consequence of lactate production, however, leads to an increase in the intramuscular $[\text{H}^+]$ (decrease $p\text{H}$ causes acidosis) linked to a high rate of ATP breakdown, non-oxidative ATP production, and strong ion movement (e.g. K^+) across the muscle cell membrane (Hargreaves, 2005). However, chronic metabolic responses to training enhance the skeletal muscle buffer capacity that nullify, to some extent, the effect of H^+ on $p\text{H}$. Therefore, rather than a dead-end product, during exercise lactate behaves as a substrate for ATP production as well as a gluconeogenic precursor (Brooks, 1998).

During prolonged exercise a fall of ATP concentration in the cell ensues the decrease in ATP production (Green, 1991). In addition, swift breakdown of ATP causes the levels of Mg^{2+} , ADP, P_i within skeletal muscle to elevate. Increased Mg^{2+} can hamper Ca^{2+} release from the sarcoplasmic reticulum and impair force production, especially in combination with lowered $[\text{ATP}]$ in muscle (Dutka and Lamb, 2004). High $[\text{ADP}]$ in muscle can reduce force and slow relaxation in muscle by adversely affecting the contractile myofilaments and Ca^{2+} uptake into the sarcoplasmic reticulum (Hargreaves, 2005 cited MacDonald and Stephenson, 2004). The elevation of P_i also reduces contractile force and Ca^{2+} release from the sarcoplasmic reticulum

(Hargreaves, 2005). Furthermore, these biochemical reactions alter several metabolic processes of the muscle excitation-contraction cycle (Green, 1991) The muscle would not, therefore, generate sufficient energy to sustain the contractile activity (Green, 1991). Curiously, single muscle fibres analyses have shown that [ATP] mainly falls in type II "fast" fibres following intense exercise, a factor that limits the contribution of the latter to force production (Casey et al., 1996). As fatigue develops, greater fibre type II recruitment follows hindering metabolic efficiency and the force production (Komi and Marconnet, 1991; Kryöläinen, Pullinen, and Candau, 2000; Davis and Thompson, 1986).

Alterations of neuromuscular function related to fatigue also impacts on energy cost of running. Scientific evidence suggests that at the end of a marathon, greater muscle recruitment takes place to produce the similar resultant force during the push-off phase (Burgess, 2010 cited Nicol, Komi and Marconnet, 1991; Kryöläinen, Pullinen, and Candau, 2000; Nicol, Komi, and Marconnet 1991). Furthermore, changes in running kinetics and kinematics were linked to the onset of fatigue during prolonged running, and related to a reduced energy cost of running (Hauswirth, Bigard and Guezennec, 1997; Nicol, Komi and Marconnet, 1991; Kryöläinen, Pullinen, and Candau, 2000). Many different types of exercise and exercise arrangements can lead to fatigue occurrence. Studies have used discrete movement fatiguing protocols (acyclic) such as isometric force production; other have implemented cyclical movement patterns such as rowing, skiing, swimming, and, obviously running to induce fatigue through different modalities, that is, long-duration steady-state exercise to high intensity interval training. In this thesis, the latter was the object of interest because it has been reported to induced fatigue in well-trained runners (Zavorski, Montgomery, and Pearsall, 1998).

2.6 Interval Training

Interval training can be defined as physical training consisting of periods of high- or moderate-exercise intensity interspaced with recovery periods of low-intensity or no exercise. Exercise bout duration could range from 30-sec to 20 min repeated for total training periods of 20 min to 60 min. The prescribed intensity of exercise and recovery periods depend on the energy system to be enhanced (ACSM, 2014). The interval training was popularised in early 1950's by the long-distance runner Emil Zatopek and was later investigated by Reindell et al 1959, 1962 examined the impact of IT and the systematic participation in an exercise program on cardiovascular response of trained individuals. From there, middle and long-distance runners have since used IT to improve running performance and to increase maximal aerobic capacity (Hickson and Rosenkoetter, 1981).

The intent of implementing HIIT into an exercise program is to stress the physiological systems that will be solicited during a specific type of exercise (Daniels and Scardina, 1984). The principle revolves around the notion that the metabolic systems must be stressed to trigger chronic responses to training (Paul and David, 2002). While interval training has been used in endurance sports to improve aerobic performance (Billat, 2001), studies have used interval training to induce fatigue in order to investigate metabolic changes in $\dot{V}O_2$, heart rate, core temperature, substrate oxidation, skeletal muscle and liver glycogen content, blood catecholamines, as well as in biomechanical efficiency (Bailey and Pate, 1991; Kalis et al., 1988; MacDougall et al., 1974; Morgan and Craib 1992; Williams and Cavanagh 1987, Zavorsky, Montgomery and Pearsall, 1998).

During interval training, at moderate-to-high intensity exercise, skeletal muscle glycogen serves as the primary fuel source (Romijn et al, 1993). Fatigue during this type of training sessions often associates with muscle glycogen depletion (Allen, Lamb and Westerblad, 2008;

Bergstrom, et al., 1967; Hultman, 1967). The high blood [lactate] reflects the contribution of the fast glycolysis during the exercise interval, especially in type II muscle fibres (Allen, Lamb and Westerblad, 2008). Fatigue results from complex step-down processes along the path from the motor cortex to the myofibril; however, high intensity short lasting exercise bouts provokes a gradual decline of energy production from the fast glycolysis. In the process [ATP] and [PCr] rapidly decrease along with increase in [ADP], [Pi], and [H⁺]. As a result, pH decreases and glycolytic enzyme activities slow down drastically altering the excitation-contraction coupling (Fitts, 1994). Therefore, in addition to the depletion of skeletal muscle and liver glycogen content during interval training, under these circumstances exercise performance deteriorates and, fatigue sets in. However, a debate remains regarding whether fatigue alters energy cost of running and its interplay with shoe type?

2.7 Footwear characteristics

The effect of footwear on running performance has generated a great deal of debate in the last forty years. Humans evolved as hunters and gatherers walking and running barefoot as a natural way of transportation. They were, therefore, well-adapted to walk and run over long distance on hard and rough surfaces (Lieberman, 2012). Even in recent years, runners like Abede Bikila, who won a gold medal and set a new world record in the Marathon at the 1960 Rome Olympic games (Bowles et al., 2012), ran on barefoot and were performing very well against western runners equipped with the new shoe technologies.

In the last decade, several peer-reviewed manuscripts reported alterations of various aspects of gait while running barefoot compared to wearing conventional shoes (Hatala et al., 2013; Jenkins and Cauthon, 2011). According to some of these scientific reports, barefoot running decreases impact at contact, as well as improves proprioception (Altman and Davis, 2012) (Hatala et al., 2013; Jenkins and Cauthon, 2011; Perl, Daoud and Lieberman, 2012).

Further to the experimental outcomes, barefoot running improved performance and reduced the risk of overuse injuries (Altman and Davis, 2012; Goss and Goss, 2012; Jenkins and Cauthon, 2011; Nigg, 2009; Nunns et al., 2013; Paulson and Braun, 2014). However, barefoot running can be limited due to hard and unsafe floor conditions or inclement weather conditions (Hollander, 2015). This has led to the identification of different types of footwear in the market today that could mimic the barefoot condition without risking injuries from unsafe ground conditions. Indeed, this topic increased attention among numerous manufacturers (Hollander, 2015). The following sections will dwell on differences between MIN and conventional footwear (SHOD).

2.7.1 Conventional

The traditional (conventional) running shoes provide great amount of cushioning giving support, protection and proper movement patterns (Altman and Davis, 2012; Divert et al., 2005B; Warne and Warrington, 2014). The SHOD are commonly designed to give protection to the foot, offer traction, control foot pronation, reduce the force of initial impact, and decrease the energy cost of running (Knapik et al., 2014). The SHOD are characterised by double density midsole, with higher cushioning heel and arch support (Altman and Davis, 2012; Bonacci et al., 2013) with the forefoot midsole approximately 11 mm thinner than the heel (Fleming, 2015; Gavilanes-Miranda, De Gandarias, and Garcia, 2012). The SHOD heel elevation decreases Achilles tendon loading by reducing range of motion at ankle joints during running; however, studies carried out to ascertain if this strategy prevent risk of injury produced contrasting results (Bowles et al., 2012). Amazingly, incidence of Achilles tendon injuries has increased steadily since the invention of modern running shoe (Richard, Magin and Callister 2008) as it relates to joint torque increase at the ankle, hip, and knee causing heel strike landing in front of body mass centre and, therefore, increasing the braking phase (Lieberman et al., 2010; Daoud et. al., 2012; Lohmann, Sackieriyas, and Swen, 2011). Furthermore, shoe mass has been described to be

particularly essential in Cr determination, as additional shoe mass increased the metabolic demand of running, i.e., hindered metabolic cost at a known workload (Divert et al., 2008). For instance, the cost of transport increased by approximately 1% for every additional 100 g in shoe mass, and in addition, Franz, Wierzbinski and Kram (2012) reported a strong relationship between shoe mass and Cr. These factors have led runners to adopt the minimalist footwear.

2.7.2 Minimalist

Minimalist running shoes suffer inextricable confounds with barefoot running regardless of flourishing evidence indicating the two are not similar (Fleming et al., 2015; Bonacci et al., 2013; McCallion et al., 2014; Nigg, 2009). Minimalist footwear (MIN) represents a hybrid between BF and SHOD. Forty-Three experts from 11 countries – mainly researchers and health care professionals – defined the MIN as “Footwear which provide negligible interference with the correct movement pattern of the foot due to its high amount of flexibility, decrease heel to toe drop, weight and stack height, and lack of movement control and stability devices” (Esculier et al., 2015). The MIN footwear offers, therefore, lightweight with malleable soles and minimal heel to forefoot offset that give reduced degree of padding (Altman and Davis, 2012; Bonacci et al., 2013; Warne and Warrington, 2014). Heels are usually 0 to 4 mm thicker than the forefoot midsole (Fleming, 2015; Gavilanes-Miranda, De Gandarias, and Garcia, 2012). These shoes imitate barefoot condition and prevent injury risk as for barefoot running. Furthermore, minimalist footwear predisposes user to increased ankle dorsiflexion and knee flexion upon foot strike (Willy and Davis 2013). In addition, minimalist shoes with a flat sole but devoid of cushioning can cause runners to make acute and immediate changes in running gait from a rear-foot strike to a fore-foot strike, to increase cadence and to reduce vertical oscillation of the centre of mass, which in turn can improved Cr (Moore, Jones and Dixon, 20014, Warne and Warrington, 2012).

Regardless of imitating the shape of the foot, or duplicating the feeling of BF, any form of MIN design remains a form of footwear. Whatever characteristics of BF the shoe displayed, it is still literally a form of footwear.

However, Esculier et al., 2005 developed a scale to rate how minimalist footwear can be, using five standard features within minimalist shoe definition that includes weight, stack height, stability and motion control technologies, heel to toe drop, and flexibility. The degree of minimalism is, then, quantified by a minimalist index score expressed in percentage with lower score associated with maximalist and higher score related to minimalist.

Several studies have investigated effect of shoes on Cr, specifically comparing barefoot with SHOD, but to the best of our knowledge no study has investigated interplay of footwear and exercise-induced fatigue on energy cost of running.

2.8 Hypothesis

We hypothesized an interplay between footwear and exercise-induced fatigue on energy cost of running and substrate utilization. Consequently, there will be shift towards lipid oxidation / utilization and an altered energy cost of running due to fatigue with lesser shift towards lipid oxidation with minimalist footwear and higher shift towards lipid oxidation with shod shoe types. Therefore, the hypothesis was aimed to answer following research questions:

- a) Is there any change in Cr following EIF?
- b) Will there be any alteration in substrate utilization following EIF?
- c) Is there any effect of footwear on Cr and substrate utilization?

3. Material and Methods

3.1 Experimental procedure

Ten active and healthy male distance runners were recruited for this study, which consists of one familiarization session and two counterbalanced experimental conditions with at least 72 hours washout period. Before each session, participants were instructed to refrain from strenuous exercise and resistance training for 36 hours and to avoid caffeine, alcohol, and other stimulants or supplement intake for 24 hours. Participants were also asked to arrive well rested for each testing session. A total of 10 male distance runners were examined in this study, however, we dropped metabolic data of one participant who did not complete post-energy cost of running test. To be eligible for this study, participants were required to have trained for minimum of five days a week, with one training session being high intensity interval over 70% of maximal aerobic speed (MAS). In addition, they were required to run a minimum of 50 km, per week and have at least one year of serious training.

All sessions were conducted in the morning at the same time of day for each participant (see Figure 1). During the familiarization session (Day one), participants read and signed the consent form, and answered a long-form physical activity readiness questionnaire to screen for health and injury risks in addition to completing a questionnaire that determines training status and minimalist shoe experience. If eligible, anthropometric measurements were recorded and participants underwent a fitness appraisal. Then both SHOD and MIN shoes were provided for the duration of the experiment. All participants were given an identical footwear to ensure they were all exposed to the same conditions during their running session. The MIN (Altra “one”) weighed 178 g and had a 0 mm heel-toe drop. This corresponds with a consensus definition

established by Esculier et al. (2015). The SHOD (Brooks “Glycerine 13”) weighed 349 g and had a 12 mm heel-toe drop. Both models of footwear were neutral that is, no anti-pronation or

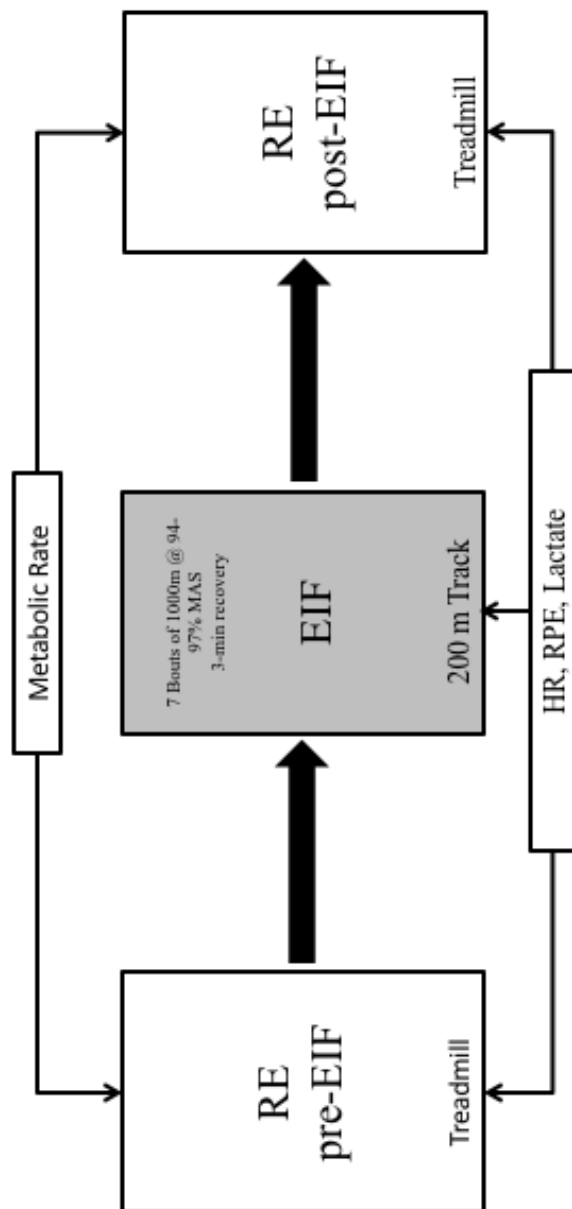


Figure 1
Experimental design and time line. Participants completed two experimental trials in counterbalanced fashion. Each experimental trial consisted of undertaking energy cost of running tests at three randomised velocities pre- and post-EIF protocol. Participants performed seven bouts of 1000 m with 3 min recovery during EIF protocol. Metabolic rate, HR and lactate measurements were collected energy cost of running tests and HR, lactate, and RPE during EIF protocol.

anti-supination elements in the outsole. During sessions two and three (Day two and three), participants underwent a pre- and post-treatment energy cost of running test interspaced with the treatment consisting of a running fatiguing task in both SHOD and MIN conditions.

DAY ONE: Maximal oxygen uptake ($\dot{V}O_{2max}$) determination test was administered to characterize the participants' aerobic fitness and to determine MAS. The MAS was needed to individualize interval training aerobic speed during the subsequent experiment sessions. The running test was performed on a motor-driven treadmill at a constant 1% slope. Prior to the test, a warm-up, consisting of running at a self-selected speed for 5 min were provided. Afterwards, the incremental test started at an initial speed of 7 km.h⁻¹ and increased by 1 km.h⁻¹ every 2 min until volitional exhaustion was reached (Leger and Boucher, 1980). Participants were then given 5 min rest before undergoing a verification phase that consisted of running at 105% of the speed reached at $\dot{V}O_{2max}$ until volitional exhaustion; a procedure implemented to ensure the participants reached $\dot{V}O_{2max}$ (Rossiter, Kowalchuk, and Whipp, 2006). A recovery period followed, until participants' heart rate decreased to 120 b.min⁻¹. The MAS corresponded to the speed reached at $\dot{V}O_{2max}$ as per Basset and Boulay (2003)

Day Two and Three: Participants underwent an energy cost of running test consisting of three randomized 8 min 1% grade treadmill runs at 2.79, 3.33, and 3.89 m s⁻¹ with a 2 min rest period between runs. A self-selected warm-up was provided for participants as recommended by Shaw, Ingham and Folland, (2014). During the Cr test, metabolic rate (MR), heart Rate (HR), blood lactate concentrations (BL) and rate of perceived exertion (RPE) were recorded. After completing the running test, participants were then directed to a 200 m indoor track to perform the exercise induced fatigue protocol (EIF) consisting of 7 bouts of 1000 m between 94% and 97 of MAS with 3 min of recovery between runs. EIF protocol deemed completed when participants

reached a RPE score of 19 (Dishman, 1994). The intensity of the bouts corresponds with a typical endurance runner's training session with the aim of developing aerobic power (Basset, Chouinard and Boulay, 2002). Upon completion of the EIF protocol, participants returned to the laboratory and underwent the same energy cost of running protocol as mentioned above.

3.2 Cardiorespiratory Measurements

Cardiorespiratory parameters were recorded during incremental and energy cost of running tests. Oxygen uptake ($\dot{V}O_2$), carbon dioxide output ($\dot{V}CO_2$), breathing frequency (f_R), and tidal volume (V_T) were recorded through real time breath-by-breath sampling using an indirect calorimetric system implemented with O_2 and CO_2 analyzers (Oxycon Pro, Jeager, Germany). Respiratory exchange ratio (RER) and minute ventilation (V_E) were calculated as the quotient of $\dot{V}CO_2$ on $\dot{V}O_2$ and as the product of f_R by V_T , respectively. Prior to testing, gas analyzers and volume were calibrated with medically certified calibration gases and automated flow calibration respectively.

3.3 Blood Lactate (BL) Measurement

The BL were sampled prior to each energy cost of running test. During the EIF, BL were sampled during three of the rest periods (i.e. the rest period following the first, third and seventh interval). Blood samples were approximately 15-20 μ L each for a total of 210-280 μ L. Lactate is an indicator of the fast glycolytic pathway that plays a major role in energy production, one of the parameters needed to accurately quantify fatigue. Blood was assayed on site with a lactate analyzer (Lactate scout+, EKF diagnostics, Cardiff, U.K.).

3.4 Heart rate (HR)

HR data were collected throughout the lab and track sessions with a heart monitor (Suunto, model Ambit2, Suunto OY, Vantaa, Finland) and uploaded to MovesCount

(www.movescount.com) and transferred to Igor Pro 6.3 (WaveMetrics Inc, Lake Oswego, Ore, USA) for determination of peak HR during fatigue protocol.

3.5 Substrate Oxidation and Partitioning

Glucose (Gox) and lipid (Lox) oxidation rates were calculated according to the following equations (Jeukendrup and Wallis, 2005).

$$G_{ox} \text{ (g min}^{-1}\text{)} = -4.21\dot{V}CO_2 + 2.96\dot{V}O_2 - 0.4N \quad \text{Eq. 2-1}$$

$$L_{ox} \text{ (g min}^{-1}\text{)} = 1.695\dot{V}O_2 - 1.701\dot{V}CO_2 - 1.77N \quad \text{Eq. 2-2}$$

where $\dot{V}O_2$ and $\dot{V}CO_2$ are expressed in $L \text{ min}^{-1}$.

N is urinary nitrogen which is 0.160 (PRO_{ox}) (Simonson and Defronzo, 1990).

Protein oxidation rate (PRO_{ox}) were estimated at 0.066 g min^{-1} based on previously published urinary urea excretion measurements made on 12-h post-absorptive men with normal CHO reserves (Haman, Legault and Weber, 2004; Haman et al., 2002).

3.6 Energy Production

EP was calculated from individual contribution of each substrate to the fuel mixture as follows:

$$EP \text{ (kcal min}^{-1}\text{)} = 4.07G_{ox} + 9.75L_{ox} \quad \text{Eq.2-3}$$

NOTE: Calculation of energy expenditure assume negligible contribution of protein oxidation for moderate to high intensity exercise (Jeukendrup and Wallis, 2005).

3.7 Metabolic Data Reduction

All metabolic data were transferred to Igor pro 6.3 (WaveMetrics Inc, Lake Oswego, Ore, USA) for further analysis. Cardiorespiratory parameters of the incremental test were first smoothed using second-order polynomial function to determine maximal values of $\dot{V}O_2$, $\dot{V}CO_2$, breathing frequency (f_R), and tidal volume (V_T) as well as peak oxygen uptake of the verification phase. Second equivalent of O_2 and CO_2 (Eq O_2 and Eq CO_2), were calculated and

plot over $\dot{V}O_2$ to determine the ventilatory threshold by identifying when equivalent O_2 abruptly departs from equivalent CO_2 as a function of $\dot{V}O_2$ (Cooper, 2004). For the energy cost of running test, the $\dot{V}O_2$ and, $\dot{V}CO_2$ were computed using the area under the curve method (AUC) applied on the middle 4 min of 8 min running bouts. From the latter values estimate of energy expenditure (kcal min^{-1}) and of disappearance rate of glucose (G_{ox}) and lipid (L_{ox}) were calculated using equations 2-1, 2-2, then the energy cost of running was calculated as per Fletcher, Esau and MacIntosh (2009) using equations 2-3.

Heart rate peak was determined using FindPeak function from Igor Pro 6.3 (WaveMetrics Inc, Lake Oswego, Ore, USA). Peak HR was detected from HR signal (Y= HR in bpm and X=time in sec) collected during the experimental sessions. First the signal was smoothed by a Box smoothing procedure that averaged an equal numbers of points before and after the averaged output (or smoothed value). Then, the peak maximum was detected [with minimum peak amplitude of 5% and a maximum peak window of 100] at the first derivative zero-crossing, where the second derivative was negative (Igor Pro Manual – volume III- chapter 9 Signal processing, 2017).

3.8 Statistical Analyses

All values are reported as mean \pm standard deviation, unless otherwise specified and an alpha level (α) of 0.05 was used to indicate statistical significance. Tests for statistical assumptions (i.e., normality and homogeneity of variance) were performed, that is, the homogeneity of variance was tested using Levene's test and normality was tested using Kolmogorov-Smirnov test. First, descriptive statistics were conducted on all parameters of interest (body mass, height, age, training profile parameters, $\dot{V}O_{2max}$, and maximal aerobic speed). Second, a 2-way [2 conditions (MIN vs. SHOD) X 2 time (pre- vs. Post-EIF)] ANOVA

with repeated measures was performed on metabolic parameters and energy cost of running. Note that owing to stoichiometric equations limitation (invalid outcomes when RER is over or under 1.0 and 0.7, respectively) treadmill velocities of 3.33, and 3.89 m s⁻¹ were discarded from the analysis. Third, a 2-way [2 conditions (MIN vs. SHOD) X 5 time (pre-, first, mid, last, and post-EIF)] ANOVA with repeated measures was conducted on blood lactate and RPE. Finally, a 2-way [2 conditions (MIN vs. SHOD) X 3 time (first, mid, last interval)] ANOVA with repeated measures was run on peak HR during the EIF. IBM SPSS Statistics 20(IBM Corporations, Armonk, New York, USA) was used for statistical analyses.

4. Results

Recall that owing to stoichiometric equations limitation (invalid outcomes when RER is over or under 1.0 and 0.7, respectively) treadmill velocities of 3.33, and 3.89 m s⁻¹ were discarded from the analysis.

4.1 Participants characteristics and training profile

As displayed in Table 1, the maximal aerobic capacity of our participants falls under the 90 percentiles score according to the ACSM value for maximal aerobic power (ACSM, 2013). The $\dot{V}O_{2\max}$ score corresponded to the predicted score from the velocity reached at exhaustion (speed \times 3.5ml min⁻¹) (Tokmaskidis et al., 1987), and confirmed aerobic fitness of participants as shown by HR_{max} that reached 100% of maximal age predicted HR (220-age).

As displayed in table 2, the training profile of our participants was screened to ensure their capability to completing the EIF protocol. Participants had to train for a minimum of 5 days a week and have one of their weekly training sessions at an intensity higher than 70% of MAS. In addition, they had to run at least 50 km per week as shown in table 2. As such they represent a good cluster of runners as demonstrated by 10 km personal best that reached 46% of the world record (Mercier scoring table) and by their weekly training load.

4.2 Exercise-induced fatigue (EIF)

Statistical analysis revealed no significant interaction on blood lactate. However, a significant main time effect was observed for blood lactate ($p=0.0001$). Pairwise comparisons showed that all blood lactate measurements significantly differ from each other (see Figure 2 top panel). Furthermore, a significant main time effect was revealed ($p=0.0001$) for RPE, although no significant interaction was present. *Post hoc* analysis showed that as for blood lactate all scores significantly differ from each other (see Figure 2 mid panel). Finally, a significant main

Table 1 Anthropometric and fitness characteristics of the participants

Age (yrs.)	Mass (kg)	Height (cm)	VO_{2max} (ml min ⁻¹ kg ⁻¹)	MAS (km hr ⁻¹)	HR_{max} (bpm)
29.0±7.5	71.0±4.8	176.3±6.5	61.6±7.3	18.0±1.1	190.3±9.0
Mean±SD					

Table 2 Training profile of the participants

	Years of Structured Training	Training Load (km week⁻¹)	PB 10k (mm:ss)	Session (Week⁻¹)	Interval training (week⁻¹)
Mean	4.8	73.0	35:46	7.1	1.7
SD	4.3	17.3	3:50	2.5	0.5

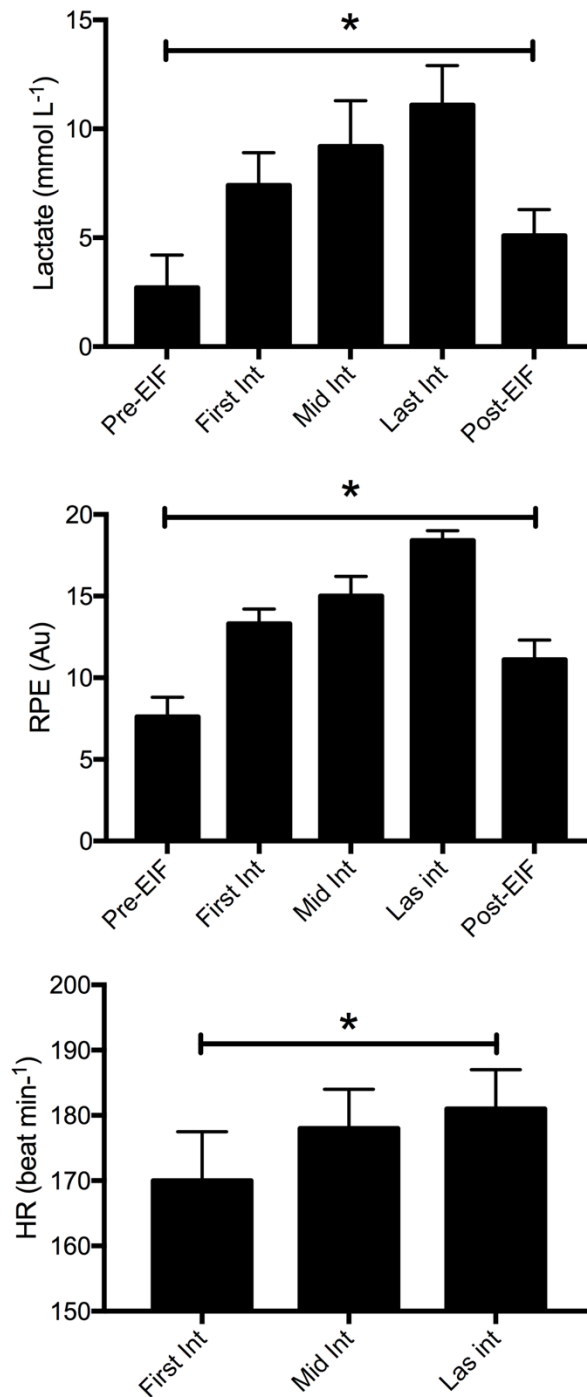


Figure 2 Metabolic and psychometric makers of exercise induced fatigue. Top panel: blood lactate concentration. Middle panel: RPE scores. Bottom panel: HR response. All parameters are displayed as a function of intensity. Significant main time effect: * $p \leq 0.05$. For blood lactate and RPE scores, all time points differ from pre EIF; for HR, mid and last intervals differ from the first interval.

Table 3 Energy cost of running, cardiorespiratory responses and substrate partitioning pre- and post EIF protocol.

	MIN		SHOD		Significance
	Pre	Post	Pre	Post	
Energy cost (kcal kg ⁻¹ km ⁻¹)	0.98±0.08	1.0±0.04	0.96±0.03	1.0±0.05	ns
$\dot{V}O_2$ (ml min ⁻¹)	2508±283	2526±215	2457±226	2562±230	ns
$\dot{V}CO_2$ (ml min ⁻¹)	2223±294	2111.6±215	2201.9±389	2181±409	ns
RER (AU)	0.88±0.08	0.83±0.06	0.89±0.09	0.84±0.09	Main significant effect time
\dot{G}_{ox} (mg min ⁻¹)	1931±866	1407±685	1980±1060	1595±1145	Main significant effect of time
L_{ox} (mg min ⁻¹)	468±370	689±382	419±346	631±382	Main significant effect of time

time effect was present for HR peak ($p=0.001$). The pairwise comparisons showed that HR peak of the first interval significantly differed from the two others (see Figure 2 bottom panel). As displayed in figure 2, blood lactate increased as a function of running intervals as for RPE score and peak HR which confirmed fatigue occurrence.

4.3 Substrate partitioning and energy cost of running

Statistical analysis revealed no main significant effect of condition or time on $\dot{V}O_2$, $\dot{V}CO_2$ and energy cost, note that energy cost trends to be higher ($p=0.088$) post- compared to pre-EIF. However, and as shown in Table 3, the analysis showed a main time effect on G_{ox} ($p=0.003$) and L_{ox} ($p=0.004$) with a decrease of 459 mg min^{-1} and an increase of 53 mg min^{-1} for the former and the latter respectively. Along with these outcomes RER was reported to be significantly different from pre- and post-EIF ($p=0.003$).

5. Discussions

The objective of the study was to assess the interplay between footwear and exercise-induced fatigue on energy cost of running and substrate contribution to energy production. The statistical analysis revealed no effect of footwear on these two dependent variables. However, this result might stem from the time interval between the final bout of EIF and post Cr test, and to the minimalist footwear's MI score that was too low (70%) to be different enough from SHOD. Therefore, from now on, the discussion will bear on the significant effect of exercise-induced fatigue on the above-mentioned variables.

An athlete utilizes a high contribution of lipid to energy production at a high percentage of $\dot{V}O_{2max}$ to complete long-distance running. A change of small magnitude in the energy cost of running could influence the performance of endurance events that depends on the interaction of numerous physiological factors such as substrate contribution to energy production. Exercising at high-intensity depletes muscle glycogen and leads to an increased contribution of lipid oxidation to energy production and subsequently influences energy cost of running (Brook, 1994). The main finding of this study showed a shift in substrate oxidation towards lipid after the EIF protocol. An increase in lipid oxidation of 53 mg min^{-1} and a reduction in carbohydrate oxidation of 459 mg min^{-1} post-EIF compare to pre-EIF was observed. Although energy cost of running did not reach significance, EP was higher post-EIF protocol.

5.1 Characteristics of participants and training profile

First, one must consider participants characteristics and training profile when examining the effect of exercise on human performance. The following section will address some of those important parameters. Trained athletes displayed three to four times higher skeletal muscle oxidative enzyme activity, in addition to increased capillaries per muscle fibres and a higher

proportion of slow twitch fibres compared to untrained individuals (Henriksson, 1992). These skeletal muscle metabolic differences result from the implementation of high intensity interval training (HIIT) into a planned exercise program (periodization). Along with those chronic training responses, cardiorespiratory variables such as $\dot{V}O_{2\max}$, and ventilatory threshold are enhanced with such a training. Since our participants had to train for a minimum of 5 days a week and had one of their weekly training session at an intensity higher than 70% of MAS, ran at least 50 km per week and had a 10 km personal best that reached 46% of the world record (Mercier scoring table), one can assume that they all displayed the same metabolic profile as above-mentioned.

Maximal oxygen uptake is a marker of running performance and widely accepted measure of aerobic fitness. As shown in table 1, our participants represent a very good cluster of runners according to the ACSM criteria (ACSM, 2013). In addition, runners' characteristics showed a coefficient of variation of 11.9% and 6.1% for $\dot{V}O_{2\max}$ and MAS, respectively, demonstrating a very homogenous group of runners.

5.2 Exercise-Induced Fatigue

High intensity interval training (HIIT) can be broadly defined as repeated bouts of short to moderate duration or distance exercise (i.e. from 10-sec to 20 min and from 200 m to 5 km) completed at an intensity that corresponds to the metabolic system to be enhanced (e.g. aerobic capacity or power). The idea of HIIT is to repeatedly stress the physiological systems that will be used during a specific endurance-type exercise (Daniels and Scardina, 1984). High intensity interval training brings about physiological responses that include, in its acute phase, cardiovascular drift, substrate depletion, lactate production and accumulation, and in its chronic phase, enhanced buffer capacity, improved maximal aerobic capacity, increased glycolytic and oxidative enzymes activities, higher mitochondrial content, and higher capillary/muscle fibre

ratio, to name a few (Pernow and Saltin, 1971; Gollnick et al., 1972; Bangsbo et al., 1992; Hargreaves et al., 1995). These acclimations to training have permitted our runners to cope with our experimental fatiguing task (EIF). Indeed, all runners did achieve at least 7 running bouts during which they experienced increased in rate of perceived exertion along with increase peak heart rate and lactate accumulation and production, confirming fatigue occurrence. It is of no surprise that our participants displayed such a metabolic response since an extensive body of literature has shown the same outcomes (MacDougall and Sale, 1981; Tsintzas et. al., 1996; Vollestad and Blom ,1985; Flectcher et. al., 2009). For instance, MacDougall and Sale (1981) showed that metabolic acidosis generated from the fast glycolytic pathway contributed to fatigue for exercise intensity of 100% of $\dot{V}O_{2max}$ and beyond. Considering the cardiovascular drift quantified from heart rate recorded during EIF, one can infer that the 94-97% running intensity increased to 100% and beyond at the end of EIF ensuring as shown by lactate accumulation and RPE score that metabolic acidosis occurred in our participants during track running (refer to fig 2).

5.3 Substrate oxidation and energy cost

The major findings of the study revealed that due to increased glycolytic flux during EIF (Brooks and Mercier 1994) a shift towards lipid oxidation occurred to sustain energy production during steady state exercise after the interval training session. This outcome might reflect glycogen depletion induced by high intensity exercise and its impact on muscle metabolism. It has been suggested that the shift towards lipid metabolism reflects an amplified muscle oxidative capacity resulting from training (Henriksson and Reitman, 1977, Gollnick and Saltin, 1982). One can assume that our participants displayed the same chronic response to training due to their fitness level and training profile. In addition, Kiens et al. (1993) also showed a decrease in carbohydrate oxidation due to a reduction in glycogenolysis and an increase in blood FFA

absorption in trained muscle that confirm augmented mitochondrial density and β -oxidation enzyme activity along with better muscle oxygen delivery during submaximal running exercise. Others have reported shift towards lipid oxidation during steady state exercise following interval training (Zavorsky, Montgomery, and Pearsall, 1998; Collin et al., 2000) or towards the end of marathon run (Kyrolainen, 2000). However, note that since the participants of our study were in fasting state throughout the experimental sessions one cannot discard the potential effect of the negative energy balance on the observed substrate contribution shift (Kelly and Basset, 2017; Albusheen et al., 2017). Most studies have focused on the relationship between physiological factor of running and biomechanical parameters but few have provided an insight into substrate partitioning during submaximal running exercise following fatiguing running bouts. As previously mentioned in methodology we have discarded running bouts corresponding to 3.33, and 3.89 m/s during steady state exercise testing due to the limitation of stoichiometric equations used to calculate substrate oxidation (Jeukendrup and Wallis, 2005). As reported by Fletcher, Esau and MacIntosh (2009) high intensity running speed shifts substrate use from lipid to carbohydrate causing increase in RER.

An unexpected outcome of this protocol resides in lack of significant cardiovascular drift during CR after EIF. Several studies have reported an increase oxygen uptake after prolonged aerobic activities (Bailey and Pate, 1991; Sproule, 1998; Xu and Montegomary, 1995; Sproule, 1998), and have postulated that increased oxygen uptake was caused by an elevation in HR to compensate for reducing stroke volume, increase core temperature due to thermal stress, blood catecholamine elevation, change in substrate oxidation towards lipid metabolism as a reduction in hepatic and muscle glycogen content, and a reduction in biomechanical efficiency (Bailey and Pate 1991; Kalis et al., 1988; MacDougall et al. 1974; Morgan and Craib, 1992; Williams and

Cavanagh 1987). Among those variables, the current experimental design did bring substrate metabolism change with no other effect. The latter outcomes are not unique in the literature. For instance, Rabital et al. (2011) did observe increase in energy cost of running with no change in $\dot{V}O_2$. Although non-significant, the energy cost of running of our runners has increased from pre- to post-EIF reflecting the change in substrate oxidation as already reported by Xu and Montgomery (1995). In parallel, Fletcher, Esau and MacIntosh (2009) also observed an increase in energy cost of running with no change in oxygen uptake as reflected by the running economy index during three different speeds. It is important to highlight that increase in energy cost of running is more pronounced for running distance greater than 15 km and that consequently no or small increase in cost of running occurs following fatiguing task using HIIT (Di prampero et al., 1986). Accordingly, when calculating the total distance covered in this protocol (16.2 km total) the runners are on the edge of that distance mark, which could explain the lack of significant results in cardiorespiratory variables recorded during the steady state exercise. The lack of significant results in cardiorespiratory parameters such as cardiovascular drift, $\dot{V}O_2$, and energy cost of running could stem from recovery time between the last running bout during EIF and CR on treadmill. As mentioned above, our runners were well-trained individuals as shown by their training profile. In addition to these characteristics, they displayed a very good heart rate recovery (HRR) during EIF. For instance, HRR was 38 ± 10 bmp, 41 ± 7 , and 41 ± 7 for the first, mid, and last running bouts, respectively, matching the results published by Lamberts et al. (2009). The outcomes have been interpreted as a consequence of parasympathetic reactivation and sympathetic withdrawal (Kaikkonen, Rusko and Martinmaki, 2008) influencing metabolic responses. Therefore, we can postulate that such a mechanism was magnified through the longer recovery time allowed between the last running bout and the CR post-EIF ($22:28 \pm 5:24$ min).

Although all efforts have been made to reduce the time elapsed between these two-time points, this aspect of the experimental design might have impacted on the expected results. However, although recovery time between EIF and CR might represent the main factor that affected the cardiorespiratory responses post-treatment, the substrate contribution to energy production then reflects the muscle glycogen depletion since the metabolic demand as quantified by energy cost of running was not statistically significant during CR.

Furthermore, one cannot put aside the combination effect of low running volume during the experimental session and recovery time between EIF and post-CR on lack of significant cardiorespiratory responses.

6. Conclusion

6.1 Response to Hypothesis

The purpose of this study was to determine the interplay of footwear and exercise-induced fatigue (EIF) on substrate partitioning and energy cost of running during steady-state running exercise. We hypothesized that there will be an altered energy cost of running after exercise-induced fatigue compare to baseline, and that consequently there will be shift towards lipid oxidation / utilization due to muscle glycogen depletion. Our finding revealed significant change in substrate utilization towards lipid oxidation following EIF in both conditions, which supported our first hypothesis, thus, rendering our null hypothesis invalid. However, energy cost of running was not significantly affected by both conditions and time, but energy cost of running tends to increase post- compare to pre-EIF, but did not reach significance which disproved our second hypothesis. Although, EIF was not enough to statistically alter energy cost of running during the 10 km h⁻¹ run, it did alter substrate partitioning. Those results might reflect a combination of low running volume during the experimental session as reported by Di Prampero et al., (1986) and recovery time effect between EIF and post-CR that could have reactivated the parasympathetic system known to impact cardiorespiratory responses.

The main finding of this study revealed a shift in substrate oxidation towards lipid following EIF. There is an increase in lipid oxidation of 53 mg min⁻¹ and a reduction in carbohydrate oxidation of 459 mg min⁻¹ post-EIF compare to pre-EIF as supported by Zavorsky, Montgomery, and Pearsall (1998); Collin et al. (2000) despite no significant increase in energy cost of running, which is in accordance with the study of Rabital et al. (2011).

6.2 Methodological Considerations

There are intrinsic methodological considerations associated with the current study. First, due to inherent limitation of stoichiometric equations adopted in calculating substrate utilization, speeds of 3.33, and 3.89 m s⁻¹ were dropped during statistical analysis because the RER values were above 1.0. Furthermore, athletes were at or above ventilatory threshold for these two running speeds. Second, the time elapsed between the last running bout and the return to the laboratory for CR was, perhaps, too long, allowing partial recovery. Furthermore, ecological consideration associated with the fatigue responses demonstrated running on a track is different than running on a treadmill.

6.3 Future Research Direction

Extensive research should be done to compare substrate partitioning and running cost on track versus treadmill during energy cost of running test following fatiguing task to address the external and internal validity. External validity because sporting events are conducted on the treadmill, and internal validity because different muscles might have been fatigued. Further research should have a longer steady state exercise to observe drift and to increase the total energy requirement for the activity, which may reveal differences in energy cost and volume to accommodate Di Prampero recommendation. In addition, recovery time between EIF and post-EIF steady state exercise should not be too long in order not to miss out cardiovascular drift associated with fatigue following EIF. Furthermore, this research has shown that there is no difference between running shoes (MIN/SHOD) in term of running performance, therefore, more research must be done on EIF and barefoot running. Finally, any research using minimalist footwear should use shoes with a MI greater than 90%.

7. References

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8. Appendices

8.1 Appendix A: Participants profile questionnaire

Participant code: _____ Date: _____

1. How old are you? _____
2. In the past 3 months, have you sustained a low-body injury (sprain, strain, tear, fracture, tendonitis, etc.)? _____
3. What is your dominant leg (which leg would you use to kick a ball)? _____
4. What is your running distance specialty (sprinting, middle- or long-distance)?

5. What are your 5K and 10K personal-best times?
5K _____ 10K _____
- a. If you have never raced either of these distances, what are your personal-best races (time and distance)? _____
6. How many years have you been actively training (in a structured training program)?

7. How many training sessions do you undergo per week (including easy runs and high-intensity training sessions; but excluding weight training)? _____
8. How many training sessions per week consist of running at a steady pace of 3-4min/km (i.e., “tempo” / “threshold” runs)? _____
9. How many training sessions per week are interval-training (high-intensity work-bouts interspersed with brief rest/recovery interval; excluding “tempo”/”threshold” run)?

10. What is your average running distance per week (how many kilometres on average do you run per week?) _____
11. What is your longest running distance in a week (how many kilometres have you run in your highest running week ever)? _____
12. What is the longest distance you have run in a single session? _____
13. How many weight-training sessions do you do per week? _____

14. How many cross-training sessions do you do per week (e.g., cycling, swimming, elliptical, yoga, etc.)? _____
15. In which period of your annual training plan are you (i.e., general preparatory phase, specific preparatory phase, competition phase, taper or transition phase)? _____
16. At which level are you competing: provincial, national, international? _____
17. Do you wear minimalist or barefoot shoes? _____
- a. When did you start wearing this footwear? _____
- b. How often per week do you use this footwear? _____
- c. For what type of training do you use this footwear? _____
18. Do you run in minimalist or barefoot shoes? _____
- a. How far do you run in them? _____
- b. What is your average “barefoot” running distance per week? _____
- c. What is the longest distance you have run in such footwear? _____
- d. What is the brand/model of your current minimalist or barefoot shoes? _____
- e. What is the size of your current minimalist or barefoot shoes? _____
- f. Do you know the mass of your current minimalist or barefoot shoes? If so, how great is their mass? _____
- g. Do you know the heel-toe drop in your current minimalist or barefoot shoes? If so, how great is it? _____
19. Do you use traditional running shoes for running? _____
- a. How often per week do you use this footwear? _____
- b. How far do you run per training session? _____
- c. What is your average “traditional” running distance per week? _____
- d. What is the longest single session distance you have run in such footwear?

- e. What is the brand/model of your current “traditional” running shoes? _____
- f. What is the size of your current “traditional” running shoes? _____

g. Do you know the mass of your current “traditional” running shoes? If so, how great is their mass? _____

h. Do you know the heel-toe drop in your current “traditional” running shoes? If so, how great is it? _____

8.2 Appendix B: Borg 6-20 Rate of perceived exertion (RPE) scale

<i>Rating of Perceived Exertion Borg RPE Scale</i>		
6 7 8 9 10 11	Very, very light Very light Fairly light	How you feel when lying in bed or sitting in a chair relaxed. Little or no effort.
12 13 14 15 16	Somewhat hard Hard	Target range: How you should feel with exercise or activity.
17 18 19 20	Very hard Very, very hard Maximum exertion	How you felt with the hardest work you have ever done. Don't work this hard!