

The Independent Influence of Aerobic Fitness and Running Economy on Thermoregulatory Responses during Treadmill Running

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THESIS

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ABSTRACT

The independent influence of maximum oxygen consumption ($\text{VO}_{2\text{max}}$) and running economy (RE) on thermoregulatory responses during treadmill exercise have not been isolated due to the complex interactions between $\text{VO}_{2\text{max}}$, RE, body mass, body surface area (BSA), and metabolic heat production (H_{prod}). The purpose of the thesis is to determine whether large differences in $\text{VO}_{2\text{max}}$ and/or running economy independently alter thermoregulatory responses during running in a neutral environment. Seven aerobically unfit (LO-FIT: $\sim 40 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) and seven aerobically fit (HI-FIT: $\sim 60 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) males, matched for body mass and BSA ran at 1) a fixed metabolic heat production of 640 W (FHP trial) and 2) 60% $\text{VO}_{2\text{max}}$ (REL trial). Also, seven high RE (HI-ECO: $\sim 185 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$) and seven low RE (LO-ECO: $\sim 220 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$) males, matched for body mass, BSA and $\text{VO}_{2\text{max}}$ ($\sim 60 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) ran at a 1) fixed H_{prod} of 640 W (FHP trial) and 2) fixed running speed of $10.5 \text{ km} \cdot \text{h}^{-1}$ (FRS trial). All trials were performed in a thermoneutral environment. The data was analyzed using a two-way mixed ANOVA, with the significance level set at an alpha of 0.05 for all comparisons. It was hypothesized that thermoregulatory responses (i.e., core temperature and sweating), during exercise will not be independently altered by $\text{VO}_{2\text{max}}$, but will be altered by any differences in heat production and running economy. The FHP trial resulted in similar changes in esophageal temperature (ΔT_{es}), changes in rectal temperature (ΔT_{re}), and WBSL between the HI-FIT and LO-FIT groups, despite vastly different % $\text{VO}_{2\text{max}}$. Whereas the REL trial resulted in greater ΔT_{eso} , ΔT_{re} , and WBSL in the HI-FIT group, in parallel with their greater H_{prod} . In groups greatly differing in RE, the FHP trial elicited similar ΔT_{es} , ΔT_{re} , and WBSL; however the HI-ECO group had to run faster to achieve the same heat production as their LO-ECO counterparts. Moreover, a FRS of $10.5 \text{ km} \cdot \text{h}^{-1}$ produced a greater H_{prod} , ΔT_{es} , ΔT_{re} , and WBSL in the LO-ECO group. In

conclusion, thermoregulatory responses are determined by H_{prod} and RE, not $VO_{2\text{max}}$, when differences in mass and BSA are eliminated between groups. Thus, these findings support the initially stated hypotheses.

- PART ONE -

THESIS INTRODUCTION AND METODOLOGICAL CONSIDERATIONS

I. INTRODUCTION

Currently, there is a widely accepted notion that thermoregulatory responses to exercise, in a physiologically compensable environment, are influenced by differences in VO_{2max} (9, 18, 20, 23, 29). Saltin and Hermansen reported that exercise at the same percentage of VO_{2max} (i.e., relative exercise intensity) yields similar core temperature responses, irrespective of aerobic capacity (VO_{2max}), under compensable conditions (46). These findings were later supported by Fritzsche and Coyle and Gant et al. (18, 20). Greenhaff also reported that individuals who are fitter have smaller changes in core temperature when exercising at the same absolute workload (and metabolic heat production) in a 23°C room (22). Furthermore, Gant et al. reported that core temperature changes and whole body sweat losses are related to relative exercise intensity, irrespective of differences in fitness (20). However, none of these studies isolated VO_{2max} as the independent variable while controlling for potential confounding factors such as body mass, body surface area (BSA) and heat production. Indeed, the difference in mass between participants in these studies was anywhere from 5.1 kg to 28.9 kg, while the difference in BSA was up to 0.48 m² (20, 22). Since the temperature increase of any body, for the same increase of heat content, is largely dependent on its mass, and the heat exchange between a body and its environment is influenced by surface area, controlling for the effects of body mass and BSA is clearly crucial.

A recent study by Jay et al., which did account for both mass and BSA, by matching participants for these characteristics, reported that the same relative exercise intensity yields significantly greater changes in core temperature and thermoregulatory sweating in fit, compared to unfit, individuals, since they were exercising at a greater metabolic heat production (27). Furthermore, at a fixed heat production, which produced different relative exercise intensities,

almost identical changes in core temperature and sweating were observed (27). These findings suggest that fitness may not be the potent modulator of thermoregulatory responses, as previously believed. However, this study only employed semi-recumbent cycling as an exercise modality, and many studies typically assess thermoregulatory response during treadmill running. There are typically greater inter-individual differences in running economy (since it is a weight-bearing exercise) than the differences in mechanical efficiency typically observed during cycling, therefore a larger inter-individual variation in heat production is more likely during running. Furthermore, less trained individuals often have a lower running economy, therefore in order to isolate the influence of fitness during treadmill running, not only should differences in mass and BSA be accounted for, but also the differences in running economy need to be independently evaluated. Indeed, the only previous study assessing the role of fitness during running, reported greater changes in core temperature and sweating in their untrained group at a fixed running speed, but these results may be simply due to a greater metabolic heat production secondary to an inferior running economy relative to their trained counterparts (20).

From a practical perspective, it is necessary to determine the factors that influence core temperature and thermoregulatory sweating during exercise for methodological purposes. These findings would potentially influence how exercise physiologists, evaluating thermoregulatory responses in various populations (15–17, 34, 45) (e.g., children, burn patients, the obese, etc.) and under various conditions (32) (e.g., hypoxia), design their experimental protocol to compare independent groups or even a repeated-measures group before and following a training intervention.

The aim of this thesis was to isolate the independent influence of VO_{2max} and running economy on changes in core temperature and thermoregulatory sweating during treadmill running in a neutral environment.

II. REVIEW OF LITERATURE

Human Heat Balance

Background

Humans are homeotherms and therefore maintain a “set point” deep body (core) temperature of $\sim 37^{\circ}\text{C}$ to ensure optimal conditions for essential physiological and chemical processes (42). This “set point” core temperature is free to vary within a specific “null zone”(7) which, during rest in a thermal neutral environment, is approximately $\pm 0.5^{\circ}\text{C}$ (42). As such, core temperature is not fixed, but in a constant dynamic balance due to the body’s interaction with the environment and the body’s circadian rhythm (2, 51).

The dynamic interaction between heat production within the body ($M - W$) and net heat exchange (loss or gain) with the environment (*sum of $K, C, R, C_{res}, E_{res}$, and E_{sk}*) can be described through a conceptual human heat balance equation:

$$(M - W) = [(\pm K \pm C \pm R) + (C_{res} + E_{res}) + E_{sk}] \pm S \dots\dots\dots W \dots\dots\dots (1)$$

Where: S is the rate of net heat storage; M is the rate of metabolic energy expenditure; W is the rate of external mechanical work; K is conduction; C is convection; R is radiation; C_{res} is respiratory heat loss through convection; E_{res} is respiratory heat loss through evaporation; and E_{sk} is the rate of heat loss via evaporation from the skin.

A combination of environmental conditions (i.e., air temperature, radiant temperature, humidity and air movement) and personal factors (i.e., clothing worn and metabolic heat generated through activity) can result in an imbalance between heat gain (i.e., metabolic heat production by the body and heat gain from the environment) and heat loss (i.e., dissipation of heat to the ambient environment) (42). For instance, during exercise and/or external heat exposure, the body will store heat causing core temperature to rise beyond its “null zone”. The body will continue to store more heat until the heat loss avenues (e.g., convection, evaporation) are sufficiently pronounced through physiological responses (e.g., sweating, vasodilatation) to attain heat balance once again. When transient periods of heat storage occur, core temperature increases to a new elevated steady-state (28). However, under conditions (e.g., exercise in a hot and humid environment) where even maximum heat loss is insufficient to attain heat balance (i.e., uncompensable heat stress), heat storage will continually occur resulting in a continuous rise in core temperature.

The following is a detailed account of the first four components of the heat balance equation and their role in the body’s dynamic thermoregulatory system.

Metabolic Heat Production (M-W)

The rate of metabolic heat production, in an organism, is the rate of transformation of chemical energy into heat (8). It is calculated using two components: metabolic energy expenditure (M) and external mechanical work (W). The body expends metabolic energy (M) which enables it to do mechanical work (W); since the body is not a 100% efficient at doing mechanical work, the remaining metabolic energy is released as heat (i.e., $M-W$) (42).

The body’s metabolic rate (M) is generated from ingested food, which consists of carbohydrates, lipids, proteins and sometimes alcohol, and inspired oxygen (8). These substrates,

primarily carbohydrates and lipids, are oxidized to generate ATP, which is used to supply the cells of the body with energy. The by-product of these biochemical processes is heat, and the more inefficient the process, the greater the heat production. Since the amount of oxygen required to mobilize carbohydrates and lipids is constant (8), indirect calorimetry can be used to quantify metabolic energy expenditure. Specifically, utilizing one liter of oxygen to oxidize carbohydrates yields 21.13 kJ of energy while the complete oxidation of lipids with 1 liter of oxygen yields 19.63 kJ of energy. As such, the following equation can be used to estimate metabolic energy expenditure (40):

$$M = VO_2 \frac{\left(\frac{RER - 0.7}{0.3} e_c \right) + \left(\frac{1 - RER}{0.3} e_f \right)}{60} \times 1000 \dots\dots\dots W \dots\dots\dots (2)$$

Where: VO_2 is the amount of consumed oxygen, in L/min; e_c is the caloric equivalent per litre of oxygen for the oxidation of carbohydrates (21.13 kJ); e_f is the caloric equivalent per litre of oxygen for the oxidation of fat (19.63 kJ); RER (i.e., respiratory exchange ratio) is the ratio of expired CO_2 to consumed O_2 .

As indicated by *Equation 2*, metabolic energy expenditure is directly influenced by oxygen consumption. It follows that running economy is indicative of how much oxygen one consumes for a distance covered(13, 38, 47). Therefore, more economical individuals require a lower oxygen consumption (per unit mass) for a given running speed compared to their less economical counterparts. Please see *Running Economy* section for more details.

Mechanical work is defined as the product of force and displacement in the direction of the force, and it can be estimated using *Equation 3*.

$$W = \frac{F \cdot d}{t} \dots\dots\dots W \dots\dots (3)$$

Where: W is the external mechanical work done, in Joules (J); F is the force of magnitude acting on an object, in Newtons (N); d is the distance moved in the direction of the force, in meters (m); and t is the elapsed time (s).

At rest, when no external mechanical work is being performed, all metabolically generated energy eventually appears as heat inside the body, due to the inefficiency of the biochemical processes (8). The metabolic heat production of an adult, at rest, is approximately 80 to 120 W (42). At the onset of exercise, the rate of metabolic heat production is almost immediately elevated (28). Depending on the type of physical activity, between 100% and no less than 75% of total energy expenditure (M) will be released as heat. Therefore, a maximum of 25%, and in many cases none, of the total energy expenditure is used for external mechanical work (W) (42).

Mechanical work can only be done on an object when it is being moved relative to the line of the acting force (30). During running at a constant speed on a level surface the object (i.e., a person) is moving in the horizontal direction and the gravity acting on the object is in the downward direction. As such, no external mechanical work ($W=0$) is being done when one is running at a constant speed on a level surface, and all of the metabolic energy (M) expended is released as heat inside the body (i.e., since $W=0$, $M-W=M$). Furthermore, during constant speed running on a level surface, one's heat production is not affected by their efficiency at performing external mechanical work (since $W=0$), but rather by their running economy (i.e., oxygen required to cover a distance per unit body mass – See *Running Economy* section).

Sensible Heat Exchange ($\pm K \pm C \pm R$)

The three components of sensible heat exchange with the environment are conduction (K), convection (C) and radiation (R). These components follow the second law of thermodynamics – i.e., heat energy will spontaneously flow from higher to lower temperature regions until reaching equilibrium (1). Conduction refers to heat transfer via direct contact between the body and a solid surface, while convection is the flow of heat between the body and a medium by movement (e.g., air) and lastly radiation refers to the flow of electromagnetic waves between objects of varying temperature. Collectively, through these sensible heat exchange avenues a person can either lose or gain heat.

Conduction (K): Under most circumstances, conductive heat transfer, in terms of whole-body heat exchange, is negligible (i.e., $K \sim 0$). However, active measures, such as placing an ice pack directly on the skin, can facilitate conductive heat exchange. Under these circumstances, conductive heat transfer depends on: 1) the cross sectional area between the two surfaces in contact, 2) the temperature difference between the two surfaces in contact and, 3) the thermal conductivity, indicated by the *conductive coefficient* (k), of the medium. Therefore, conduction (K , or Q in the equation below) can be estimated using Fourier’s law of conduction (*Equation 4*).

$$Q = kA \frac{T_2 - T_1}{d} \dots\dots\dots W \dots\dots\dots (4)$$

Where: Q equates the rate of heat transfer by conduction, in W; k is the thermal conductivity of the medium, in $W \cdot m^{-2} K^{-1}$; A is the cross-sectional area normal to conductive direction in m^2 ; $T_2 - T_1$ equals the temperature difference across the medium, in K and d equals the distance between the objects at temperatures T_2 and T_1 , in m.

Convection (C): At ambient temperatures below skin temperature, a rise in skin temperature increases the temperature gradient between the skin and the air, thus aiding convective heat transfer from the body to the environment. Convective heat exchange between the skin and the environment is also dependent upon: 1) the net flow of the medium over the surface of the object (e.g., air particles over the skin surface), and 2) the effective surface area exposed to the medium (primarily depends on clothing and posture).

The net flow of the medium over the skin surface is used to determine the convective heat transfer coefficient. For air velocities between 0.2 and 4.0 m·s⁻¹, the convective heat transfer coefficient can be estimated using *Equation 5* (36).

$$h_c = 8.3v^{0.6} \dots\dots\dots \text{W}\cdot\text{m}^{-2}\cdot\text{K}^{-1} \dots\dots\dots (5)$$

Where: h_c is the convective heat transfer coefficient, in W·m⁻²·K⁻¹; and v is the air velocity in m·s⁻¹.

Once the convective heat transfer coefficient is determined, the rate of convective heat exchange can be estimated using *Equation 6* (4).

$$C = f_{cl}h_c(t_{cl} - t_a)A_D \dots\dots\dots \text{W} \dots\dots\dots (6)$$

Where: f_{cl} is the clothed area coefficient factor (i.e., the surface area of the clothed body divided by the surface area of the nude body); h_c is the convective heat transfer coefficient, in W·m⁻²·K⁻¹ – dependent upon a person’s physical position in space and the resultant relative

velocity of the surrounding air; t_{cl} is the mean temperature of the clothed body, in °C; and t_a is the surrounding air temperature, in °C; A_D is total body surface area, in m^2 .

Radiation (R): All bodies above the temperature of absolute zero emit thermal radiation via electromagnetic waves. The amount of heat exchange that occurs through radiation between two bodies depends on: 1) the orientation of the body relative to the source, 2) the temperature of the objects, and 3) the movement of the heat source in relation the body. While outside, the weather (e.g., sunny or cloudy), the angle of the solar projection and the type and colour of clothing worn will collectively influence the rate of radiant heat load imposed on the body. Indoors however, the rate of radiative heat exchange can be quantified more simply, particularly in the absence of a large radiant source (e.g., radiant warmer). The radiative heat transfer coefficient (h_r) can be estimated using *Equation 7* (36).

$$h_r = 4\varepsilon\sigma \frac{A_r}{BSA} \left[273.2 + \frac{t_{cl} + t_r}{2} \right]^3 \dots\dots\dots W \cdot m^{-2} \cdot K^{-1} \dots\dots\dots (7)$$

Where: ε is the area weighted emissivity of the clothed body surface; σ is the Stefan-Boltzmann constant, $5.67 \times 10^{-8} W \cdot m^{-2} \cdot K^{-4}$; A_r is the effective radiative area of body, in m^2 ; BSA is the total body surface area, in m^2 ; t_{cl} is the mean temperature over the clothed body, in °C; t_r is the mean radiant temperature (assumed to be equal to t_a when inside), in °C.

Subsequently, radiative heat exchange (R), when indoors, can be estimated using the following equation (4).

$$R = f_{cl} h_r (t_{cl} - t_r) A_D \dots\dots\dots W \dots\dots\dots (8)$$

Where: f_{cl} is the clothed area coefficient factor (i.e., the surface area of the clothed body divided by the surface area of the nude body); h_r is the radiative heat transfer coefficient, in $W \cdot m^{-2} \cdot K^{-1}$; t_{cl} is the mean temperature of the clothed body, in $^{\circ}C$; t_r is the mean radiant temperature, in $^{\circ}C$ – in an indoor environment, with no radiant source, $t_r = t_a$ (i.e., air temperature); A_D is total body surface area, in m^2 .

Evaporation (E_{sk})

Evaporation refers to heat transfer between the body and a medium that requires an initial change in state from liquid to vapour at the skin surface (42). In the heat, evaporative heat loss at the skin (E_{sk}) is more effective at dissipating heat from the body than all the other heat loss avenues combined – provided that evaporation at the skin is permitted (i.e., vapour permeable clothing) and that the partial pressure gradient between the skin and the environment facilitates evaporation. The body secretes sweat on to the skin surface via eccrine sweat glands; the sweat vaporizes from the skin surface resulting in energy transfer from the body to the environment. More specifically, for every one gram of sweat that is vaporized from the skin to the environment, at a constant temperature, 2.426 kJ of energy is transferred from the body to the environment (52). In an absolute sense, evaporation is determined by the partial pressure gradient between the sweat on the skin’s surface and the water in the ambient air (i.e., humidity). Total evaporative heat loss is also influenced by air velocity, body surface area, skin wettedness, and clothing worn. To estimate evaporative heat loss, the evaporative heat loss coefficient (h_e) must be estimated first using *Equation 9*.

$$h_e = 16.5h_c \dots\dots\dots W \cdot m^{-2} \cdot kPa^{-1} \dots\dots\dots (9)$$

Where: h_e is the evaporative heat transfer coefficient, in $\text{W}\cdot\text{m}^{-2}\cdot\text{kPa}^{-1}$; 16.5 is the Lewis Relation; and h_c is the convective heat transfer coefficient (*Equation 5*), in $\text{W}\cdot\text{m}^{-2}\cdot\text{K}^{-1}$.

Subsequently, evaporative heat loss from the skin can be estimated using *Equation 10* (3).

$$E_{sk} = \frac{w(P_{sk,s} - P_a)}{\left[R_{e,cl} + \frac{1}{f_{cl}h_e} \right]} A_D \dots\dots\dots \text{W} \dots\dots\dots (10)$$

Where: w equals skin wettedness, from 0.06 to 1.00, where 1.00 equals 100% skin wettedness (Note: $E_{sk} = E_{max}$ when skin wettedness is at its maximum – 0.85 for unacclimated and 1.00 for acclimated individuals); $P_{sk,s}$ is the saturated water vapour pressure at the skin, in kPa (calculated using Antoine’s equation (42)); P_a is the water vapour pressure in the ambient air, in kPa; $R_{e,cl}$ is the evaporative heat transfer resistance of clothing, in $\text{m}^2\cdot\text{kPa}\cdot\text{W}^{-1}$; f_{cl} equals the clothed area coefficient factor; h_e is the evaporative heat transfer coefficient, in $\text{W}\cdot\text{m}^{-2}\cdot\text{kPa}^{-1}$ and; A_D is total body surface area, in m^2 (see *Equation 8*).

Respiratory Heat Loss ($C_{res} + E_{res}$)

Heat is also lost through respiration by means of convection (C_{res}) and evaporation (E_{res}). Inhaled air (i.e., cooler than body temperature) is heated to body temperature inside the lungs and upper respiratory tract (convection); the warmer air is able to retain more moisture, thus it is saturated with water from the lungs and upper respiratory tract (evaporation). Once the warmer and more humid air is exhaled into the environment, respiratory heat loss through convection and evaporation occurs. Therefore, respiratory heat loss depends on the physical properties of the inspired air (i.e. temperature and water vapour pressure) and a person’s rate and depth of

respiration. Empirically, the combined respiratory heat loss from convection and evaporation can be estimated using *Equation 11* (3).

$$C_{res} + E_{res} = [0.0014M(34 - t_a) + 0.0173M(5.87 - P_a)] \dots\dots\dots W \dots\dots\dots (11)$$

Where: M is the metabolic heat production, in W; P_a is the partial pressure of water vapour of ambient air, in kPa; and t_a is the ambient air temperature, in °C.

Biophysical Aspects of Human Heat Balance

The biophysical aspects of body mass and body surface area (BSA) are key components influencing whole body heat balance. The temperature change of any body, for a given change in heat content, is largely dependent on its mass. For example, a liter of stirred water has a greater change in temperature than three liters of stirred water, for the same amount of heat energy put in (i.e., change in heat content). Theoretically, the same concept applies to the human body; for the same change in heat content a smaller person will have a greater change in mean tissue temperature, and presumably core temperature, compared to a larger person. Furthermore, the evaporative requirements for heat balance (E_{req}), in a fixed environment, are determined by the body's absolute heat production ($M - W$) (5, 21, 48). The sweat rate for a given E_{req} is also theoretically influenced by BSA, at high skin wettedness values (i.e., $w \geq 0.50$) due to decrements in sweating efficiency (i.e., the proportion of sweat that evaporates) (5); thus, for high fixed absolute rates of heat production, individuals with a smaller BSA would have a greater sweat rate, compared to individuals with a larger BSA. It follows that in order to evaluate the independent influence of aerobic fitness on thermoregulatory responses, body mass and BSA must be controlled for (i.e., matching groups for mass and BSA).

Thermal Physiology

Thermoreception

The preoptic/anterior hypothalamus (PO/AH), located immediately above the brain stem, is the central integrator of information from cold and warm temperature sensors (thermoreceptors) located in the deep (core) tissues, the skin and the central nervous system (CNS) (53). The central thermoreceptors are located in the spinal cord, brain stem, and brain and are predominantly warm-sensitive. Peripheral thermoreceptors, are located in the epidermis (skin), blood vessels, and deep (visceral) tissues and are primarily cold-sensitive (24, 53). The afferent signals, derived collectively from central and peripheral thermoreceptors, are integrated at the PO/AH and are used to initiate and modulate the principal autonomic (e.g., sweating and vasodilatation) and behavioural (e.g., removing clothing) thermoregulatory effector responses (53).

Sweating and Heat Activated Sweat Glands

Anatomically, human sweat glands can be divided into two types; the apocrine and the eccrine glands. The apocrine glands are mainly found in the armpit and pubic regions; they produce sweat and are responsible for the distinct odour of those regions. The eccrine glands are found across most of the body and are abundant on the torso and forehead (31); these are the glands primarily responsible for human thermoregulation. Sweat is secreted into these glands through membrane water channel proteins, called aquaporins, from interstitial fluid and blood plasma (42, 49).

The body loses heat through the evaporation of sweat from the surface of the skin. The rate at which sweat is secreted to the skin surface is controlled by the central nervous system through the integration of core temperature and skin temperature (39). At the peripheral level the

rate of sweating is influenced by the density of heat activated sweat glands and the mean output of each individual sweat gland (14, 26). Effectively, both whole-body and local sweat rates are determined by the rate of evaporation required for heat balance (E_{req}) and skin wettedness required for heat balance (E_{req}/E_{max}) irrespective of absolute core temperature and aerobic fitness (i.e., VO_{2max}) (11, 19). Absolute E_{req} during exercise is primarily determined by the rate of metabolic heat production, whereas E_{max} is determined by body surface area, maximal skin wettedness, ambient humidity, air velocity and water vapour permeability of the clothing worn (5, 21, 27, 48). To attain heat balance E_{req} must be matched by E_{sk} .

Thermoregulation during Running Exercise

Thermoregulatory Responses to Exercise

Metabolic heat production increases immediately following the onset of exercise, but it is not immediately matched by the heat lost to the surrounding environment, thus resulting in an increase in body heat content and an increase in body temperature. During exercise there is an initial sympathetic vasoconstriction response, allowing blood flow to be directed to active muscles (42). If heat dissipation is required, based on the central and peripheral feedback from thermoreceptors, the anterior hypothalamus responds by initiating heat loss responses (42). Initially, vasodilatation occurs, leading to a small redistribution of body heat content to the periphery. As a result skin temperature rises, increasing the temperature gradient between the skin surface and the ambient environment, leading to an elevated rate of dry heat loss via convection and radiation (42). Secondly, a sweating response is initiated; resulting in an increased partial water vapour pressure at the skin; although, heat loss through evaporation already occurs via respiration, this allows for even greater evaporative heat loss. In a neutral

thermal environment, heat dissipation can occur through both dry (C+R+K) and evaporative heat loss avenues.

Earlier studies examining thermoregulatory responses during cycling exercise concluded that relative exercise intensity is responsible for yielding similar core temperatures in individuals of different aerobic capacities ($VO_{2\text{peak}}$) (18, 22, 46). Furthermore, it has been reported that fitter individuals have greater local and whole body sweat rates for a set relative exercise intensity (25, 26, 46, 50). The prevailing logic is that despite fitter individuals having a greater metabolic heat production for a given relative exercise intensity, their heat loss mechanisms are proportionally greater, resulting in similar heat storage and body temperatures, under conditions where heat loss is not impaired by climate (23). Therefore, there is a widely held notion in the literature that relative exercise intensity determines thermoregulatory responses. However, Jay et al. recently demonstrated that when matched for mass and BSA, fitter individuals ($VO_{2\text{max}}$ of 60.1 ± 4.5 $\text{mLO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) display much greater changes in core temperature and thermoregulatory sweating at the same relative intensity (60% $VO_{2\text{max}}$) than their less fit counterparts ($VO_{2\text{max}}$ of 40.3 ± 2.9 $\text{mLO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$), during cycling exercise in a neutral environment (27). Furthermore, they demonstrated that exercising at a fixed heat production (540 W), which elicited vastly different relative exercise intensities, resulted in almost identical changes in core temperature and sweating, when comparing fit and unfit individuals matched for mass and BSA. Based on these findings the authors concluded that, during cycling exercise in a neutral environment, changes in core temperature and sweating are determined by heat production, body mass and BSA, not $VO_{2\text{peak}}$ (27).

The study of Jay et al. employed cycle ergometry (27) and the only study that has examined the influence of aerobic fitness on thermoregulatory responses during exercise on a

treadmill was conducted in 2004 by Gant et al. (20). Their study used relative and absolute (i.e., fixed running speed) treadmill exercise bouts, in a neutral environment, to compare thermoregulatory responses between groups of high and moderate fitness. Their results suggested that core temperature and whole body sweat losses were related to relative exercise intensity, irrespective of differences in fitness (VO_{2max}), thus supporting the long-held findings of Saltin & Hermansen (20, 46) and disagreeing with the recent findings of Jay et al (27). However, there are some key differences between the experimental design of these two studies (i.e., Jay et al. and Gant et al.) that may have led to the apparently contradictory findings: 1) Jay et al. matched for body mass (i.e., ~ 0.5 kg difference between groups), whereas the Gant et al. did not (i.e., ~ 5.1 kg difference between groups); 2) Gant et al. compared individuals who are moderately fit and very fit (59.4 ± 0.7 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ vs. 72.8 ± 0.8 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$), where as Jay et al. compared individuals who are aerobically unfit and fit (40.3 ± 2.9 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$ vs. 61.1 ± 4.5 mL $O_2 \cdot kg^{-1} \cdot min^{-1}$) (20, 27); 3) Gant et al. did not consider potential differences in running economy (RE) between their two groups; this is an important factor to consider in a study that uses running as the mode of exercise as the inter-individual differences in economy are much greater for running than cycling (See section: *Running Economy*). Therefore, the greater sweat losses of the moderate VO_{2max} group, compared to the high VO_{2max} group at the same running speed were probably indicative of differences in RE and not an influence of fitness *per se*, i.e. the moderate fitness group had a greater heat production for a given running speed because of a lower running economy and greater mass, eliciting a greater E_{req} and thus a greater rate of sweat production needed for heat balance. Due to these numerous flaws, the independent influence of VO_{2max} , on thermoregulatory responses, needs to be re-evaluated while accounting for biophysical aspects (i.e., body mass and BSA), running economy and metabolic heat production.

Running Economy

Running economy (*RE*) has been defined as the steady-state aerobic demand (VO_2) per unit mass for a given submaximal running speed (13, 37, 47). *RE* is estimated from steady-state VO_2 , in relative terms (i.e., $\text{mLO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$), and running speed (e.g., $\text{km} \cdot \text{h}^{-1}$) (13, 37, 38), using the following equation.

$$RE = \frac{VO_2}{s \cdot 60} \dots\dots\dots \text{mlO}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1} \dots\dots\dots (12)$$

Where: VO_2 is the amount of consumed oxygen, in $\text{mLO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$, and s is the running speed, in $\text{km} \cdot \text{h}^{-1}$, multiplied by 60 to convert $\text{km} \cdot \text{h}^{-1}$ to $\text{km} \cdot \text{min}^{-1}$.

Running economy is influenced by many factors, both biomechanical and physiological in nature. The major biomechanical factors affecting running economy are anthropometry (e.g., stride length influenced by height and weight), flexibility (e.g., elastic potential), joint moments, and kinetics (e.g., ground reaction force) (47). Whereas, physiological factors affecting running economy include composition of muscle fibres, muscle temperature (i.e., warm-up), aerobic fitness (i.e., $\text{VO}_{2\text{max}}$), and metabolic factors (e.g., number of mitochondria) (47). The fact that *RE* is affected by so many factors results in a lot of room for individual variability.

The individuality component of running economy is identified in multiple studies, as well as demonstrated in *Figure 1*. Running economy can vary greatly among individuals of different fitness levels and training status (i.e., fit and trained individuals tend to have a better *RE* compared to those who are unfit and untrained) (13, 37, 47). However, *RE* can also vary by as much as 30% among trained runners with a similar $\text{VO}_{2\text{max}}$ (13, 47). *Figure 1* demonstrates that *RE* values vary within and between different “subject categories”, ranging from elite runners

(i.e., Category 1) to untrained runners (i.e., Category 4) (37). Furthermore, there is overlap in the RE values between “subject categories”, thus showing that running economy is a very individual characteristic, although there is a general trend of more elite runners having a better RE than untrained runners.

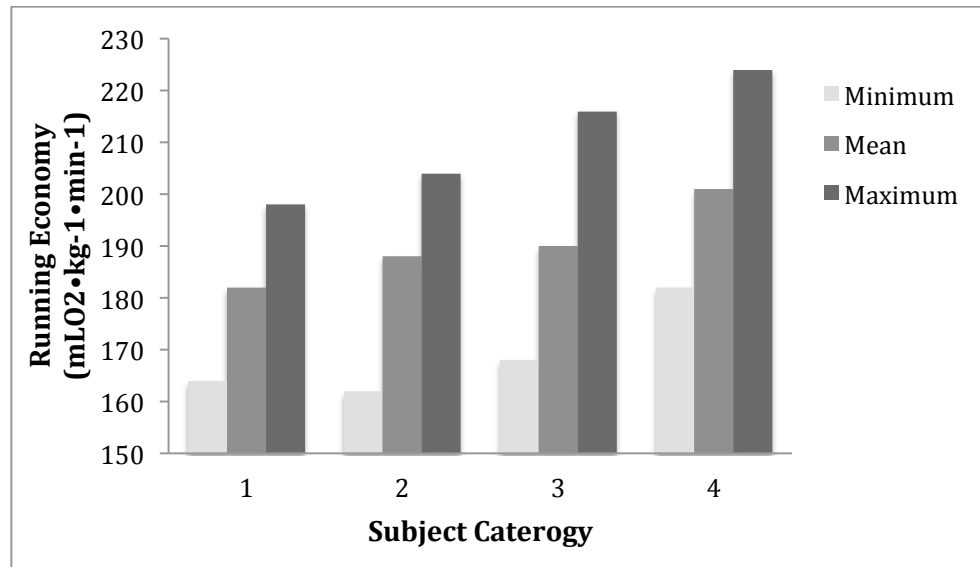


Figure 1: Minimum, mean, and maximum oxygen demand values for: elite runners [VO_{2max} : 75.6 ± 3.2 $mLO_2 \cdot kg^{-1} \cdot min^{-1}$] (Category 1), sub-elite runners [VO_{2max} : 70.5 ± 4.0 $mLO_2 \cdot kg^{-1} \cdot min^{-1}$] (Category 2), good runners [VO_{2max} : 59.2 ± 4.1 $mLO_2 \cdot kg^{-1} \cdot min^{-1}$] (Category 3) and untrained subjects [VO_{2max} : 51.4 ± 3.9 $mLO_2 \cdot kg^{-1} \cdot min^{-1}$] (Category 4). Subjects ran at speeds eliciting $\sim 70\%$ VO_{2max} (37).

Furthermore, at different running speeds, intra-individual variations in *RE* has been shown to be between 2 and 11% (38); this was not accounted for in the results presented in Figure 1 (37). Therefore, RE also varies within an individual for various conditions (e.g.,

different running speed). Taking this into account, running economy must be evaluated on an individual basis (not assumed for a group based on training and fitness), and also for the same conditions (e.g., fixed running speed for all groups), so that a between groups comparison can be made.

III. PROPOSED PROJECT

Rationale

There has only been one study, to date, that has attempted to evaluate the influence of aerobic fitness (VO_{2max}) on thermoregulatory responses during running (20). However, it is clear from the literature that these authors did not isolate the influence of VO_{2max} on thermoregulatory responses independently of heat production, body mass, BSA. The only study that has been able to isolate the independent influence of VO_{2peak} on thermoregulatory responses (during cycling) demonstrated that fixed heat production, not relative exercise intensity ($\%VO_{2max}$), determined the changes in core temperature and sweating (27). Relative exercise intensity elicits a much greater heat production in fitter individuals when matched for body mass, because they are working at the same percentage of a much larger VO_{2max} (see *Figure 2*). Furthermore, Gant et al. did not account for differences in running economy between fitness groups for their common running speed trial. Even when matching for body mass and VO_{2max} , a common (i.e., fixed) running speed elicits a greater heat production in less economical runners due to a higher oxygen uptake (VO_2) (see *Figure 2*). It follows that to truly isolate the influence of VO_{2max} on thermoregulatory responses during running, fit and unfit individuals must be compared at the same metabolic heat production (and therefore VO_2) irrespective of running speed or relative intensity (*Figure 2*).

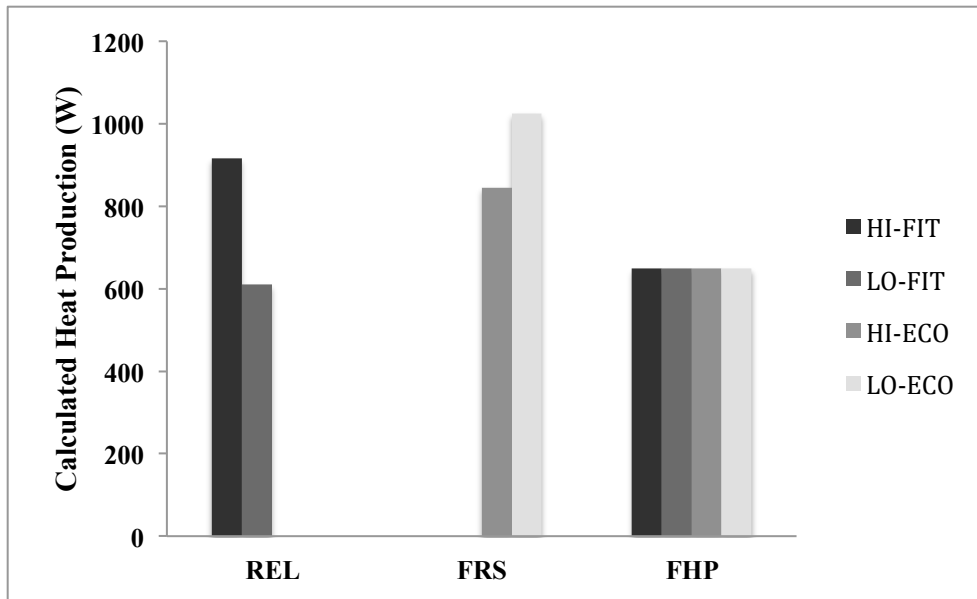


Figure 2: Calculated heat production values, in Watts, for four independent groups [two groups matched for VO_{2max} with 1) a low running economy (LO-ECO group) and 2) a high running economy (HI-ECO group); and two groups matched for running economy with 1) a high VO_{2max} (HI-FIT) and 2) low VO_{2max} (LO-FIT group)] during three different exercise trials [1) a relative exercise intensity of 60% VO_{2max} (REL) to compare LO-FIT vs. HI-FIT; 2) a fixed heat production of 650 W (FHP) administered to all four groups; and 3) a fixed running speed of 10.5 $km \cdot h^{-1}$ (FRS)] to compare HI-ECO vs. LO-ECO. Calculations were done assuming, a body mass of 75 kg (groups matched for body mass), a high VO_{2max} of 60 $mLO_2 \cdot kg^{-1} \cdot min^{-1}$, a low VO_{2max} of 40 $mLO_2 \cdot kg^{-1} \cdot min^{-1}$, a high RE of 190 $mLO_2 \cdot kg^{-1} \cdot km^{-1}$, a low RE of 230 $mLO_2 \cdot kg^{-1} \cdot km^{-1}$ (RE based on preliminary findings).

It is important, for methodological purposes, to determine whether changes in core temperature and thermoregulatory sweating are determined by aerobic fitness (VO_{2max}) or by heat production, body mass, BSA, and running economy. That will be the aim of this thesis.

Research Questions

The two research questions for this thesis were:

- 1) Do large differences in $\text{VO}_{2\text{max}}$ independently alter changes in core temperature and sweating during treadmill running in a neutral environment?
- 2) Do large differences in running economy, in individuals of equal aerobic fitness (same $\text{VO}_{2\text{max}}$) independently alter changes in core temperature and sweating during treadmill exercise in a neutral environment?

Experimental Hypothesis

Based on the previously discussed literature and concepts, it was hypothesized that:

- 1) Changes in core temperature and sweating during treadmill exercise in a neutral environment would be: A) The same, irrespective of $\text{VO}_{2\text{max}}$, at a fixed metabolic heat production (650 W) despite different relative exercise intensities between the two groups; and B) significantly greater in the high $\text{VO}_{2\text{max}}$ (HI-FIT) group at the same relative workload (60% $\text{VO}_{2\text{max}}$) compared to the low $\text{VO}_{2\text{max}}$ (LO-FIT) group due to differences in metabolic heat production.
- 2) Changes in core temperature and sweating during treadmill running in a neutral environment, when groups are matched for fitness, would be A) the same at a fixed metabolic heat production (650 W) despite large differences in running economy, and consequently running speed and B) significantly greater in the high $\text{VO}_{2\text{max}}$ and low running economy (LO-ECO) group at the same running speed ($10.5 \text{ km}\cdot\text{h}^{-1}$) compared to the high $\text{VO}_{2\text{max}}$ and high running economy (HI-ECO) group.

V. METHODOLOGY

Participants

Prior to commencing the study, approval of the experimental protocol was obtained from the University of Ottawa Research Ethics Committee that conforms to the Declaration of Helsinki. All participants who volunteered for the study completed a Physical Activity Readiness Questionnaires (PAR-Q) form and provided written informed consent.

A power calculation using thermometry data from an earlier publication from our laboratory (27) was performed using the calculated effect size of 0.80, an α of 0.05 and a β of 0.2 which determined that seven participants were required for a sufficient level of statistical power. The participants selected were required to be healthy, non-smoking, and normotensive males, in the age range of 18-40 years old. To isolate the influence of aerobic fitness (VO_{2max}) on thermoregulatory responses, 7 low VO_{2max} [$\sim 45 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ (LO-FIT group)] and 7 high VO_{2max} [$\sim 60 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ (HI-FIT group)] males matched for mass and body surface area (BSA) were tested. Furthermore, to isolate the influence of running economy (RE) on thermoregulatory responses, 7 low running economy [$\sim 220 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$ (LO-ECO group)] and 7 high running economy [$\sim 185 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$ (HI-ECO group)] males matched for VO_{2max} [$\sim 60 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$], body mass and BSA were tested. The participants across the compared groups (i.e., HI-FIT vs. LO-FIT and LO-ECO vs. HI-ECO) were matched within one kilogram of body mass and within 0.05 m^2 of body surface area (BSA). Participants ranged from 60 to 85 kg in body mass and from ~ 10 to $\sim 20\%$ in body fat percentage, since a recent study showed no influence of body fat percentage within this range on human thermoregulatory responses (27). All participants performed one preliminary trial and two experimental trials specific to the group that they were in (see *Table 1*). The experimental trials were the following: 1) a fixed metabolic

heat production of 650 W (FHP trial); 2) a 60% of VO_{2max} (REL trial); and 3) a fixed running speed of $10.5 \text{ km}\cdot\text{h}^{-1}$ (FRS trial).

Table 1: The trials performed by the subjects of each group are indicated with a check mark (✓).

GROUP	TRIAL		
	FHP	FRS	REL
LO-FIT	✓		✓
HI-FIT	✓		✓
LO-ECO	✓	✓	
HI-ECO	✓	✓	

Preliminary Trial

The preliminary trial protocol is illustrated in *Figure 3*. During the preliminary trial, total body mass, height, body composition and maximum oxygen consumption (VO_{2max}) were measured. BSA was calculated using measurement of height and weight, according to DuBois and DuBois (1916). Body composition (including body fat percentage) of each participant was measured using dual energy x-ray absorptometry (DEXA). VO_{2max} was measured using a treadmill (TRUE 850, TRUE Fitness Technology Inc., O’Fallon, MO, USA) and a V_{MAX} Encore Metabolic Cart (CareFusion, San Diego, CA, USA). The protocol consisted of a 12-minute warm-up [Fit participants: four minutes at 8.5, 10.5, and 12.5 $\text{km}\cdot\text{h}^{-1}$; Unfit participants: four minutes at 6.5, 8.5 and 10.5 $\text{km}\cdot\text{h}^{-1}$] followed by a ten-minute recovery period, prior to running at a self-selected speed between 8 and 12 $\text{km}\cdot\text{h}^{-1}$ and a 1% grade increase every minute until

physical exhaustion. This protocol is based on recommendations from the Canadian Society of Exercise Physiology (12).

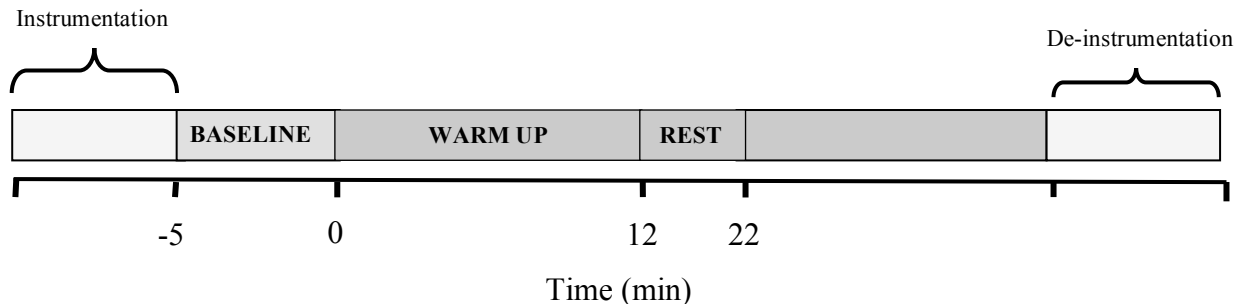


Figure 3: Schematic representation of the preliminary trial protocol.

Instrumentation

Core Temperature: Rectal temperature (T_{re}) and esophageal temperature (T_{es}) were measured using a pediatric thermocouple probe (Mon-a-therm Temperature Probe, Mallinckrodt Medical, St. Louis, MO, USA). The rectal temperature probe was inserted, by the participant, 12 cm past the anal sphincter. The esophageal temperature probe was inserted by Jovana Smoljanić (approved by the Office of Risk Management, University of Ottawa), through the participant's nostril into the esophagus. The location of the probe's tip in the esophagus is estimated to be at the level of the eighth and ninth thoracic vertebrae reflecting the location of the left ventricle and aorta (35).

Skin Temperature (T_{sk}): was measured at four sites (upper chest, deltoid, anterior thigh, and calf) using T-type (copper/constantan) thermocouples integrated into heat flow sensors (Concept Engineering, Old Saybrook, CT, USA). The heat flow sensors were attached to the skin using double-sided stick disks (3M, D-41453, Neuss, Germany) and surgical tape (Blenderm,

3M, St. Paul, MN, USA). Prior to the placement of the heat flow sensors, the test sites were shaved to remove any excess body hair and wiped down with an alcohol swab to remove body oils. Mean skin temperature (T_{sk}) was calculated using the four skin temperatures weighted to the regional proportions as determined by Ramanathan: chest 30%, shoulder 30%, thigh 20%, calf 20% (43).

All temperature data was collected using a National Instruments data acquisition module (model NI cDAQ-9172) at a sampling rate of 5 seconds. The data was displayed in real time and recorded in a spreadsheet format on a personal computer (Dell Inspiron 545) with LabVIEW 2009 software (National Instruments, TX, USA).

Whole Body Sweat Rate (WBSR): was estimated by measuring body mass to the nearest 2 grams using a platform scale (Combics 2, Sartorius, Mississauga, ON, Canada). Measurements were taken at rest, directly prior to the start of exercise, and then immediately after completing the 15th, 30th, 45th and 60th minute of exercise (Figure 3). The participants stopped exercise for each measurement period, during which three body mass measurements were taken. Participants were not be towelled down prior to these measurements. An average value of the three measurements was calculated for each 15-minute period to give whole body sweat rate values in grams. Whole body sweat losses were adjusted for respiratory mass losses (calculated using Eq. 8), as well as saliva (collected from the mouthpiece) and urine (if applicable) losses.

Local Sweat Rate (LSR): was measured using one ventilated sweat capsule located on the lower back, approximately 5 cm above the posterior superior iliac spine. The ventilated capsule was attached to the skin using a double-sided stick disk (3M, D-41453, Neuss, Germany), collodion glue (Fisher Scientific, Ottawa, Canada) and surgical tape (Blenderm, 3M, St. Paul, MN, USA). Prior to attaching the capsule, the area was shaved and wiped down with an alcohol

swab. Anhydrous compressed air was passed through the capsule over the skin surface at a flowrate of 1.80 L/min. The flow rate of the anhydrous compressed air was measured using an Omega FMA-A2307 flow rate monitor (Omega Engineering, Stamford, CT). Humidity and temperature of the effluent air were measured using a Vaisala HMT330 Series Humidity and Temperature Transmitter (Vaisala Oyj, Vantaa, Finland) and displayed in real time on a personal computer (Dell Inspiron 545) with Vaisala MI70 Link (Version: 1.15) software (Vaisala Oyj, Vantaa, Finland). The local sweat rate of the lower back (LSR_{back}) was calculated using the flow rate and the difference in water content between effluent and influent air. The value was normalized for the skin surface area under the capsule (4.0 cm^2) and expressed in $\text{mg} \cdot \text{min}^{-1} \cdot \text{cm}^{-2}$. Sweating onset threshold and thermosensitivity for each participant was determined by plotting LSR_{back} against change in T_{es} and performing a segmental linear regression analysis using Graphpad Prism 6 software.

Metabolic data: was measured during the entire 60 min of exercise using a V_{max} Encore Metabolic Cart (CareFusion, San Diego, CA, USA). Subjects were equipped with a mouthpiece and a nose clip and were instructed to breathe normally. Metabolic energy expenditure (M) was obtained from minute-average values for oxygen consumption (VO_2) in litres per minute, and the respiratory exchange rate (RER) using Eq. 1 (40).

Heart Rate (HR): was monitored continuously throughout the trial using a Polar RS400X coded transmitter, and stored with a Polar Advantage interface and Polar Precision Performance software (Polar Electro Oy, Kempele, Finland).

Urine Specific Gravity (USG): Participants were asked to provide two urine samples during the experimental trials, one before and one after the trial. The samples were analyzed for

urine specific gravity using a TS400 refractometer (Reichert Technologies, Depew, NY), to determine hydration status. Each sample was measured twice to ensure consistency.

Experimental Protocol

Participants were instructed to refrain from ingesting caffeine and alcohol, as well as from partaking in exercise 24 hours prior to the experimental trials. Furthermore, participants were instructed to drink plenty of fluids the night before testing. They were asked to arrive at the Thermal Ergonomics Laboratory in Ottawa, Ontario, Canada, after eating a small meal. All trials were conducted in the morning, starting between 8 and 10 AM. Testing was conducted throughout the year (spring, summer, fall, and winter months); it should be noted that previous research found no summer acclimatization in this geographical region (6). The room was regulated at an ambient air temperature and relative humidity of 25°C and 30%, respectively. To ensure proper hydration, urine specific gravity (USG) was measured prior to and immediately after exercise. No fluids were ingested during the 60 minutes of exercise.

The experimental protocol is illustrated bellow in *Figure 4*. Upon arrival participants were asked to drink 250 mL of water (to ensure hydration), provide a urine sample (for USG measurement), and change into athletic clothing. The trials were completed seminude, thus clothing consisted of only shorts (provided by the lab – Tempo Shorts, New Balance), athletic shoes, and light socks, which have an estimated clothing insulation value of $0.1clo$ (10). The participant was then be weighed and instrumented (as described in the “Instrumentation” section). Once instrumented, the participants rested (in a standing position) for 30 minutes so baseline values can be obtained. In the last two minutes of baseline the participants were weighed; three body mass measurements were taken. Subsequently, all subjects ran for 60

minutes at either 1) a fixed metabolic heat production of 650 W (FHP trial), 2) a relative exercise intensity eliciting 60% of $\text{VO}_{2\text{max}}$ (REL trial), or 3) a fixed running speed of $10.5 \text{ km}\cdot\text{h}^{-1}$ (FRS trial). The 60 minutes of running was divided into four 15-minute blocks; after each 15-minute block (i.e., after 15, 30, 45, and 60 min of exercise) the participant stopped for a maximum of two minutes to allow for three body mass measurements to be taken. During the trial, three mechanical fans stacked vertically, producing an air velocity of $\sim 1.3 \text{ m/s}$, were placed 1.2 meters in front of the participant. These conditions were selected to ensure a physiologically compensable environment and full evaporation at the highest rates of metabolic heat production [$\sim 930 \text{ W}$ – for fit subjects working at 60% of their $\text{VO}_{2\text{max}}$ (estimated assuming body mass to be 75 kg, a $\text{VO}_{2\text{max}}$ of $60 \text{ mL O}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$ and a RER of 0.90)] expected in this study. The environmental conditions were also comparable to previous studies investigating the influence of $\text{VO}_{2\text{max}}$ on thermoregulatory responses during exercise (20, 27).

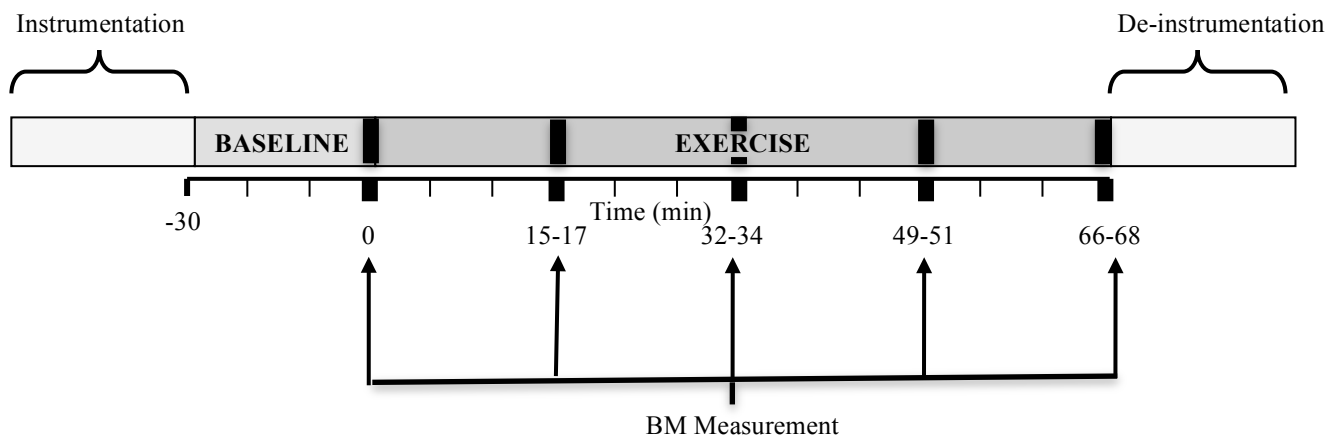


Figure 4. Schematic representation of the protocol for all experimental trials. Body mass (BM) measurements were obtained at the indicated times.

Data Analysis

All the data is expressed and was analyzed within each exercise trial (i.e., REL, FRS, and FHP). A two-way mixed ANOVA was used to analyze the dependent variables of T_{re} , T_{eso} , and WBSR, with a repeating factor of “time” and a non-repeating factor of “ VO_{2max} group”. The dependent variables of T_{re} , and T_{eso} were analyzed at five levels of “time” (i.e., rest, 15, 30, 45 and 60 min of exercise), whereas WBSR was analysed at four levels of “time” (i.e., 15, 30, 45 and 60 min of exercise, and 0-15, 15-30, 30-45, 45-60 min of exercise, respectively). All dependent variables were analyzed at two levels of “ VO_{2max} group” (i.e., low VO_{2max} (LO-FIT) vs. high VO_{2max}); and at two levels for “running economy” (i.e. high running economy (HI-ECO) vs. low running economy (LO-ECO). If significant differences were found between LO-FIT and HI-FIT (i.e., evaluating the independent influence of VO_{2max}) and/or between HI-ECO and LO-ECO (i.e., evaluating the independent influence of running economy), the individual differences were assessed using an independent samples *t*-test. Additionally, sweating onset threshold and thermosensitivity, and whole-trial means of H_{prod} (in W, $W \cdot kg^{-1}$, and $W \cdot m^{-2}$), E_{req} , VO_2 , % VO_{2max} , WBSL, T_{sk} and running speed were analyzed using an independent samples *t*-test. All data are expressed as a mean \pm SD. The significance level was set at an alpha of 0.05 for all comparisons. The probability of making a Type I error in all tests was maintained at 5% by using a Holm-Bonferroni correction. The data was analyzed using GraphPad Prism (version 6.0, GraphPad Software, La Jolla, CA).

- PART TWO -
RESULTS OF THESIS

Running Economy, not Aerobic Fitness, Independently Alters Thermoregulatory Responses during Treadmill Running

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Running head: Running economy, fitness and thermoregulation

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ABSTRACT: We sought to determine the independent influence of running economy (RE) and aerobic fitness (VO_{2max}) on thermoregulatory responses during treadmill running by conducting two studies. Study 1: Seven high (HI-FIT: $61 \pm 5 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) and seven low (LO-FIT: $45 \pm 4 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) VO_{2max} males matched for physical characteristics and RE (HI-FIT: 200 ± 21 ; LO-FIT: $200 \pm 18 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$) ran for 60 min at 1) $60\% VO_{2max}$ and 2) a fixed metabolic heat production (H_{prod}) of 640W. Study 2: Seven high (HI-ECO: $189 \pm 15.3 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$) and seven low (LO-ECO: $222 \pm 10 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1}$) RE males matched for physical characteristics and VO_{2max} (HI-ECO: 60 ± 3 ; LO-ECO: $61 \pm 7 \text{ mL O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) ran for 60 min at a fixed 1) speed of $10.5 \text{ km} \cdot \text{h}^{-1}$ and 2) H_{prod} of 640W. Environmental conditions were $25.4 \pm 0.8^\circ\text{C}$, $37 \pm 12\% \text{ RH}$. Study 1: At H_{prod} of 640W, similar changes in esophageal temperature (ΔT_{es} ; HI-FIT: 0.63 ± 0.20 , LO-FIT: $0.63 \pm 0.22^\circ\text{C}$; $P=0.986$) and whole-body sweat losses (WBSL; HI-FIT: 498 ± 66 , LO-FIT: $497 \pm 149 \text{ g}$; $P=0.984$) occurred despite different relative intensities (HI-FIT: 55 ± 6 ; LO-FIT: $39 \pm 2\% VO_{2max}$; $P < 0.001$). At $60\% VO_{2max}$, ΔT_{es} ($P=0.029$) and WBSL ($P=0.003$) were greater in HI-FIT ($1.14 \pm 0.32^\circ\text{C}$; $858 \pm 130 \text{ g}$) compared to LO-FIT ($0.73 \pm 0.34^\circ\text{C}$; $609 \pm 123 \text{ g}$), as was H_{prod} (HI-FIT: 12.6 ± 0.9 , LO-FIT: $9.4 \pm 1.0 \text{ W} \cdot \text{kg}^{-1}$; $P < 0.001$) and the evaporative heat balance requirement (E_{req} ; HI-FIT: 691 ± 74 , LO-FIT: $523 \pm 65 \text{ W}$; $P < 0.001$). Similar sweating onset ΔT_{es} and thermosensitivities occurred between VO_{2max} groups. Study 2: At $10.5 \text{ km} \cdot \text{h}^{-1}$, ΔT_{es} (1.16 ± 0.31 vs. $0.78 \pm 0.28^\circ\text{C}$; $P=0.017$) and WBSL (835 ± 73 vs. $667 \pm 139 \text{ g}$; $P=0.015$) were greater in LO-ECO, as was H_{prod} (13.5 ± 0.6 vs. $11.3 \pm 0.8 \text{ W} \cdot \text{kg}^{-1}$; $P < 0.001$) and E_{req} (741 ± 89 vs. $532 \pm 130 \text{ W}$; $P=0.007$). At H_{prod} of 640W, ΔT_{es} ($P=0.910$) and WBSL ($P=0.710$) were similar between HI-ECO ($0.55 \pm 0.31^\circ\text{C}$; $501 \pm 88 \text{ g}$) and LO-ECO ($0.57 \pm 0.16^\circ\text{C}$; $483 \pm 88 \text{ g}$) but running speed was different (HI-ECO: 8.2 ± 0.6 , LO-ECO: $7.2 \pm 0.4 \text{ km} \cdot \text{h}^{-1}$; $P=0.025$). In

Running economy, fitness and thermoregulation

conclusion, thermoregulatory responses during treadmill running are not altered by $\dot{V}O_{2\max}$, but by RE due to differences in H_{prod} and E_{req} .

Keywords: Core temperature, Experimental design, Heat balance, Sweating, $\dot{V}O_{2\max}$

INTRODUCTION

Exercise physiologists wishing to determine whether factors such as age (19, 44), obesity (16, 17), injury (such as skin burns (33)), and disease (15, 47) lead to thermoregulatory impairments must employ an independent-group experimental design to compare changes in core temperature and sweating to a reference. However the exercise intensity selected to generate a thermal challenge is vitally important since any systematic differences between groups in heat production relative to specific morphological characteristics (i.e. mass and body surface area) may lead to different thermoregulatory responses that are not due to an underlying influence of the factor under investigation (12).

To date, the most common approach for between-group thermoregulatory comparison studies has been to prescribe a relative exercise intensity (i.e. % $\text{VO}_{2\text{max}}$) due to the prevailing belief that aerobic fitness profoundly alters thermoregulatory responses during exercise (20, 24, 26, 46). However, we have recently demonstrated that under physiologically compensable conditions, aerobic fitness and therefore % $\text{VO}_{2\text{max}}$, do not independently alter changes in core temperature (12, 27), whole-body sweating (12, 23, 27) or local sweating (12, 27). Rather, changes in core temperature are determined by heat production (H_{prod}) per unit total body mass, in $\text{W}\cdot\text{kg}^{-1}$ (12), and whole-body sweat rate (in $\text{g}\cdot\text{min}^{-1}$) and local sweat rate (in $\text{mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$) are determined by the evaporative requirement for heat balance (E_{req} , which is primarily governed by H_{prod}) in W and $\text{W}\cdot\text{m}^{-2}$, respectively (12, 27).

Nevertheless, all of these recent studies employed cycle ergometry as their exercise modality, and although a fixed H_{prod} with the desired units can be reliably attained using a fixed external workload of the same units due to the relatively low individual variability in mechanical efficiency on a standard laboratory ergometer (45), many exercise physiologists and sport

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scientists often use treadmill running. It follows that running economy (RE) on a treadmill at a fixed running speed can differ between individuals by as much as 30%, independently of aerobic fitness (14). It is thus unclear whether unbiased thermoregulatory comparisons of mass-matched groups can be performed using a fixed running speed (in $\text{km}\cdot\text{h}^{-1}$), or if differences in RE can lead to alterations in H_{prod} and E_{req} that are sufficient to elicit systematic differences in core temperature and sweat rate between groups that would otherwise respond similarly.

Contrary to our recent findings using cycle ergometry (27), a study by Gant et al. (24) supports the use of $\%VO_{2\text{max}}$ for between-group comparisons of thermoregulatory responses during treadmill running. The authors reported a greater change in core temperature in a moderately fit ($VO_{2\text{max}} > 55 \text{ mlO}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) group compared to a group of very fit ($VO_{2\text{max}} > 70 \text{ mlO}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) competitive runners, running at a fixed speed of $10.5 \text{ km}\cdot\text{h}^{-1}$, which was considered a fixed absolute intensity (24). However, the two groups were not well matched for mass and indirect calorimetry was not employed, therefore the greater change in core temperature in the group with a lower $VO_{2\text{max}}$ may have simply arisen due to a greater H_{prod} secondary to an inferior RE (24), and not due to $VO_{2\text{max}}$ per se.

It is therefore clear that the independent influence of both $VO_{2\text{max}}$ and RE on thermoregulatory responses during treadmill running must be evaluated in order to establish the optimal method for between-group comparisons of core temperature and sweating with this exercise modality. To this end, two studies were performed. Firstly, two groups matched for body mass, BSA, age, body fat%, sex and RE, but vastly different in $VO_{2\text{max}}$ ran on a treadmill at i) a relative intensity of $60\%VO_{2\text{max}}$ (REL trial), and ii) a fixed H_{prod} of 640 W (FHP trial). In a second study, two groups matched for body mass, body surface area (BSA), age, body fat%, sex and $VO_{2\text{max}}$, but distinctly different in RE ran on a treadmill at i) a fixed running speed of 10.5

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km·h⁻¹ (FRS trial), and ii) a fixed H_{prod} of 640 W (FHP trial). In study 1, it was hypothesized that in the REL trial greater changes in core temperature and thermoregulatory sweating would be observed in the high (HI-FIT) compared to the low (LO-FIT) VO_{2max} group, due to a greater H_{prod} and E_{req}; but in the FHP trial thermoregulatory responses would be similar despite a greater %VO_{2max} in the LO-FIT group. In study 2, it was hypothesized that in the FRS trial greater changes in core temperature and thermoregulatory sweating would be observed in the low (LO-ECO) compared to high (HI-ECO) running economy group, due to a greater H_{prod} and E_{req}; but in the FHP trial no differences in thermoregulatory responses would be observed but treadmill speed would be slower in the LO-ECO group.

METHODS

Participants

Prior to commencing the study, ethical approval of the experimental protocol was obtained from the University of Ottawa Research Ethics Committee that conforms with the Declaration of Helsinki. All participants who volunteered for the study completed a Physical Activity Readiness Questionnaires (PAR-Q) form and provided written informed consent. A power calculation using thermometry data from an earlier publication from our laboratory (27) was performed using the calculated effect size of 0.80, an α of 0.05 and a β of 0.2 which determined that seven participants were required for a sufficient level of statistical power.

In study 1, to isolate the influence of aerobic fitness [i.e. maximum oxygen consumption (VO_{2max})] on thermoregulatory responses, 7 aerobically-fit (HI-FIT group) and 7 unfit (LO-FIT group) males matched for mass, BSA, age, body fat% and RE but who differed greatly in VO_{2max} were recruited (Table 1). In study 2, to isolate the influence of running economy (RE) on thermoregulatory responses, 7 low economy (LO-ECO group) and 7 high economy (HI-ECO

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group) males matched for VO_{2max} , body mass, BSA, age and body fat% but who differed greatly in RE were recruited (Table 1). The majority of the HI-ECO group was composed of runners whereas the majority of the LO-ECO group was composed of non-running athletes (i.e. cyclists and ice hockey players).

Experimental Design

All participants performed one preliminary trial and two experimental trials. In study 1, the experimental trials were: 1) a 60% of VO_{2max} (REL trial) and 2) a fixed H_{prod} of 640 W (FHP trial). In study 2, the experimental trials were: 1) a fixed running speed of $10.5 \text{ km}\cdot\text{h}^{-1}$ (FRS trial) and 2) a fixed H_{prod} of 640 W (FHP trial). During the preliminary trial, total body mass, height, steady state oxygen consumption (VO_2) and maximum oxygen consumption (VO_{2max}) were measured. Steady state VO_2 was determined using a treadmill protocol consisting of three, 12-min stages (Fit participants: four minutes at 8.5 , 10.5 , and $12.5 \text{ km}\cdot\text{h}^{-1}$; Unfit participants: four minutes at 6.5 , 8.5 and $10.5 \text{ km}\cdot\text{h}^{-1}$). VO_{2max} was determined following a 10-min recovery period; participants ran at a self-selected speed between 8 and $12 \text{ km}\cdot\text{h}^{-1}$ and a 1% grade increase every min until physical exhaustion. This protocol was based upon recommendations from the Canadian Society of Exercise Physiology (13).

Body composition of each participant was measured using dual energy x-ray absorptiometry (DEXA). BSA was calculated using the DuBois and DuBois formula (5). RE was calculated using steady state oxygen consumption (i.e., the average VO_2 during the last two minutes of the four-minute stage) at $10.5 \text{ km}\cdot\text{h}^{-1}$, as shown in Equation 1 (14):

$$RE = \frac{VO_2}{s \cdot 60} \dots \dots \dots \text{mlO}_2 \cdot \text{kg}^{-1} \cdot \text{km}^{-1} \dots \dots \dots (1)$$

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Where: $\dot{V}O_2$ is the amount of consumed oxygen, in $\text{mLO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$, and s is the running speed, in $\text{km} \cdot \text{h}^{-1}$, divided by 60 to convert $\text{km} \cdot \text{h}^{-1}$ to $\text{km} \cdot \text{min}^{-1}$.

Instrumentation

All instrumentation was identical for studies 1 and 2. Rectal (T_{re}) and esophageal (T_{es}) temperatures were measured using pediatric thermocouple probes (Mon-a-therm General Purpose Temperature Probe, Mallinckrodt Medical, St. Louis, MO). The rectal probe was inserted, by the participant, 12 cm past the anal sphincter. The esophageal probe was inserted, by the researcher, through the participant's nostril into the esophagus; the location of the probe's tip in the esophagus is estimated to be at the level of the eighth and ninth thoracic vertebrae reflecting the location of the left ventricle and aorta (34). Skin temperature (T_{sk}) was measured on the left side of the body at 4 sites using T-type thermocouples. The probes were attached to the skin using double-sided stick disks (3M, D-41453, Neuss, Germany) and surgical tape (Blenderm, 3M, St. Paul, MN, USA). Mean skin temperature was calculated using the 4-point Ramanathan weighting: chest 30%, shoulder 30%, thigh 20%, calf 20% (42). All temperature data was collected using a National Instruments data acquisition module (model NI cDAQ-9172) at a sampling rate of 5 seconds. The data was displayed in real time and recorded in a spreadsheet format on a personal computer (Dell Inspiron 545) with LabVIEW 2009 software (National Instruments, TX, USA).

Whole-body sweat rate (WBSR) was estimated by measuring body mass to the nearest 2 grams using a platform scale (Combics 2, Sartorius, Mississauga, ON, Canada). Measurements were taken in triplicate at rest, directly prior to the start of exercise, and then immediately after completing the 15th, 30th, 45th and 60th min of exercise. Participants were not towed down prior to these measurements. An average value of the three measurements was calculated for each 15-

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min period, which was subsequently divided by 15 min to give WBSR values in $\text{g}\cdot\text{min}^{-1}$.

Additionally, the sweat losses from each 15-min interval were summed to give a cumulative whole-body sweat loss (WBSL) in g.

Local sweat rate of the lower back (LSR_{back}) was measured using one ventilated sweat capsule located approximately 5 cm above the right posterior superior iliac spine. The ventilated capsule was attached to the skin using a double-sided stick disk (3M, D-41453, Neuss, Germany), Collodion glue (Fisher Scientific, Ottawa, Canada) and surgical tape (Blenderm, 3M, St. Paul, MN, USA). Anhydrous compressed air was passed through the capsule over the skin surface at a flow rate of 1.80 L/min. The flow was measured using an Omega FMA-A2307 monitor (Omega Engineering, Stamford, CT). Humidity and temperature of the effluent air were measured using a capacitance hygrometer (Series HMT333, Vaisala, Helsinki, Finland) that was factory calibrated and accurate to $0.035 \text{ mg}\cdot\text{cm}^{-2}\cdot\text{min}^{-1}$, and values were displayed in real time on a personal computer (Dell Inspiron 545) with Vaisala MI70 Link (Version: 1.15) software (VaisalaOyj, Vantaa, Finland). LSR_{back} was calculated using the flow rate and the difference in water content between effluent and influent air. The value was normalized for the skin surface area under the capsule (4.0 cm^2) and expressed in $\text{mg}\cdot\text{min}^{-1}\cdot\text{cm}^{-2}$. Sweating onset threshold and thermosensitivity for each participant was determined by plotting LSR_{back} against change in T_{es} and performing a segmental linear regression analysis using Graphpad Prism 6 software. Sweating thermosensitivity was defined as the increase in sweating slope relative to changes in T_{es} after the onset threshold for sweating (9). The onset threshold for sweating was defined as the intercept of the thermosensitivity slope with the resting sweat rate (9).

Metabolic data was measured during the entire 60 min of exercise using a V_{max} Encore Metabolic Cart (CareFusion, San Diego, CA, USA). Subjects were equipped with a mouthpiece

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and a nose clip and were instructed to breathe normally. Metabolic energy expenditure (M) was obtained from minute-average values for oxygen consumption (VO_2) in liters per minute, and the respiratory exchange ratio (39). The rate of metabolic heat production (H_{prod}) was assumed to be equal to metabolic energy expenditure, as external work rate during running on a flat surface at a constant speed is equal to zero (31). Subsequently, the evaporative requirement for heat balance (E_{req}) was calculated by subtracting the sum of the estimated rate of heat lost to the environment through dry heat transfer avenues [i.e. convection (C) and radiation (R), determined using air speed, ambient temperature and T_{sk}] and the rate of respiratory heat loss via convection and evaporation ($C_{\text{res}} + R_{\text{res}}$), from H_{prod} , (i.e. $E_{\text{req}} = M - R - C - E_{\text{res}} - C_{\text{res}}$) (21, 28). For the complete breakdown of these calculations, the reader is referred to previous publications from our laboratory (12), original sources (22), and reviews (21, 28, 39).

Experimental Protocol

In both studies, participants were instructed to refrain from ingesting caffeine and alcohol, as well as from partaking in exercise 24 h prior to the experimental trials. Furthermore, participants were instructed to drink plenty of fluids the night before testing. They were asked to arrive at the Thermal Ergonomics Laboratory in Ottawa, Ontario, Canada, after eating a small meal. Testing was conducted throughout the year; it should be noted that previous research has demonstrated that no summer acclimatization occurs in this geographical region (4) and the number of participants from each group tested at particular times of the year were balanced. The room was regulated at an ambient air temperature and relative humidity of $25.4 \pm 0.8^\circ\text{C}$ and $37 \pm 12\%$ RH, respectively. Throughout all trials, three mechanical fans, stacked vertically were placed 1.2 m in front of the participant and produced an air velocity of $\sim 2.0 \text{ m}\cdot\text{s}^{-1}$. These environmental conditions were selected to ensure a physiologically compensable environment at

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the highest H_{prod} (~930 W – for fit subjects at 60% $VO_{2\text{max}}$) expected in the overall study. The environmental conditions are also comparable to previous studies investigating the influence of $VO_{2\text{max}}$ on thermoregulatory responses during exercise (24, 27).

In both studies, upon arrival at the laboratory, subjects were asked to provide a urine sample, which was analyzed for urine specific gravity (USG) using a refractometer (Reichert TS 400; Depew, NY) to ensure that all participants were euhydrated prior to each experimental session. Participants were required to have a USG below 1.020 (3) prior to commencing a trial. After confirmation of hydration status, participants changed into athletic clothing. The trials were completed seminude, thus clothing consisted of only shorts (Tempo Shorts, New Balance), athletic shoes, and light socks, which have an estimated clothing insulation value of 0.1 clo (8). Following a body mass measurement and instrumentation, the participants rested (in a standing position) for 30 min to obtain baseline values. In the last two minutes of baseline, body mass measurements were taken in triplicate. Subsequently, in study 1, participants ran on a flat treadmill for 60 minutes at either 1) a relative exercise intensity of 60% of $VO_{2\text{max}}$ (REL trial) and 2) a fixed H_{prod} of 640 W (FHP trial) equivalent to a VO_2 of 1.85 to 2.00 $L \cdot \text{min}^{-1}$. In study 2, participants ran on a flat treadmill for 60 minutes at 1) a fixed running speed of 10.5 $\text{km} \cdot \text{h}^{-1}$ (FRS trial); and 2) a fixed H_{prod} of 640 W (FHP trial). The order in which the trials were performed was balanced between participants. In both studies, every 15 min, the participants briefly stopped and body mass measurements were taken in triplicate.

Data Analysis

All data are expressed as a mean \pm SD and analyzed within each exercise trial (i.e., REL, FRS, and FHP trials). Sweating onset threshold and thermosensitivity, and whole-trial means of H_{prod} (in W, $W \cdot \text{kg}^{-1}$, and $W \cdot \text{m}^{-2}$), E_{req} , VO_2 , % $VO_{2\text{max}}$, WBSL, T_{sk} and running speed were

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analyzed using an independent samples *t*-test. To analyze the dependent variables of T_{re} , T_{es} , and WBSR, a two-way mixed ANOVA was used with the repeated factor of time (five levels for T_{re} and T_{es} : rest, 15, 30, 45, and 60 min of exercise; four levels for WBSR: 0-15, 15-30, 30-45, 45-60 min of exercise) and the non-repeated factor of group (two levels: HI-FIT vs. LO-FIT (Study 1) or HI-ECO vs. LO-ECO (Study 2)). When significant main effects or interactions were found in either study, between-group differences at individual time points were assessed using a one-tailed independent samples *t*-test. The significance level was set at an alpha of 0.05 for all comparisons. The probability of making a Type I error in all tests was maintained at 5% by using a Holm-Bonferroni correction. All statistical analyses were performed with GraphPad Prism (version 6.0, GraphPad Software, La Jolla, CA).

RESULTS

Physical characteristics

Mean participant characteristics for both studies 1 and 2 are presented in Table 1. Participants were successfully selected to ensure no morphological differences between HI-FIT and LO-FIT groups, and HI-ECO and LO-ECO groups for body mass, BSA and body fat%. By design, in study 1 the HI-FIT group had a significantly greater VO_{2max} ($P<0.001$) relative to the LO-FIT group with no concurrent differences in RE; and in study 2 the HI-ECO group had significantly better ($P<0.001$) RE than the LO-ECO group but the same VO_{2max} .

Heat production, running speeds and the evaporative requirement for heat balance

Average values for H_{prod} , running speed and E_{req} for both studies are presented in Table 2.

Study 1: In the REL trial, H_{prod} (in W, $W \cdot kg^{-1}$, and $W \cdot m^{-2}$), E_{req} and running speed were all significantly greater ($P<0.001$) in the HI-FIT group compared to the LO-FIT group, but relative exercise intensity was, by design, almost identical ($P=0.856$). In the FHP trial, H_{prod} was

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successfully maintained at the same levels for between HI-FIT and LO-FIT participants, and consequently E_{req} was also similar between HI-FIT and LO-FIT groups. However, relative exercise intensity was significantly greater in the LO-FIT group ($P < 0.001$). Due to the similar RE between groups, the treadmill running speed required to attain a fixed level of H_{prod} (and therefore E_{req}) in the FHP trial was similar between the HI-FIT and LO-FIT group ($P = 0.486$).

Study 2: In the FRS trial, running speed was fixed at $10.5 \text{ km} \cdot \text{h}^{-1}$ but H_{prod} was greater (in W , $W \cdot \text{kg}^{-1}$, and $W \cdot \text{m}^{-2}$) in the LO-ECO group due to an inferior RE. In addition, E_{req} ($P < 0.001$) and relative exercise intensity ($P = 0.006$) was significantly greater in the LO-ECO group. In the FHP trial, H_{prod} was, by design, similar between HI-ECO and LO-ECO participants ($P = 0.558$), as was E_{req} ($P = 0.221$). However, in order to maintain the same H_{prod} , the HI-ECO group had to run at a significantly faster treadmill speed ($P = 0.025$). The resultant relative exercise intensity was similar between the HI-ECO and LO-ECO group ($P = 0.921$) because they were matched for VO_{2max} .

Core temperatures

Study 1: In the REL trial, there was a distinct interaction between VO_{2max} group and exercise time for both T_{re} ($P = 0.049$) and T_{es} ($P = 0.006$), and after 60 min of exercise a greater change in T_{re} (HI-FIT: $1.23 \pm 0.37^\circ\text{C}$, LO-FIT: $0.90 \pm 0.30^\circ\text{C}$; $P = 0.047$) and T_{es} (HI-FIT: $1.14 \pm 0.32^\circ\text{C}$, LO-FIT: $0.73 \pm 0.34^\circ\text{C}$; $P = 0.029$) in the HI-FIT group was observed (Figure 1). In the FHP trial, no interaction between VO_{2max} group and exercise time was observed for T_{re} ($P = 0.812$) or T_{es} ($P = 0.843$). After 60 min of exercise, almost identical changes in T_{es} (HI-FIT: $0.63 \pm 0.20^\circ\text{C}$; LO-FIT: $0.63 \pm 0.32^\circ\text{C}$; $P = 0.986$) and T_{re} (HI-FIT: $0.86 \pm 0.26^\circ\text{C}$; LO-FIT: $0.92 \pm 0.32^\circ\text{C}$; $P = 0.703$) were observed between VO_{2max} groups.

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Study 2: In the FRS trial, an interaction between RE group and exercise time was observed for both T_{re} ($P < 0.001$) and T_{es} ($P = 0.005$), and the LO-ECO group demonstrated greater changes in T_{re} (HI-ECO: $1.03 \pm 0.33^\circ\text{C}$, LO-ECO: $1.51 \pm 0.29^\circ\text{C}$; $P = 0.007$) and T_{es} (HI-ECO: $0.78 \pm 0.28^\circ\text{C}$, LO-ECO: $1.16 \pm 0.31^\circ\text{C}$; $P = 0.017$) after 60 min of exercise (Figure 2). In the FHP trial, no interaction between RE group and exercise time was observed for T_{re} ($P = 0.926$) or T_{es} ($P = 0.966$). After 60 min of exercise, very similar changes in T_{re} (HI-ECO: $0.74 \pm 0.32^\circ\text{C}$; LO-ECO: $0.73 \pm 0.19^\circ\text{C}$; $P = 0.940$) and T_{es} (HI-ECO: $0.55 \pm 0.31^\circ\text{C}$; LO-ECO: $0.57 \pm 0.16^\circ\text{C}$; $P = 0.910$) were observed between RE groups.

Skin temperature

Study 1: mean skin temperature was the same between $\text{VO}_{2\text{max}}$ groups in both the REL (HI-FIT: $31.75 \pm 0.54^\circ\text{C}$, LO-FIT: $31.61 \pm 0.30^\circ\text{C}$; $P = 0.561$) and FHP (HI-FIT: $31.70 \pm 0.46^\circ\text{C}$, LO-FIT: $31.34 \pm 0.35^\circ\text{C}$; $P = 0.124$) trials.

Study 2: Similarly to study 1, there were no differences between RE groups in mean skin temperature in the FRS (HI-ECO: $31.58 \pm 0.56^\circ\text{C}$, LO-ECO: $32.00 \pm 0.58^\circ\text{C}$; $P = 0.185$) or the FHP (HI-ECO: 31.80 ± 0.36 , LO-ECO: 31.72 ± 0.32 ; $P = 0.667$) trial.

Whole-body sweating

Study 1: In the REL trial, WBSR was greater in the HI-FIT group ($P = 0.003$) and an interaction between $\text{VO}_{2\text{max}}$ group and exercise time was also observed ($P = 0.009$) (Figure 3). After 60 min of exercise, WBSR was greater in the HI-FIT group ($P = 0.001$) compared to the LO-FIT group (Figure 3). Cumulative WBSL over 60 min of exercise was also greater ($P = 0.003$) in the HI-FIT group (858 ± 130 ml) compared to the LO-FIT group (609 ± 123 ml). In the FHP trial, WBSR was similar between the HI-FIT and LO-FIT group ($P = 0.984$) and no interaction between $\text{VO}_{2\text{max}}$ and exercise time ($P = 0.970$) was observed (Figure 3). Similarly, the cumulative

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WBSL over the 60-min of exercise was almost identical (HI-FIT: 498 ± 66 ml, LO-FIT: 497 ± 149 ml; $P=0.984$).

Study 2: In the FRS trial, WBSR was significantly greater in the LO-ECO group ($P=0.015$) furthermore, no interaction between RE group and exercise time was observed ($P=0.525$) (Figure 4). Additionally, cumulative WBSL over the 60-min bout of exercise was greater ($P=0.015$) in the LO-ECO group (835 ± 73 ml) relative to the HI-ECO group (667 ± 139 ml). In the FHP trial, WBSR was similar between HI-ECO and LO-ECO groups ($P=0.710$) and there was no interaction between RE group and exercise time ($P=0.178$) (Figure 4). Similarly, the cumulative WBSL throughout the 60-min trial was similar between RE groups (HI-ECO: 501 ± 88 ml, LO-ECO: 483 ± 88 ml; $P=0.710$).

Sweating onset thresholds and thermosensitivity

The sweating onset threshold and thermosensitivity data for studies 1 and 2 are displayed in Table 3. It should be noted that two LO-FIT participants in study 1 and one HI-ECO participant in study 2 were unable to tolerate the esophageal temperature probe, and thus thermosensitivities were calculated using 10 participants (5 vs. 5) in study 1 and 12 participants (6 vs. 6) in study 2.

Study 1: The change in esophageal temperature at the onset of sweating was similar between HI-FIT and LO-FIT groups in both the REL ($P=0.681$) and FHP ($P=0.152$) trials. Similarly, the sweating thermosensitivity was the same in between HI-FIT and LO-FIT groups in both the REL ($P=0.126$) and FHP ($P=0.559$) trials.

Study 2: The onset threshold for sweating was similar between HI-ECO and LO-ECO groups in both FRS ($P=0.179$) and FHP ($P=0.835$) trials. Also, sweating thermosensitivity was

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similar between HI-ECO and LO-ECO groups in both the FRS ($P=0.437$) and FHP ($P=0.221$) trials.

DISCUSSION

To date, no study has truly evaluated the influence of aerobic fitness (VO_{2max}) and running economy (RE) on thermoregulatory responses during treadmill running, independently of the potentially confounding factors of body mass, body surface area (BSA) and body fat. Collectively, the present data demonstrate that during running, large differences in VO_{2max} do not independently influence changes in core temperature or sweating. Rather, differences in these thermoregulatory responses occur due to alterations in metabolic heat production (H_{prod}) and the associated evaporative requirement for heat balance (E_{req}), arising from, a) differences in absolute exercise intensity when running at a fixed $\%VO_{2max}$ (REL trial, study 1); and b) differences in RE when exercising at a fixed running speed (FRS trial, study 2). On the other hand, when exercise was performed at a fixed H_{prod} (and therefore fixed E_{req}), similar sweating responses and changes in core temperature were observed despite a large difference in $\%VO_{2max}$ between HI-FIT and LO-FIT groups (FHP trial, study 1), and significant differences in running speed between HI-ECO and LO-ECO groups (FHP trial, study 2). Together these data clearly demonstrate that the optimal method for performing unbiased comparisons of thermoregulatory responses during treadmill running between groups or individuals of the same physical characteristics is to prescribe exercise that elicits the same H_{prod} (and therefore E_{req}) irrespective of $\%VO_{2max}$ and running speed.

The findings of the present study associated with the influence of VO_{2max} on thermoregulatory responses are in line with previous research from our group reporting nearly identical changes in core temperature between aerobically-fit (VO_{2max} : $\sim 60 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) and

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unfit ($\text{VO}_{2\text{max}}$: $\sim 40 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) participants matched for body mass and body surface area during semi-recumbent cycling at a fixed H_{prod} of $\sim 540 \text{ W}$ (27). We also showed that during cycling at 60% $\text{VO}_{2\text{peak}}$ fitter individuals demonstrate much greater changes in core temperature and sweating, precipitated by a greater H_{prod} (27). However, the present study shows for the first time that these previous findings are not restricted to one mode of exercise and that no independent influence of $\text{VO}_{2\text{max}}$ on thermoregulatory responses exists, even during weight-bearing exercise that recruits a much greater proportion of active musculature. While the principles of heat balance remain the same irrespective of exercise modality, the present study illustrates that the method that must be used to elicit a fixed H_{prod} and E_{req} are different. During cycling, the same external workload can be used between mass-matched groups to elicit the same H_{prod} and E_{req} due to the fact that gross mechanical efficiency during cycling, particularly on standard laboratory ergometers, varies between individuals by a relatively small amount. For example, our previous study employing semi-recumbent cycling (27) reported a maximum and minimum gross mechanical efficiency value of 18.2% and 13.5% respectively across all participants at a fixed metabolic heat production of $\sim 540 \text{ W}$. However, even in trained runners with same $\text{VO}_{2\text{max}}$ and physical characteristics, large differences (e.g. $\sim 30\%$) in RE (which can be altered by both biomechanical and physiological factors) commonly occur (14, 35, 36). At a fixed running speed of $10.5 \text{ km}\cdot\text{h}^{-1}$ (FRS condition) in the present study, differences in RE were sufficient to alter VO_2 , and thus H_{prod} and E_{req} , to an extent that significantly different elevations in core temperature (Fig. 2) and sweating (Fig. 4) were observed. Similarly, a different running speed (Table 2) was required to elicit the same H_{prod} and E_{req} (and therefore thermoregulatory responses) between the HI-ECO and LO-ECO group. While there is a tendency for more skilled runners to be more economic, both high and low economy runners are present in all skill groups

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(35). Therefore, the present observations suggest that a fixed running speed should not be used to perform between-group thermoregulatory comparisons during treadmill running, regardless of skill level. Rather VO_2 should be measured and a fixed H_{prod} and E_{req} should be employed between groups similar in mass and BSA, irrespective of running speed.

From a practical perspective, matching independent groups for mass and BSA is difficult, and in some cases impossible (e.g. children vs. adults (37)). Due to the morphological matching in the present study, the fixed absolute H_{prod} (in W) in the FHP trials simultaneously elicited the same H_{prod} per unit mass ($\text{W}\cdot\text{kg}^{-1}$) and E_{req} in W and per unit BSA ($\text{W}\cdot\text{m}^{-2}$). Another recent study from our laboratory reported that for groups with different body sizes, changes in core temperature are determined by H_{prod} in $\text{W}\cdot\text{kg}^{-1}$, whole-body sweat losses are determined by E_{req} in W, and local sweat rates are determined by E_{req} in $\text{W}\cdot\text{m}^{-2}$ (12). Therefore an appropriate experimental approach in future treadmill studies examining thermoregulatory differences between groups unmatched for body size would be to adjust treadmill speed to elicit a fixed heat production relative to the physical characteristic most relevant for the primary dependent variable of interest (10).

In opposition to the present findings, Gant et al. (24) concluded that $\text{VO}_{2\text{max}}$ does influence changes in core temperature and sweating during treadmill running. However, their comparison groups were extremely fit ($\text{VO}_{2\text{max}}$: $73 \text{ mlO}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$) and moderately fit ($\text{VO}_{2\text{max}}$: $59 \text{ mlO}_2\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$); and most importantly any potential between-group differences in RE were not considered (24). Furthermore, the authors compared thermoregulatory responses using an “absolute exercise intensity” of a fixed running speed and reported greater changes in core temperature and greater sweat rates in their moderately fit group suggesting this was an independent influence of a lower $\text{VO}_{2\text{max}}$. Yet, since RE tends to be lower in less trained

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individuals (35), a higher H_{prod} likely occurred in the lower $VO_{2\text{max}}$ group at a fixed running speed leading to a greater change in core temperature, and a greater sweat rate arising from a greater E_{req} (23); not due to a lower fitness *per se*, but because they were poorer runners. The results of the present study demonstrate that when a true absolute exercise intensity (i.e. a fixed H_{prod}) is administered, there are no fitness-related differences in sweating or changes in core temperature. Moreover, the fixed running speed which was selected to match the condition previously used by Gant et al. ($10.5 \text{ km} \cdot \text{h}^{-1}$) (24), yielded significantly greater changes in core temperature and sweating in the LO-ECO runners, even though the groups were matched for $VO_{2\text{max}}$. Collectively, these observations suggest that the previously reported differences in thermoregulatory responses ascribed to differences in fitness (24) were actually due to differences in H_{prod} and E_{req} secondary to differences in RE.

In both studies 1 and 2, no differences in the change in esophageal temperature before the onset of sweating or the thermosensitivity of sweating were found in any trials. Previous research has reported lower onset thresholds for sweating in fit individuals (11, 38), while other studies have reported a greater sweating thermosensitivity due to a heat-related adaptation of peripheral structures (sweat glands) following athletic training (1, 2, 25, 38). As such, it may be expected the onset thresholds would be lower and/or the thermosensitivity values would be greater in the HI-FIT compared to LO-FIT group. Sweating onset and thermosensitivity data were only available for 6 and 5 pairs of participants for the HI/LO-FIT comparisons in the FHP and REL trials respectively; therefore this diminished sample size could have contributed to the lack of difference between groups. Nonetheless, any (non-significant) differences suggested lower onsets and greater thermosensitivities in the LO-FIT group, which are opposite to fitness/training-related effects on these variables proposed in the literature. Moreover, the present

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observations agree with an earlier study in cyclists reporting no difference in sweating onset or thermosensitivity between aerobically-fit and unfit groups (27).

Perspectives

In addition to the practical benefits for experimental design, the findings of this study also demonstrate why fitter and less economical runners may be at a greater risk of developing heat-related illnesses. By definition, a less economic runner will consume more oxygen at a given running speed, which will lead to a greater H_{prod} and possibly a greater increase in core temperature. Indeed, a low RE has been previously suggested as a likely contributor to heat intolerance (18). Additionally, a greater aerobic fitness is logically a strong predictor of running speed during a race (30, 36) and running faster will inherently result in a greater H_{prod} per unit body mass ($\text{W}\cdot\text{kg}^{-1}$) and thus greater changes in core temperature and subsequently greater sweat rates due to a greater E_{req} (12, 23). Indeed, past studies have demonstrated higher post-marathon core temperatures in runners with faster finishing times (32, 40).

Nonetheless, recent research indicates fitter individuals may be afforded a greater thermal tolerance at a given core temperature relative to unfit individuals via a greater expression of heat shock proteins (29). Moreover, maximal sweat rate, skin wettedness, and evaporation may be altered by a partial acclimation associated with a regular training regimen that leads to a greater aerobic fitness (6, 7, 25, 43). In which case, as the boundaries of thermoregulatory compensability are reached, a separation in core temperature would be expected between the aerobically-fit and unfit groups (i.e. core temperature continues to rise in the aerobically-unfit group due to a lower maximum rate of heat dissipation). Future research is needed however to quantify the influence of aerobic fitness on maximum skin wettedness since this is not yet known. Furthermore, future research should evaluate female participants using the methods of

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this study. Finally, the assessment of thermoregulatory responses of individuals with a very low aerobic fitness ($<30 \text{ mlO}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) should also be conducted in order to extend the relevance of this work to sedentary clinical populations.

CONCLUSION

When aerobically-fit and unfit groups were matched for body morphology and ran on a treadmill at a fixed $\% \text{VO}_{2\text{max}}$, the fitter group demonstrated greater changes in core temperature and greater whole-body sweat rates due to a greater H_{prod} and E_{req} , respectively. However, when these two groups ran on a treadmill at an intensity that elicited the same H_{prod} and E_{req} , these differences in thermoregulatory responses were abolished demonstrating that aerobic fitness exerts no independent influence on the change in core temperature or sweating during running in a physiologically compensable environment. Similarly, when high and low running economy groups were matched for morphological characteristics and ran on a treadmill at a fixed running speed, the less economic runners demonstrated greater changes in core temperature and greater whole-body sweat rates precipitated by a greater H_{prod} and E_{req} respectively. However, when running speeds were modified to elicit the same H_{prod} and subsequent E_{req} in both groups, the ensuing thermoregulatory responses were the same. Therefore, in keeping with our previous research performed on cyclists, researchers conducting between-group thermoregulatory comparisons during treadmill running should employ exercise intensities that elicit similar H_{prod} and E_{req} between groups irrespective of $\% \text{VO}_{2\text{max}}$ or running speed.

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