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Review

Human behavioral thermoregulation during exercise in the heat

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The human capacity to perform prolonged exercise is impaired in hot environments. To address this issue, a number of studies have investigated behavioral aspects of thermoregulation that are recognized as important factors in determining performance. In this review, we evaluated and interpreted the available knowledge regarding the voluntary control of exercise work rate in hot environments. Our analysis indicated that: (a) Voluntary reductions in exercise work rate in uncompensable heat aid thermoregulation and are, therefore, thermoregulatory behaviors. (b) Unlike thermal behavior during rest, the role of thermal comfort as the ultimate mediator of thermal behavior during exercise in the heat remains uncertain. By contrast, the rating of perceived exertion appears to be the key perceptual controller under such conditions, with thermal perception playing a more modulatory role. (c) Prior to increases in core temperature (when only skin temperature is elevated), reductions in self-selected exercise work rate in the heat are likely mediated by thermal perception (thermal comfort and sensation) and its influence on the rating of perceived exertion. (d) However, when both core and skin temperatures are elevated, factors associated with cardiovascular strain likely dictate the rate of perceived exertion response, thereby mediating such voluntary reductions in exercise work rate.

It is beyond any doubt that the human capacity to perform prolonged exercise is impaired in hot environments (Cheung & Sleivert, 2004; Gonzalez-Alonso et al., 2008; Nybo, 2008; Nybo et al., 2014). The rationale underlying such observations has been the focus of much research and debate over the past two decades. While most studies focused their attention on the autonomic branches of the thermoregulatory, central nervous, and cardiovascular systems, a number of studies have investigated the behavioral aspects of thermoregulation under such circumstances. This is because behavioral thermoregulation is often considered to be the first line of defense in the maintenance or restoration of heat balance during rest and – perhaps even more so – during exercise in a hot environment. Among the most obvious behavioral responses observed during exercise in a hot environment are voluntary reductions in exercise work rate (Flouris, 2011; Schlader et al., 2010). Thus, behavioral thermoregulation appears to be an important factor in determining exercise performance in the heat.

The concept that behavior plays an important role in physiological function and homeostasis is not new. In fact, qualitative studies of conscious homeostatic behavior have been circulating since the time of Aristotle, who was the first to highlight the contribution of the brain in the maintenance of body integrity through the regulation of food intake and behavior related to body temperature (Lanza & Vegetti, 1996). The first quantitative experiment on behavioral thermoregulation was conducted by Kinder (1927), yet the work by Bernard Weiss and Victor Laties (Weiss, 1957a,b; Laties & Weiss, 1959, 1960; Weiss & Laties, 1960) including their seminal paper in Science entitled "Behavioral Thermoregulation" (Weiss & Laties, 1961) formally established behavior as a subdiscipline of thermoregulation. Since then, a large number of studies have been conducted aiming to understand the mechanisms by which behavioral responses are elicited to defend or restore heat balance. A PubMed search using the search terms "behaviour" (or "behavior") and "thermoregulation" between the years 1950 and 2013 reveals a total of 4644 articles that appear with increasing frequency through time reaching a record of 187 articles in 2013. Figure 1 illustrates the evolution of publications in the field of behavioral thermoregulation in relation to the seminal paper by Weiss and Laties (1961) and the major international thermoregulation conferences. This graph clearly shows that the work by Weiss and Laties paved the way for the emergence of quantitative behavioral thermoregulation research. An emerging concept in this rapidly growing field of behavioral thermoregulation is that during exercise in the heat. In light of the relatively recent reviews encompassing

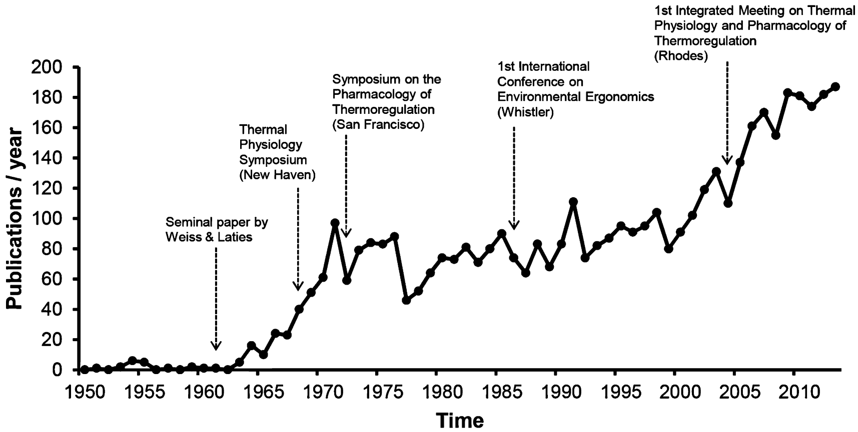

Fig. 1. The evolution of the behavioral thermoregulation field in relation to the seminal paper by Weiss and Laties (1961) and the major international thermoregulation conferences. The graph shows the total number of published articles appearing on PubMed per year using the search terms “behaviour” and “thermoregulation.” It becomes clear that quantitative behavioral thermoregulation research emerged following the work by Weiss and Laties and was supported by the major international thermoregulation conferences (publications were reduced during the inaugural year of each conference suggesting that investigators postponed publishing their work to present at these major scientific events). Note: the search includes articles appearing under the term “behavior.”

general behavioral thermoregulation (Flouris, 2011; Schlader et al., 2010), the purpose of this review is to critically evaluate and interpret the available knowledge regarding human behavioral thermoregulation during exercise in hot environments. Within the context of this review, “exercise” refers to any condition in which metabolic rate is elevated due to the production of external work. Thus, exercise refers to occupational and recreational situations alike. Given the profound attention this topic has received to date, an emphasis will be placed on the voluntary control of exercise work rate in the heat. That said, the importance of other thermal behaviors that are commonly elicited during exercise in the heat (e.g., modification of fluid intake, clothing alterations) should not be downplayed and warrant consideration in future research. Moreover, given the purpose of this review, emphasis is placed on uniform thermal environments (as would occur in a hot environment) and static comfort (as the causal relationships between perception and adaptive behavior during self-paced exercise in the heat are the objectives of the review). The ultimate goal of this work is to stimulate further mechanistic research in this field. Understanding the mechanisms and modulators of self-selected exercise work rate in the heat will undoubtedly enhance our understanding of human behavioral temperature regulation during instances of both rest and exercise. Such understanding is of critical importance given the global concerns of increasing ambient temperatures and the fact that an increasing number of people will undoubtedly exercise, work, and play in hot environments in the years to come.

Thermoregulation during exercise in the heat

During exercise, the vast majority of food’s chemical energy is converted to heat, and only a fraction is converted to mechanical energy to do external work. For example, producing an external workload of 100 W during cycling ergometry – generally considered one of the most efficient physical tasks (~ 20% of converted energy is used for external work) – requires ~ 500 W of energy conversion, with ~ 400 W released as heat in the muscle cell (Whipp & Wasserman, 1972). Thus, a significant portion of the metabolic rate required to do external work is liberated as heat that must be dissipated.

The excess heat production during exercise is a major determinant of behavior and, therefore, performance. This is because as muscle metabolic rate is increased during the early stages of exercise, a progressive increase in the muscle-to-core temperature gradient occurs such that the heat content of the active musculature exceeds that of the core region (Kenny et al., 2003, 2006). The heat released in the muscle during cellular respiration is transferred to the body core through conductive and convective heat exchange between the working muscle and the blood, and from the working muscle to the surrounding tissues and compartments (Kenny et al., 2003, 2006; Kenny & Flouris, 2014). In circumstances where exercise work rate and mechanical efficiency are constant, the rate of metabolic heat production reaches a steady-state level within ~ 10 min and remains elevated throughout the duration of exercise (Webb et al., 1970; Webb, 1986; Kenny et al., 2008). As exercise continues, the increase in body heat content and, thus, core temperature will, at some threshold value, activate autonomic heat loss responses of skin vasodilation and sweating (Flouris & Cheung, 2010).

When ambient temperature is higher than skin temperature and/or the relative humidity is high (impeding evaporative heat loss), heat balance cannot be achieved despite near-maximal stimulation of the body’s autonomic heat loss responses. In such instances, the situation is uncompensable. It is important to note that an uncompensable situation can occur even in thermoneutral environments when the individual is wearing protective clothing and/or when there are impairments in sudomotor (sweating) and/or vasomotor (skin blood flow) capacity (Flouris & Cheung, 2009; Crandall & Davis, 2010; Davis et al., 2010; Kenny & Flouris, 2014; Stapleton et al., 2014). Moreover, heat dissipation is impaired in individuals with chronic health conditions taking prescribed medications such as lithium, anticholinergic, and neuroleptic drugs (Weir, 2002), as well as in individuals with type II diabetes mellitus (Kenny et al., 2013), especially those with associated comorbidities such as obesity and/or cardiovascular disease (Bar-Or et al., 1969; Kenny & Flouris, 2014; Stapleton et al., 2014). In these situations, unless exercise is terminated or the rate of metabolic heat production is reduced via behavioral means, the body will continually store heat, preventing the attainment of heat balance, and potentially leading to dangerous increases in core temperature (Flouris et al., 2014a,b,c). Therefore, heat production – as a by-product of metabolism – can be a determinant of performance during exercise in a hot environment.

Neuronal pathways of warm sensation

Thermal perception and sense play pivotal roles in behavioral thermoregulation. The mechanism by which temperature is sensed is largely dependent on a temperature-specific family of transient receptor potential (TRP) ion channels (Guler et al., 2002; Fink, 2005; Romanovsky, 2007). Moreover, it is clear that certain TRP channels are involved in behavioral thermoregulation. For instance, a number of knockout mouse studies have confirmed that the TRP family V3 and V4 channels are likely active contributors in nocifensive behavior and in thermotaxis in the presence of warm or hot stimuli (Caterina, 2007; Caterina et al., 2000; Davis et al., 2000; Guler et al., 2002; Liedtke & Friedman, 2003; Suzuki et al., 2003; Moqrich et al., 2005). Moreover, the M8 channel is actively involved in cold-defense thermoregulation as M8 knockout mice demonstrate a preference for cooler environments, yet they retain the ability to avoid noxious cold (Bautista et al., 2007; Colburn et al., 2007; Dhaka et al., 2007).

Likely via TRP channel activation, thermal stimuli activate peripheral warm-specific C-fiber receptors or cool-specific Aδ thermoreceptors. These are small-diameter afferent fibers that project to lamina I (the superficial dorsal horn of the spinal cord) or to the medullary nucleus of the solitary tract (Craig, 2002, 2011). In turn, the output neurons of these regions project to the hypothalamus and the brainstem conveying the afferent activity relating to the thermal status of the body (Craig, 2011, 2013). Notably, the mammalian upper brainstem is known to control emotional whole-body homeostatic behaviors, including behavioral thermoregulation (Heimer & Van Hoesen, 2006; Craig, 2011). Interestingly, this neural pathway reveals a combined autonomic and behavioral opponent organization whereby the lamina I (i.e., "sympathetic") and the medullary nucleus of the solitary tract (i.e., "parasympathetic") pathways are combined (Swanson, 2000; Chandler et al., 2002; Potts, 2006), providing an energy-efficient method for precise control of behavioral thermoregulation (Craig, 2011). This principle of "opponent organization" is well known throughout physiology (Craig, 2011) and we previously proposed that it may also contribute to fatigue development during exercise in the heat (Cheung & Flouris, 2009; Flouris, 2011).

Subjective thermal perception during exercise in the heat

Upon the activation of peripheral thermosensors, a conscious change in subjective thermal perception occurs. This thermal perception includes both affective and discriminative components. The affective components are that of comfort and pleasure while discriminative perceptions are those of thermal sensation. By definition, thermal comfort is subjective indifference with the thermal environment (Mercer, 2001), thermal pleasure is perceived when a stimulus aims to restore thermal comfort (Attia, 1984) (providing an indication of the importance of the thermal status of the body to homeostasis; Cabanac, 1971), and thermal sensation identifies the relative intensity of the temperature being sensed (Attia, 1984). Quantification of these indices allows for identification of the combined sensations "which we have often experienced in the winter as 'pleasantly warm' and in the summer as 'pleasantly cool' (Gagge et al., 1967)." Importantly, although pleasantness is a useful perceptual tool indicating the magnitude and direction of changes in thermal comfort (Attia, 1984), the quantification of thermal comfort is perhaps most important as, during resting conditions, thermal discomfort (the reciprocal of thermal comfort) is the affective perception that ultimately provides the motivation for thermal behavior (Gagge et al., 1967; Satinoff, 1996; Schlader et al., 2011b). During exercise, however, the role of thermal comfort in behavior is less clear (Fanger, 1970). In fact, recent evidence suggests that the perception of effort (or perceived exertion) may be the ultimate modulator of behavior during self-paced exercise in the heat (Schlader et al., 2010).

Thermal comfort

Traditionally, research has aimed to understand what conditions produce thermal comfort, while less emphasis has been placed on why thermal comfort (or discomfort) is perceived (Parsons, 2002). Thus, our understanding of the latter remains rather incomplete. Nevertheless, it is well accepted that thermal comfort is often intimately related to skin and core temperatures. At normothermic core temperatures, thermal comfort is largely determined by skin temperature (Gagge et al., 1967; Cabanac et al., 1971, 1972; Mower, 1976; Bulcao et al., 2000; Pellerin et al., 2004; Yao et al., 2007; Nakamura et al., 2008, 2013). However, should core temperature be displaced from normothermia, thermal discomfort ensues, while improvements in thermal comfort occur as a result of a thermal stimulus (i.e., skin cooling or warming) that aims to restore normothermia (Chatonnet & Cabanac, 1965; Cabanac et al., 1972; Mower, 1976; Attia & Engel, 1981, 1982). Thus, a given thermal stimulus produces thermal discomfort when it displaces body temperatures from "neutral" and improves thermal comfort when it corrects a deviation in body temperatures (Cabanac, 1971, 1992; Attia, 1984).

During exercise, thermal comfort decreases as a function of the increase in core temperature (Cabanac et al., 1971; Bleichert et al., 1973; Scarperi & Bleichert, 1983). However, similar to that occurring during rest, this discomfort can be modified by skin temperature, such that when exercise is undertaken in both hot and more moderate ambient conditions thermal discomfort is greater in the heat even at time points when core temperature is similar (Maw et al., 1993; Tucker et al., 2006; Schlader et al., 2011c,d). Furthermore, during exercise in the heat, cooling stimuli improve thermal comfort even despite elevations in core temperature (Armada-da-Silva et al., 2004; Mundel et al., 2007; Simmons et al., 2008; Schlader et al., 2011b), while warming stimuli further attenuate comfort (Schlader et al., 2011c). Overall, these findings indicate that, similar to rest, skin temperature is the primary determinant of thermal comfort during exercise in the heat until hyperthermia ensues. When exercising in the heat at a hyperthermic state, thermal comfort is primarily driven by core temperature, while changes in skin temperature generate relatively small changes in comfort.

Thermal comfort during exercise in the heat may also be modulated by skin wetness. That is, during instances of profuse sweating, as it occurs during exercise in the heat, skin temperature has been postulated to be relatively unimportant in determining thermal comfort due to the cooling effect of sweat evaporation (Winslow et al., 1937; Gagge et al., 1969; Hardy, 1970). The activation of sweating does not directly reduce thermal comfort (Gagge et al., 1971). Therefore, the accumulation of non-evaporated sweat on the skin (i.e., increased skin wetness) contributes to thermal discomfort in hot conditions (Winslow et al., 1937; Gagge et al., 1969; Fukazawa & Havenith, 2009). Specifically, recent studies indicate that skin wetness is perceived via thermal- and mechano-afferent signals evoked through contact with wet stimuli which the brain compares with a neural representation of a "typical wet stimulus" developed from prior sensory experience (Filingeri et al., 2014a,b; Filingeri et al., 2015). Unfortunately, however, the relationship between skin wetness and thermal comfort during exercise remains uncertain. For instance, a given level of sweating is likely a requirement for thermal comfort during exercise (Fanger, 1970). Therefore, any relationships between skin wetness and thermal comfort that occur during rest likely do not apply during exercise (Havenith et al., 2002). Nevertheless, skin wetness is likely a modulator of thermal comfort during exercise in the heat, but further research is necessary in order to elucidate any such relationships. Notably, however, the influence of skin wetness on thermal comfort during exercise in the heat will be heavily influenced by the choice of clothing (Havenith et al., 2008). In this regard, research regarding interactions between clothing and skin wetness on thermal comfort during exercise in the heat is warranted.

Thermal sensation

Data collected over the past 40 years have repeatedly shown that thermal sensation generally provides the body with information regarding the thermal environment. Thus, thermal sensation is largely dictated by skin temperature, independent of core temperature (Mower, 1976; Attia & Engel, 1981; Yao et al., 2007; Zhang et al., 2010). This also remains valid during exercise, as changes in thermal sensation have been shown to reflect dynamic increases or decreases in skin temperature throughout exercise, despite ongoing increases in core temperature (Schlader et al., 2011c). However, it is notable that, compared with rest, a larger change in skin temperature is required during exercise to induce a change in thermal sensation of similar magnitude (Kemppainen et al., 1985; Ouzzahra et al., 2012; Gerrett et al., 2014). This indicates that thermal sensitivity is blunted during exercise. Nevertheless, the impact of exercise in the heat on perceptual thermal sensitivity remains uncertain.

Perception of effort

The perception of effort during exercise is an indicator of perceived strain, which is measured on a subjective scale, e.g., the Borg Ratings of Perceived Exertion (RPE) scale (Borg, 1982). By definition, RPE is intended to integrate signals both central (e.g., cardiorespiratory, central nervous system) and peripheral (e.g., muscles, joints) in origin. During exercise, neural activation of skeletal muscle raises the RPE in a dose-dependent manner (Noble & Robertson, 1996). However, no single physiological variable consistently explains RPE (Hampson et al., 2001). Yet, depending on the circumstances, a single specific physiological cue may take precedence and become the predominant mediator of the RPE response (Pandolf, 1982).

The available evidence indicates that RPE is higher during exercise in the heat at a given exercise work rate, and that this occurs prior to elevations in core temperature (Bergh et al., 1986; Pivarnik et al., 1988; Maw et al., 1993). This suggests that factors associated with elevated skin temperature are dictating the RPE response (see Pandolf, 1982). However, should core temperature become elevated, regardless of the underlying mechanisms, RPE rises as a function of the magnitude of hyperthermia (Nybo & Nielsen, 2001a; Nielsen & Nybo, 2003; Rasmussen et al., 2004). Nevertheless, several studies have shown that skin temperature can modulate this response because RPE can be reduced during exercise in the heat by applying a cool stimulus to the skin despite elevated core temperatures (Armada-da-Silva et al., 2004; Mundel et al., 2007; Simmons et al., 2008; Schlader et al., 2011b), while RPE becomes further elevated via application of a warm stimulus (Schlader et al., 2011b). Strikingly, this arrangement mirrors the thermal modulation of comfort, whereby thermal comfort is mediated predominantly by elevations in skin temperature, unless there is a change in core temperature, at which point this thermal stimulus becomes the primary dictator of discomfort and skin temperature plays a more modulatory role.

Self-selected exercise work rate in the heat

It is abundantly clear that aerobic exercise performance is impaired in the heat. For instance, exercise performance is inversely related to ambient temperature within a given competition (Ely et al., 2007a,b, 2008; Vihma, 2010; Wegelin & Hoffman, 2011). These findings have been confirmed in laboratory studies that have demonstrated that fixed work rate exercise time to exhaustion is also reduced in a hot environment (MacDougall et al., 1974; Galloway & Maughan, 1997; Gonzalez-Alonso et al., 1999; Parkin et al., 1999). Most relevantly, self-paced exercise performance, in which the exerciser is in control of his exercise work rate, is similarly impaired in a hot environment, and is characterized by voluntary reductions in exercise work rate (Fig. 2) (Tatterson et al., 2000; Tucker et al., 2004, 2006; Altareki et al., 2009; Ely et al., 2009, 2010; Abbiss et al., 2010; Lorenzo et al., 2010; Periard et al., 2011a; Schlader et al., 2011d,e). During such exercise, skin temperatures are elevated throughout. However, the magnitude of hyperthermia (i.e., the increase in core temperature) is largely dependent on the duration of exercise, with longer self-paced exercise tasks being associated with a greater level of hyperthermia than more moderate and shorter duration tasks (Tatterson et al., 2000; Tucker et al., 2004, 2006; Altareki et al., 2009; Ely et al., 2009, 2010; Abbiss et al., 2010; Lorenzo et al., 2010; Periard et al., 2011b; Schlader et al., 2011d,e). Interestingly, however, reductions in exercise work rate are frequently observed even when the magnitude of hyperthermia is minimal, and is similar throughout exercise in both moderate and hot conditions (Tatterson et al., 2000; Tucker et al., 2004, 2006; Ely et al., 2010; Lorenzo et al., 2010; Schlader et al., 2011d,e). These voluntary reductions in exercise work rate have been found to be, at least partially, consciously mediated and act to reduce the rate of metabolic heat production (Schlader et al. 2011a,d). Such reductions in metabolic heat production attenuate the rate of rise in core temperature (Fig. 2) (Schlader et al., 2011a), thereby providing the likely rationale underlying the commonly observed minimal degree of hyperthermia that accompanies self-paced exercise in the heat. Thus, this behavior aids thermoregulation, and therefore voluntary reductions in exercise work rate in the heat are, by definition, thermoregulatory behaviors (Schlader et al., 2011a; Flouris, 2011). Now, the question arises as to how this behavior is controlled. Specifically, what factors dictate this behavior and how are these factors ultimately integrated into the decision to voluntarily reduce exercise work rate? As shown below, the available evidence indicates that RPE plays a key role.

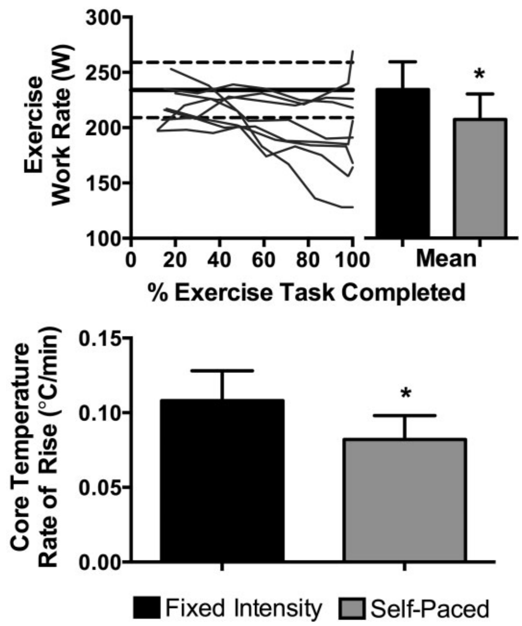

Fig. 2. Exercise work rate (i.e., power output) during exercise in uncompensable heat (40 °C) when exercise work rate is fixed [mean ± SD (thick black line ± dashed line)] and when exercise work rate is self-paced (each thin line is an individual subject; top pane), and the corresponding core temperature rate of rise (bottom pane). Data are mean ± SD ($n = 8$). These data indicate that exercise work rate in the heat is reduced when given the opportunity to behave, and that the voluntary reductions in exercise work rate decrease the rate of rise in core temperature. Note: * indicates different from fixed work rate ($P < 0.05$). Data are modified from Schlader et al. (2011a) with permission.

Perceived exertion and the perceptual control of self-selected exercise work rate in the heat

Thermal discomfort has been suggested to decrease work and athletic performance in the heat (Vanos et al., 2010). Anecdotally, this is probably due to its influence on the motivation to continue exercising in a hot environment (Cotter et al., 2001). However, unlike during rest where the role of thermal comfort in the initiation of thermal behavior is well defined, the precise role of thermal discomfort in the initiation of behavior during exercise in the heat remains ambiguous. This uncertainty is likely explained by distinct changes in the expectations of "comfort" (or discomfort) occurring with exercise (Havenith et al., 2002). For example, despite profuse sweating and the redistribution of blood, an exercising individual is prepared and expectant of being uncomfortable (Parsons, 2002; Cabanac, 2006), while sensations of pleasure, productivity, and achievement may also be associated with physical and thermal strain (Havenith et al., 2002; Ekkekakis, 2003). Alternatively, current evidence indicates that the perception of effort may be the ultimate modulator of exercise work rate (Joseph et al., 2008; Johnson et al., 2009; Tucker, 2009), and during exercise in the heat thermal discomfort may modulate this response (Schlader et al., 2010). Now the question arises as to how RPE dictates the selection of exercise work rate in the heat.

There is evidence indicating that voluntary force production and muscle fatigue may be limited perceptually, rather than physiologically *per se* (Banister, 1979). Therefore, it is likely that an increased perception of effort in order to sustain a given work rate plays a large role in the manifestation of exercise fatigue and initiation of subsequent voluntary reductions in exercise work rate (Enoka & Stuart, 1985). During exhaustive fixed work rate exercise, RPE increases linearly over time in a manner proportionate to the relative trial duration (Horstman et al., 1979; Noakes, 2004; Eston et al., 2007). Thus, the rate of rise in RPE early during exercise seemingly explains exercise duration (Horstman et al., 1979). Interestingly, this phenomenon likely contributes to the accelerated exhaustion that occurs in the heat. For instance, compared with cooler conditions, the premature cessation of fixed work rate exercise in the heat is predicted by a higher rate of rise in RPE during the early stages of exercise (Crewe et al., 2008). Given that fixed work rate exercise exhaustion, independent of ambient temperature, is associated with the attainment of near-maximal RPE (e.g., Galloway & Maughan, 1997; Gonzalez-Alonso et al., 1999), it is possible that the attenuated exercise duration in the heat can be attributed, at least partially, to an increased rate of rise in RPE. Unfortunately, however, the precise reason for this increased rate of rise in RPE remains uncertain.

During self-paced exercise, where the exercise end point is known, RPE rises relative to the proportion of the exercise task completed, with near-maximal RPE being achieved during the final stages of exercise (Albertus et al., 2005; Joseph et al., 2008; Johnson et al., 2009). Furthermore, when expressed in proportion to the relative task length, this RPE response is well preserved and increases independent of ambient temperature (Abbiss et al., 2010; Periard et al., 2011a; Schlader et al., 2011d,e; Tucker et al., 2004) or skin temperature (Schlader et al., 2011c; Levels et al., 2012) (Fig. 3). Thus, the available data suggest that the exerciser appears to be comparing how the exerciser feels to how they expect themselves to feel at that moment in time and are adjusting their exercise work rate in order to protect this relationship (Joseph et al., 2008). The selection of exercise work rate, therefore, is dependent on RPE and if any factor, or combination of factors (e.g., ambient temperature, drugs: caffeine, Doherty & Smith, 2005; dopamine reuptake inhibitors, Roelands et al., 2009), impacts RPE, exercise work rate will be adjusted accordingly.

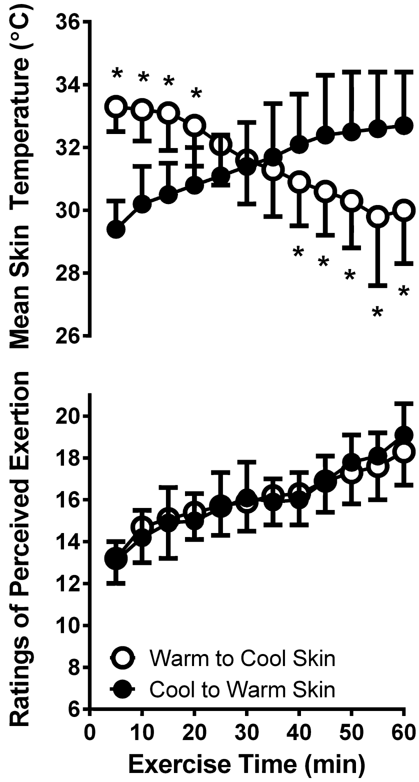

Fig. 3. Despite skin temperature being cooled (warm to cool skin) or warmed (cool to warm skin) throughout 60 min of self-paced exercise (top pane), perceived exertion increases similarly throughout self-paced exercise (bottom pane, mean ± SD, $n = 8$). These data suggest that the increase in perceived exertion during self-paced exercise is independent of skin temperature. Note: * indicates different from cool to warm skin ($P < 0.05$). Data are modified from Schlader et al., 2011c with permission.

In summary, the studies published to date suggest that RPE may modulate the voluntary selection of exercise work rate in the heat as follows: RPE is elevated at a given exercise work rate in the heat (Bergh et al., 1986; Pivarnik et al., 1988; Maw et al., 1993). Yet, RPE increases throughout self-paced exercise independent of the thermal environment (Abbiss et al., 2010; Periard et al., 2011a; Schlader et al., 2011d,e; Tucker et al., 2004) and skin temperature (Schlader et al., 2011c; Levels et al., 2012). Thus, a voluntary reduction in exercise work rate must transpire. If core temperature is normothermic, such reductions will be mediated predominantly via factors associated with elevated skin temperatures (Tatterson et al., 2000; Tucker et al., 2004; Ely et al., 2010; Schlader et al., 2011d,e). By contrast, if core temperature becomes elevated, factors associated with such hyperthermia will likely dictate changes in exercise work rate (Marino et al., 2000; Marino, 2004; Altareki et al., 2009; Periard et al., 2011a). Notably, this integrative arrangement likely explains both the direct and indirect mechanisms known and/or proposed to modulate exercise work rate in the heat.

Mechanisms underlying voluntary reductions in exercise work rate in the heat

The mechanisms by which a high ambient temperature influences self-selected exercise work rate are likely multifaceted and has been hypothesized to include the direct stimulation of peripheral thermosensors and the corresponding changes in thermal perception (Schlader et al., 2010) as well as cardiovascular strain and subsequent reductions in peak oxygen uptake (Cheuvront et al., 2010; Sawka et al., 2011, 2012). Notably, both of the aforementioned factors are probably at play during each bout of exercise in the heat, with their relative roles likely being influenced by the magnitude of hyperthermia, perhaps in addition to other, yet unknown, factors.

During self-paced exercise in the heat, elevations in core temperature are typically limited – even compared with that occurring in thermoneutral environments. Moreover, self-selected reductions in exercise work rate typically occur prior to discernable differences in core temperature (Tatterson et al., 2000; Tucker et al., 2004, 2006; Altareki et al., 2009; Abbiss et al., 2010; Ely et al., 2010; Periard et al., 2011a; Schlader et al., 2011d,e). Therefore, elevated skin temperature has been mostly implicated as the driving factor mediating reductions in exercise work rate in the heat (Ely et al., 2009, 2010; Cheuvront et al., 2010; Schlader et al., 2010, 2011c; Sawka et al., 2012). Indeed, elevated skin temperature has direct effects on thermal perception via the stimulation of peripheral thermosensors (see above). Current evidence indicates that these temperature-induced changes in thermal perception influence perceived exertion, and thus the voluntary selection of exercise work rate in the heat (Fig. 4). For example, when subjects are instructed to adjust their exercise work rate in order to maintain a constant RPE in uncompensably hot conditions, work rate predictably decreases (Tucker et al., 2006; Schlader et al., 2011b). However, when their face is thermally cooled (via fanning), which improves thermal comfort and decreases sensations of warmth, reductions in exercise work rate under these conditions are attenuated, despite no impact on core and/or mean skin temperatures (Schlader et al., 2011b). More strikingly, however, when the face is nonthermally cooled (via the application of menthol, a TRPM8 agonist), which elicits similar improvements in thermal comfort and decreases sensations of warmth, reductions in exercise work rate are also attenuated (Schlader et al., 2011b). These findings indicate that during exercise in the heat, changes in thermal perception directly modulate the voluntary selection of exercise work rate (Tucker et al., 2006; Schlader et al., 2011b). Notably, however, these findings are not unanimous, as the application of menthol at the start of exercise, and associated improvements in thermal comfort and attenuated sensations of warmth, have also been shown to have little influence on the selection of exercise work rate in the heat (Barwood et al., 2012). Although these divergent findings should not be discounted, they are likely explained by various aspects of methodology including the manner in which thermal perception was modulated [5% menthol spray over a shirt (Barwood et al., 2012) vs 8% menthol gel applied to the face (Schlader et al., 2011b)], the experimental exercise protocol [time trial (Barwood et al., 2012) vs fixed RPE (Schlader et al., 2011b)], and that the hot environmental conditions (32 °C, 50% relative humidity) were likely compensable, as evidenced by a plateau in core temperature during the latter stages of exercise (Barwood et al., 2012), as opposed to uncompensable (Schlader et al., 2011b). In support of this latter point, it has been recently shown that transient changes in ambient temperature (from 20 to 35 °C) do not influence the voluntary selection of work rate during exercise at a fixed RPE (Hartley et al., 2012). The rationale underlying this finding, and likely those of Barwood et al. (Barwood et al., 2012), is that heat balance is readily achieved across a wide range of ambient temperatures (i.e., 5–36 °C) and exercise work rates (Nielsen, 1938). Therefore, during compensable situations (and/or during moderate thermal transients), modulating the rate of metabolic heat production via voluntary

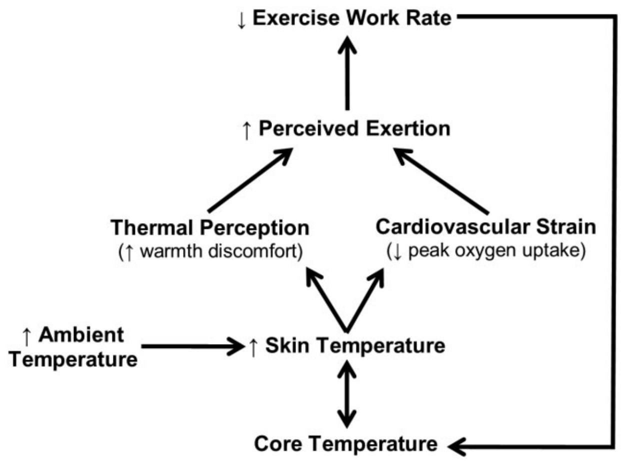

Fig. 4. The proposed manner in which thermal perception and/or cardiovascular strain mediate reductions in exercise work rate in the heat through their impact on perceived exertion. The reductions in exercise work rate are modulated predominantly via increased skin temperature and ultimately control the rate of rise in core temperature.

changes in exercise work rate is not likely necessary for the purposes of thermoregulation and achieving heat balance. Nevertheless, during uncompensably hot situations, thermal perception appears to play an important role in dictating exercise work rate in the heat (Schlader et al. 2011b).

Increased skin temperature may also indirectly influence voluntary reductions in exercise work rate via cardiovascular strain (Cheuvront et al., 2010; Sawka et al., 2011, 2012). According to this hypothesis, the selection of exercise work rate in the heat is ultimately modulated by heat-induced displacement of blood to the cutaneous vasculature, which reduces peak cardiac output (Rowell et al., 1966) and, as a consequence, blood flow to the active muscle via an inability to maintain blood pressure (Gonzalez-Alonso & Calbet, 2003). In turn, peak oxygen uptake is reduced (Arngrimsson et al., 2003, 2004; Wingo et al., 2005), and thus any given exercise work rate elicits a higher relative exercise intensity (i.e., percentage of peak oxygen uptake) and increased perception of effort (Pandolf et al., 1984; Berry et al., 1989) (Fig. 4). Notably, both peak oxygen uptake and relative exercise intensity are factors known to limit aerobic exercise performance (Bassett & Howley, 2000; di Prampero, 2003). Current evidence supports this hypothesis as reductions in peak oxygen uptake and cardiovascular strain (i.e., increases in heart rate and reductions in stroke volume and cardiac output) are associated with decreases in self-selected exercise work rate in the heat (Periard et al., 2011a). However, this may be constrained only to instances in which both skin and core temperatures are elevated (Periard et al., 2011a). For instance, at normothermic core temperatures, peak cardiac output, peak oxygen uptake, and relative exercise intensity have been found to be minimally affected during self-paced exercise in the heat (Schlader et al., 2011e). Such findings argue against cardiovascular strain as a modulator of self-selected exercise work rate in the heat prior to elevations in core temperature. Interestingly, these findings mirror the observations that peak oxygen uptake is minimally affected when hyperthermia is negligible and only skin temperatures are elevated (Arngrimsson et al., 2004).

It is likely that the relative roles of thermal perception and cardiovascular strain in modulating self-selected exercise work rate in the heat are largely dependent on the magnitude of hyperthermia. That is, during the early stages of self-paced exercise in the heat, prior to any increases in core temperature, reductions in self-selected exercise work rate are mediated via increased thermal discomfort and sensations of warmth. However, as exercise progresses and core temperature becomes elevated, it is likely that cardiovascular strain, i.e., reductions in peak oxygen uptake and corresponding increases in relative exercise intensity, begins to mediate reductions in self-selected exercise work rate in the heat. Thus, perceptual and cardiovascular factors are not independent modulators of exercise work rate. Rather, they are both capable controllers of self-selected exercise work rate in the heat, with the relative contributions of these two potential mechanisms likely being dependent on the magnitude of hyperthermia (Fig. 5). However, while we have previously proposed the above arrangement based on indirect findings (Cheung & Flouris, 2009; Schlader et al., 2010; Flouris, 2011), direct, experimental evidence in support of this hypothesis has yet to be presented.

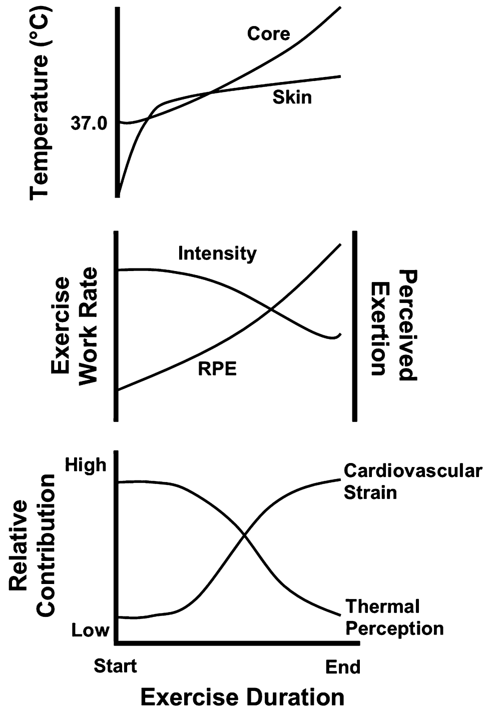

Fig. 5. Proposed relationship between cardiovascular strain (i.e., reductions in peak oxygen uptake and increased relative exercise intensity) and thermal perception (i.e., reduced thermal comfort and increased sensations of warmth) as mechanisms dictating thermoregulatory behavior during self-paced exercise in uncompensable heat. Specifically, during the early stages of exercise, when only skin temperatures are elevated (top pane), thermal behavior during self-paced exercise in the heat (i.e., reductions in exercise work rate; middle pane) is dictated largely by thermal perception (bottom pane). However, as exercise progresses, and both core and skin temperatures are elevated (top pane), reductions in exercise work rate are mediated predominantly via the increased cardiovascular strain (bottom pane). Importantly, both thermal perception and cardiovascular strain influence the voluntary selection of exercise work rate via their impact on perceived exertion (RPE, middle pane).

It is also important to note that thermal perception and cardiovascular strain are probably not the sole controllers of exercise work rate in the heat; they simply represent those factors known and recently hypothesized to influence the selection of exercise work rate under such circumstances. In fact, any factor known to modulate RPE, particularly during exercise in the heat, is a likely candidate mediating self-selected reductions in exercise work rate in the heat. For instance, processes associated with cerebral (Nielsen et al., 2001; Nybo et al., 2002a,b;

Rasmussen et al., 2004) and neuromuscular (Nybo & Nielsen, 2001b; Morrison et al., 2004, 2006, 2009; Thomas et al., 2006) functioning are likely involved, particularly during the latter stages of exercise when core temperature is elevated, but there is also evidence against this contention (Periard et al., 2011b; Racinais & Girard, 2012). Unfortunately, however, the precise role of these processes in the modulation of exercise work rate in the heat remains uncertain.

Perspectives

Our purpose in this review was to critically evaluate and interpret the available knowledge regarding human behavioral thermoregulation during exercise in hot environments as it pertains to the voluntary selection of exercise work rate. In this light, our analysis indicates that: (a) Voluntary reductions in exercise work rate in uncompensable heat aid thermoregulation and are, therefore, thermoregulatory behaviors. (b) Unlike thermal behavior during rest, the role of thermal comfort as the ultimate mediator of thermal behavior during exercise in the heat remains uncertain. By contrast, RPE appears to be the key perceptual controller under such conditions, with thermal perception playing a more modulatory role. (c) Prior to increases in core temperature (when only skin temperature is elevated), reductions in self-selected exercise work rate in the heat are likely mediated by thermal perception (i.e., thermal comfort and sensation) and its influence on RPE. (d) However, when both core and skin temperatures are elevated, factors associated with cardiovascular strain (i.e., reductions in peak oxygen uptake) likely dictate the RPE response, thereby mediating such voluntary reductions in exercise work rate.

The ultimate goal of this review was to stimulate further research aiming to increase our knowledge of the mechanisms underlying the control of self-selected exercise work rate in the heat. Such research will undoubtedly allow for a more complete understanding of the control of human thermoregulatory behavior during both exercise and rest. In this light, future research should focus on: (a) The relative contributions of different mechanisms dictating the selection of exercise work rate throughout the duration of exercise. It is likely that the mechanisms involved in the decision to reduce exercise work rate in the heat are different depending on the magnitude of hyperthermia, but direct experimental evidence is required. (b) Identifying whether voluntary reductions in exercise work rate in the heat are only advantageous when the environment is uncompensable. If this were the case, the mechanisms dictating the voluntary selection of exercise work rate in the heat would likely depend on thermal compensability. (c) Understanding the role of clothing and other behaviors (e.g., fluid intake) on the mechanisms dictating the voluntary selection of exercise work rate in the heat. This is important as such work will improve the external validity of the research conducted to date, extending beyond the laboratory to applications more specific to occupational and/or recreational settings.

Key words: Exercise work rate, metabolic heat production, temperature regulation, perceived exertion, thermal perception, cardiovascular strain.

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