



The independent roles of temperature and thermal perception in the control of human thermoregulatory behavior

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ABSTRACT

The present study independently evaluated temperature and thermal perception as controllers of thermoregulatory behavior in humans. This was accomplished using a self-paced exercise and heat stress model in which twelve physically active male subjects exercised at a constant subjective rating of perceived exertion (16, 'hard – very hard') while their face was thermally and non-thermally cooled, heated, or left alone (control trial). Thermal cooling and heating were achieved via forced convection, while non-thermal cooling and heating were accomplished via the topical application of menthol and capsaicin solutions. Evidence for thermoregulatory behavior was defined in terms of self-selected exercise intensity, and thus exercise work output. The results indicate that, in the absence of changes in temperature, non-thermal cooling and warming elicited thermal sensory and discomfort sensations similar to those observed during thermal cooling and warming. Furthermore, the perception of effort was maintained throughout exercise in all trials, while the initial and final exercise intensities were also similar. Thermal and non-thermal cooling resulted in the highest work output, while thermal warming the lowest. Non-thermal warming and control trials were similar. Heart rate, mean skin and core (rectal) temperatures, and whole body and local (neck) sweat rates were similar between all trials. These data indicate that changes in temperature are not a requirement for the initiation of thermoregulatory behavior in humans. Rather, thermal sensation and thermal discomfort are capable behavioral controllers.

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1. Introduction

By definition, a thermoregulatory behavior establishes a preferred condition for heat exchange between an organism and its environment [1], thereby helping to ensure survival and optimize comfort [2]. Compared to the relatively restricted capacity of autonomic thermoregulatory responses, behavioral responses are considered to be nearly limitless [3] and are thus regarded as the 'first line of defense' in maintaining body temperatures [4].

Via their influence on thermal sensation [5] and thermal discomfort [6], both skin and core body temperatures are capable initiators of thermoregulatory behavior [7–14]. However, when given behavioral freedom, core temperature changes too slowly for it to be the primary thermal signal [15], indicating that skin temperature is most likely the preferred behavioral input [9,13]. This arrangement effectively prevents unnecessary activation of water and/or energy consuming autonomic thermoregulatory responses [16], while suitably defending core body temperature [17].

The voluntary control of exercise intensity (work output), and therefore metabolic heat production, when exposed to both cold and hot environments provides valuable insights into the control of human thermoregulatory behavior [17]. For example, in the cold, thermal discomfort is improved by increases in exercise intensity [18,19], while in the heat, voluntary reductions in work/exercise intensity effectively prevent body temperatures from rising excessively [20–22]. Thus, self-paced exercise under environmental stress provides meaningful information concerning the control of thermoregulatory behavior in humans [17,23].

Given the causal relationships between body temperatures and the perception thereof, the fundamental mechanisms controlling human thermoregulatory behavior remain uncertain. For instance, skin temperature, and the associated thermal perceptions, influences the voluntary selection of exercise intensity [14], but it is unclear as to whether a change in temperature must occur in order for this thermal behavior to be initiated. Indeed, it is highly possible that a change in thermal sensation, and thus discomfort, independent of changes in temperature is capable of commencing thermal behavioral responses.

Utilizing the aforementioned self-paced exercise model, the purpose of this study was to independently evaluate temperature and thermal perception as controllers of human thermoregulatory behavior. Under heat stress, subjects were instructed to exercise at a

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constant (fixed) subjective rating of perceived exertion [e.g. 24] while their face was either thermally or non-thermally cooled, warmed, or left alone (control trial). Evidence for thermoregulatory behavior was defined in terms of self-selected exercise intensity, and thus total exercise work output, in a given trial.

Thermal cooling and heating were accomplished via forced convection, while non-thermal cooling and heating were achieved via the topical application of an 8.0% menthol gel and a 0.025% capsaicin cream. Acting mostly via the activation of the Transient Receptor Potential (TRP) ion channel Melastatin 8 (TRPM8) [25], during both rest [26,27] and exercise [28] menthol elicits a cooling sensation, thereby inhibiting the perception of warmth [26,29,30]. Conversely, capsaicin, principally through the activation of the TRP ion channel Vanilloid 1 (TRPV1) [25], elicits a warm, burning sensation [31] thus enhancing sensations of warmth [30]. The perceptual effects of both menthol and capsaicin transpire independent of changes in local (skin) temperature. Therefore, this paradigm permitted an investigation into the distinct roles that both temperature and thermal perception may play in the control of human thermoregulatory behavior.

2. Methods

2.1. Experimental overview

Twelve volunteers each completed five experimental trials in which they cycled at a constant (fixed) rating of perceived exertion (fixed-RPE) under significant heat stress. Exercise intensity (power output) was freely adjustable and dependent upon cycling cadence. During exercise, the face was either thermally or non-thermally cooled, warmed, or left alone (control trial). All trials took place at the same time of day and there were a minimum of 7 days between each trial. The trials were conducted in a randomized manner, to minimize any order effects.

2.2. Subjects

Twelve healthy, physically active males agreed to participate in the study. The subjects' characteristics were (mean \pm SEM): age, 23 \pm 1 y; height, 1.81 \pm 0.03 m; weight, 84.0 \pm 4.8 kg; body surface area, 2.04 \pm 0.07 m²; and percent body fat, 11.7 \pm 1.5%. Each subject was fully informed of the experimental procedures and possible risks before giving informed, written, consent. Given that aerobically well-trained subjects have an altered perception of their physiological thermal strain during exercise [32], well-trained subjects were excluded. In the present study well-trained was defined in terms of the number of days per week a potential subject underwent aerobic exercise, and whether this exercise was recreational or more formal. All subjects who participated in this study exercised aerobically a maximum of 3 days per week, but were not taking part in any formal exercise training. This protocol was approved by the University Human Ethics Committee and performed according to the Declaration of Helsinki.

2.3. Preliminary session

Seven days before the familiarization session, subjects reported to the laboratory for anthropometric measurements and an incremental exercise test. These tests were conducted in a moderate environment (19.4 \pm 0.4 °C), with the exercise tests taking place on an electronically braked cycle ergometer (Lode Excalibur, Groningen, The Netherlands) set in the pedal rate independent mode. All subsequent exercise tests were completed on the same cycle ergometer. The incremental exercise test started at a power output of 50 W for 3 min. Thereafter, power output increased by 50 W every 3 min until volitional exhaustion. This test was used to anchor the 'high' end

(i.e. 19) of the rating of perceived exertion (RPE) scale [33]. Five min following the completion of the incremental exercise test, a power output and an optimal cadence that elicited an RPE of 16 was determined for each subject. This was later used to construct the fixed-RPE protocol. During these exercise tests power output, cadence, and elapsed time were blinded from the subjects.

2.4. Familiarization session

Seven days following the preliminary session all subjects underwent a familiarization session. This session was conducted in a moderate environment (20.7 \pm 0.3 °C) and all experimental procedures were followed. This session fully familiarized the subjects with all of the experimental procedures and the fixed-RPE protocol.

2.5. Experimental protocol

At least 7 days following the familiarization session, subjects arrived at the laboratory to participate in one of five experimental trials. During these trials the subjects were instructed to cycle at a fixed-RPE while wearing a hot liquid conditioning garment (LCG). During these trials the face was either thermally or non-thermally warmed, cooled, or left alone. Thermal cooling/warming was expected to elicit a change in both temperature and perception, while non-thermal cooling/warming was expected to elicit a change in thermal perception in the absence of a change in temperature. All experimental trials took place in the laboratory in similar ($P > 0.05$) moderate ambient conditions of: 20.3 \pm 0.2 °C, 48 \pm 3% relative humidity. The subjects were not informed of the experimental conditions and were unaware of the research hypotheses, but due to the changes in thermal sensation complete blinding was impossible. It was assumed that the subjects were not heat acclimatized as the testing was conducted during the southern hemisphere autumn/winter (mean outdoor temperature: 14.2 \pm 1.0 °C).

All subjects arrived at the laboratory for the experimental trials having refrained from strenuous exercise, alcohol, caffeine, and tobacco for a period of 24 h. To minimize variations in pre-exercise muscle glycogen content and hydration status, subjects were required to complete a 48 h diet and activity log before the familiarization session, and were instructed to follow the same diet and activities prior all experimental trials. To ensure a hydrated state subjects drank a pre-measured bolus of water (5 ml/kg of body weight) 2 h prior to each trial and adequate hydration was confirmed by a nude body weight within 200 g, core temperature within 0.2 °C, and resting heart rate within six beats of the values in the previous trial [34]. Subjects were not permitted to drink during any of the experimental procedures.

On arrival at the laboratory, the subjects voided, nude body weight was measured, and a rectal thermistor was self-inserted. A heart rate monitor, skin thermistors, and the ventilated capsule were then applied and this was followed by putting on the LCG. The subjects then rested, seated on the cycle ergometer for ~5 min. This was followed by a warm-up and the fixed-RPE protocol. When the exercise bout was complete the LCG and the remainder of the experimental equipment was promptly removed and nude body weight was measured. The duration of the procedures from the initial to final nude body weight was ~50 min.

2.6. Experimental procedures

2.6.1. Fixed-RPE protocol

Prior to commencing the fixed-RPE protocol, subjects completed a 10 min warm-up which required them to cycle for 4 min at an RPE of 11, 3 min at an RPE of 13, 2 min at an RPE of 15, and 1 min at an RPE of 17. This warm-up was modified from Lander et al. [35] and was

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