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RESEARCH PAPER

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Head temperature modulates thermal behavior in the cold in humans

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ABSTRACT

We tested the hypothesis that skin temperature, specifically of the head, is capable of modulating thermal behavior during exercise in the cold. Following familiarization 8 young, healthy, recreationally active males completed 3 trials, each consisting of 30 minutes of self-paced cycle ergometry in 6°C. Participants were instructed to control their exercise work rate to achieve and maintain thermal comfort. On one occasion participants wore only shorts and shoes (Control) and on the 2 other occasions their head was either warmed (Warming) or cooled (Cooling). Work rate, rate of metabolic heat production, thermal perceptions, rectal, mean weighted skin and head temperatures were measured. Exercise work rate was reduced during Warming and augmented during Cooling after the first and second minutes of exercise, respectively ($P \leq 0.04$), with the rate of metabolic heat production mirroring work rate. At this early stage of exercise (≤5 min) the changes over time for rectal temperature were negligible and similar (0.1 ± 0.1°C, $P = 0.51$), while the decrease in mean skin temperature was not different between all trials (1.7 ± 0.6°C, $P = 0.13$). Mean head temperature was either decreased (Control: 1.5 ± 1.1°C, Cooling: 2.9 ± 0.8°C, both $P < 0.01$) or increased (Warming: 1.7 ± 0.9°C, $P < 0.01$). Head thermal perception was warmer and more comfortable in Warming and cooler and less comfortable in Cooling ($P < 0.01$). Participants achieved thermal comfort similarly in all trials ($P > 0.09$) after 10 ± 7 min and this was maintained until the end of exercise. These results indicate that peripheral temperatures modulate thermal behavior in the cold.

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Introduction

Behavior is the most effective form of temperature regulation,[1] as compared to autonomic thermoregulatory responses (e.g. shivering, sweating or changing cutaneous vasomotor tone) behavior's capacity is limitless.[2] However, while behavior plays a comparatively large role in temperature regulation,[3] paradoxically relatively little is known of its control in humans.[4]

Several behavioral models have been used to examine the control of thermal behavior in humans. A notable example is voluntary exercise,[5] as it is the only model where heat is produced endogenously. The rate of metabolic heat production, which is largely a function of the selected exercise work rate, has been found to be inversely related to ambient temperature when participants are given the freedom to select their work rate.[6] Therefore, it is not surprising that work rate is voluntarily reduced in heat[7] and voluntarily increased in the cold.[8] Unfortunately, the control of this behavior remains poorly understood.

Evidence from non-exercise models demonstrates that central (core) and peripheral (skin) body temperatures are capable initiators and transducers of thermal behavior.[9] However, these 2 effector systems are differentially driven by input from the core and skin, with autonomic thermo-effectors being strongly influenced by the core (>5:1 [core:skin], see refs. 10-11) whereas the skin influences alliesthesial/behavioral thermo-effectors equally (1:1 [core:skin], see ref. 12). The skin is more responsive to changes in the ambient thermal environment than the core.[13] The arrangement for skin temperature as the preferred thermal behavioral input minimises energy- and water-costly responses brought about by an increase in core temperature and is aimed at escaping forthcoming thermal insults.[14] When exercising in the heat, the skin and alliesthesial responses are independently capable of determining behavior without any difference in core temperature.[15,16] However, Caputa and Cabanac[8] concluded that "increased motivation for muscular

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activity in a cold environment appears to be governed chiefly by [core] brain temperature." Thus, and as discussed further below because different ambient temperatures can modify thermal and perceptual responses, whether our previous observations in the heat[15,16] can be extended to the cold, thereby conflicting with the data of Caputa and Cabanac,[8] remains to be determined.

Further complicating the matter is that the alliesthesial effects of changes in skin temperature are heterogeneous. For example, the hands and feet 'feel' the cold more whereas the face 'feels' the heat more, with whole-body thermal comfort following these biggest responders.[17] Moreover, Nakamura and colleagues[18,19] demonstrated that in the cold humans preferentially maintain a warm trunk and in the heat preferentially cool the head. However, of all regions the head (face, scalp and neck) appears most promising as a behavioral initiator given that this region: i) possesses greater thermosensitivity per unit area than other body parts,[20] ii) is responsible for a strong drive for corrective behavior,[18,19] and iii) is (at least partially) uncovered in most circumstances and thus, is available for intervention. *Therefore, the aims of this study were to evaluate if peripheral temperatures are capable of modulating exercise behavior in the cold, and to identify if local head temperature can modify this behavior.*

Materials and methods

Experimental overview

Eight males completed 3 trials each consisting of 30 minutes of self-paced cycling exercise on an ergometer in an environmental chamber at ~6°C. Participants were instructed to cycle to achieve and maintain thermal comfort for the duration of the trial.[8] On one occasion, participants wore only shorts and shoes without head manipulation (Control), whereas on 2 other occasions their head was either warmed (Warming) or further cooled (Cooling). Trials were conducted at the same time of day, separated by a week and randomized. Additionally, all trials were completed during the New Zealand autumn (mean ± SD outdoor daytime temperature of 14.6 ± 4.1°C).

Participants

Eight healthy and recreationally active males volunteered to participate in this study. Their characteristics were (mean ± SD): age 24 ± 3 y, height 1.8 ± 0.1 m, weight 82 ± 11 kg, body surface area (BSA) 2.03 ± 0.19 m^2 and percent body fat 10 ± 3%. The study was approved by the Massey University Human Ethics Committee and performed in accordance with the 1975 Helsinki Declaration, with each participant providing informed, written consent.

Preliminary session

Approximately one week before the first experimental trial, participants reported to the laboratory for anthropometric measurements and a familiarization to the experimental protocol. The cycle tests were conducted in a cold environment (5.6 ± 0.6°C, 45 ± 8 % r.h.), with exercise being performed on a mechanically-braked cycle ergometer (Monark 818, Varberg, Sweden) at an exercise work rate that was freely adjustable based on the resistance of the braking pendulum and the pedal rate of each individual (self-paced). All subsequent exercise tests were completed on the same cycle ergometer with the same self-selected preferences for seat and handlebar height. The preliminary session required subjects to cycle for 15 minutes and familiarize themselves with the cycle ergometer (both resistance and cadence adjustment) to achieve thermal comfort while fully instrumented (see below).

Experimental procedure

Approximately seven days following the preliminary session, participants arrived to complete one of 3 trials: during the Control trial the head was left uncovered whereas during the Warming trial the head was heated (55°C) via a liquid conditioned hood (Delta Temax Inc., Canada), while during the Cooling trial a fan (Fantech Pty Ltd., China) was placed to blow the cold ambient air at a speed of 20 km·h^{-1} toward the head. In the Warming trial a silicone swim cap (Aqualine, China) was worn on top of the hood to ensure maximal compression of the tubes being pressed to the head. Although participants could not be blinded to the experimental manipulation, they were unaware of the research aims and hypotheses.

All participants arrived at the laboratory having refrained from strenuous exercise, alcohol and caffeine for a period of 24 hours. To minimize variations in pre-exercise muscle glycogen content and hydration status, participants were required to complete a

24 hour diet and physical activity log before each trial and asked to replicate this for subsequent trials. Participants were not allowed to drink during the trials and wore only shorts and training shoes. Upon arrival to the laboratory, participants voided, measured their nude body weight, and then self-inserted a rectal thermistor (Mon-a-therm, Tyco Healthcare Group, USA) 10 cm beyond the anal sphincter for the measurement of rectal temperature (T_{Rec}). A heart rate monitor and skin thermistors were applied, resting heart rate was recorded, and participants then entered the environmental chamber for completion of the experimental trial. Upon completion of exercise, the participants were promptly removed from the chamber, and the heart rate monitor, skin thermistors and rectal thermistor were removed. Nude body weight was measured again following towel drying. The duration of the procedures from the initial nude body weight to the final nude body weight was ~60 minutes.

Cycling exercise

When participants entered the environmental chamber, 5 minutes was allowed for full instrumentation and to adjust the cycle ergometer to their preferences. During the Warming and Cooling trials, the hood and fan were placed, respectively, but not switched on until exercise commencement. Upon commencement of the 30 minutes, the cycle ergometer had no resistance on the flywheel. Participants were instructed to cycle to attain and maintain thermal comfort by continually being allowed to adjust their cadence and load of the cycle ergometer, and once thermal comfort was achieved participants continued to adjust their power output so that they could maintain thermal comfort.

Measurements

The subject's height and weight were measured using a stadiometer (Seca, Bonn, Germany; accurate to 0.1cm and scale (Jadever, Taiwan; accurate to 0.01kg), from which BSA was estimated.[21] Seven site skinfold thickness was determined using a Harpenden Skinfold Caliper (Baty International, West Sussex, UK) at the chest, axilla, triceps, subscapular, abdomen, supraill-iac, and thigh, and subsequently, percent body fat[22] was estimated from body density.[23]

Heart rate and work completed were acquired (Powerlab, ADInstruments, Australia) and recorded through Chart (Chart5, ADInstruments, Australia) via modification of the cycle ergometer which had a magnet placed on the flywheel of the Monark to measure revolutions per minute. A channel was then set up to calculate power using the measured cadence and load on the flywheel. A channel for work rate was then developed by incorporating the variables of power and time. Heart rate was monitored using a Polar heart rate monitor (Polar Vantage XL, Polar Electro). Expired gases were collected for 1 minute via standard Douglas bags every 5 min. The expired gases were analyzed for CO_2 and O_2 concentrations (AEI Technologies, USA) and volume (dry gas meter, Harvard, UK), and values were converted to STPD. The rate of O_2 uptake (VO_2) and respiratory exchange ratio (RER) were used to calculate the rate of metabolic heat production (in W/m^2) as follows[24]: $M = (352\ (0.23\ RER + 0.77)\ VO_2/BSA)$-rate external work.

Six calibrated surface thermistors (Grant Instruments Ltd., Cambridgeshire, UK; accurate to 0.2°C) were secured in place with Transpore Surgical Tape (3 M Healthcare, St. Paul, Minnesota, USA) to the chest, thigh, leg and arm on the right side of the body for determination of mean weighted skin temperature.[25] The remaining 2 surface thermistors were placed on the middle of the forehead and on the back of the neck for determination of head temperature (T_{Head}, mean of head and neck temperature).

Ratings of perceived exertion were measured on the 15-point Borg scale (from 6 to 20; [26]). Thermal discomfort and thermal sensation were determined on 4 [from 1 (comfortable) to 4 (very uncomfortable)] and 7 [from 1 (cold) to 7 (hot)] point scales.[27]

Data and statistical analyses

Data are reported at pre-exercise, every 5 min of exercise, as well as every minute during the first 5 min of exercise for rectal temperature, mean skin temperature, mean head temperature, and work completed. This latter approach allowed for examination of the effect of acute differences in peripheral temperature on thermal behavior. Work completed, the rate of metabolic heat production, and rectal temperature data were also analyzed as the change (Δ) from the preceding time point in order to examine dynamic changes occurring in these variables during exercise. One subject was unable to achieve thermal comfort in any of the trials. This may have been due to this subject not understanding the experiment, even despite thorough familiarization. Nevertheless, this subject's data has been not included in the analyses, resulting in an n = 7.

Total work completed during each trial was analyzed using a one-way repeated measures analysis of variance (ANOVA). All other data were analyzed using 2-way (main effects: trial × time) repeated measures ANOVA. In all instances, *post hoc* Holm-Sidak adjusted pair-wise comparisons were made where appropriate. Data were analyzed using Prism software (Version 6, GraphPad Software Inc., La Jolla, CA, USA). *A priori* statistical significance was set at $P \leq 0.05$ and actual p-values are reported where possible. All data are reported as mean ± SD.

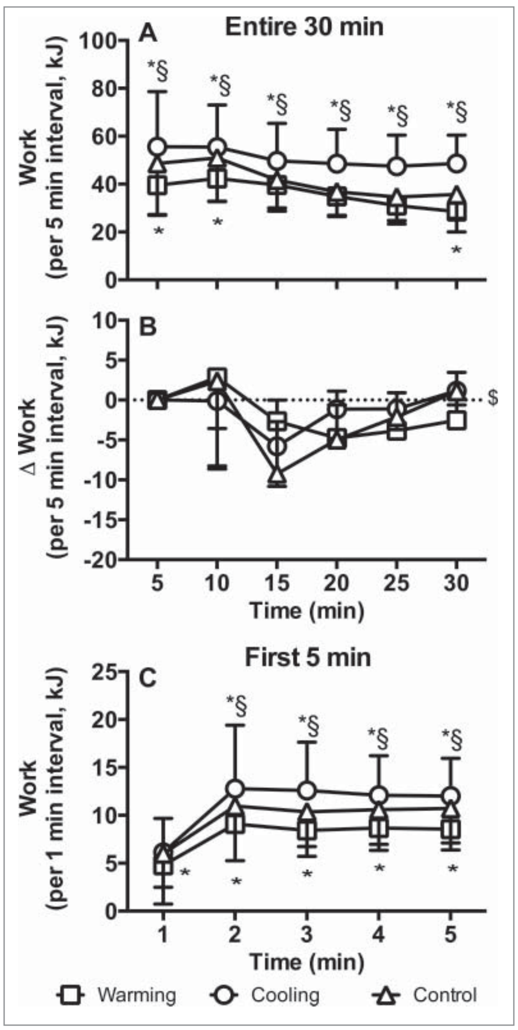

Figure 1. Work completed during every 5 min interval (A), the change (Δ) in work completed from the preceding 5 min interval (B), and work completed every minute during the first 5 min of exercise (C) during the Warming, Cooling, and Control trials. * Different from Control trial ($P \leq 0.05$), § Different from Warming trial ($P \leq 0.04$), $ Main effect of time ($P < 0.01$).

Results

Thermal behavior

Total work completed was higher ($P \leq 0.04$) in the Cooling trial (291 ± 97 kJ) compared to both the Control (241 ± 77 kJ) and Warming (210 ± 49 kJ) trials, which were not different ($P = 0.25$). Upon closer examination, however, work completed over the first 10 min of exercise was different between all trials ($P = 0.01$, Fig. 1A). These differences were observed as early as the second minute of exercise ($P = 0.04$, Fig. 1C). Importantly, changes in work completed over time did not differ between trials ($P = 0.15$, Fig. 1B). The rate of metabolic heat production mirrored work completed, with differences observed between all trials early during the exercise ($P = 0.03$, Fig. 2A), with no differences over time between trials ($P = 0.99$, Fig. 2B).

Body temperatures

Pre-exercise rectal temperatures were lower ($P<0.01$) during the Warming trial (37.0 ± 0.3°C) compared to both the Cooling (37.2 ± 0.4°C) and Control (37.2 ± 0.3°C) trials, which were not different ($P = 0.70$).

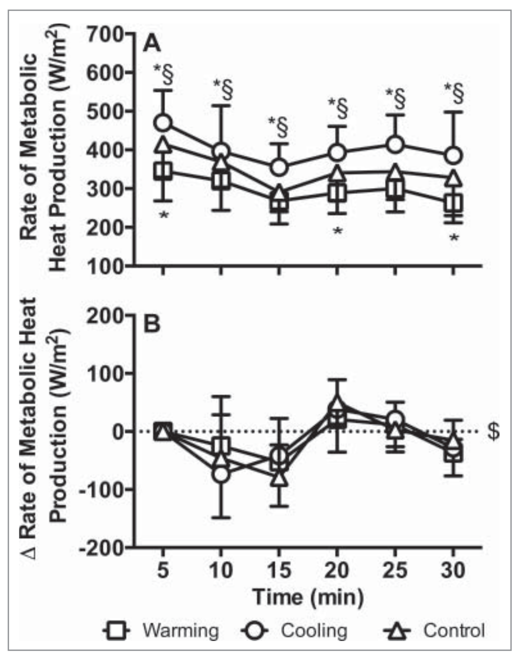

Figure 2. The rate of metabolic heat production every 5 min (A) and the change (Δ) in the rate of metabolic heat production from the preceding time point (B) during the Warming, Cooling, and Control trials. * Different from Control trial ($P \leq 0.04$), § Different from Warming trial ($P < 0.01$), $ Main effect of time ($P < 0.01$).

These differences persisted throughout the 30 min of exercise (P = 0.02, Fig. 3A), but changes occurring over time were not different between trials (P = 0.07, Fig. 3B), which also held true for the first 5 min of exercise (P ≥ 0.26, Figs. 3E and 3F). Pre-exercise mean skin temperatures were not different (P ≥ 0.63) between trials (mean: 26.7 ± 0.8°C). However, mean skin temperatures decreased over time during exercise (P < 0.01), the magnitude of which differed by trial (P < 0.01, Fig. 3C), differences that were observed as early as the first minute of exercise (P ≤ 0.02, Fig. 3G). Pre-exercise mean head temperatures were highest (P < 0.01) in the Warming trial (29.6 ± 1.2°C) compared to the Cooling (28.1 ± 1.6°C) and Control (27.9 ± 1.3°C) trials, which were not different (P = 0.63), and these differences persisted throughout the 30 min of exercise (P < 0.01, Figs. 3D and 3H).

Thermal perceptions

Pre- and throughout exercise, whole-body thermal discomfort was not different between trials (P=0.09,

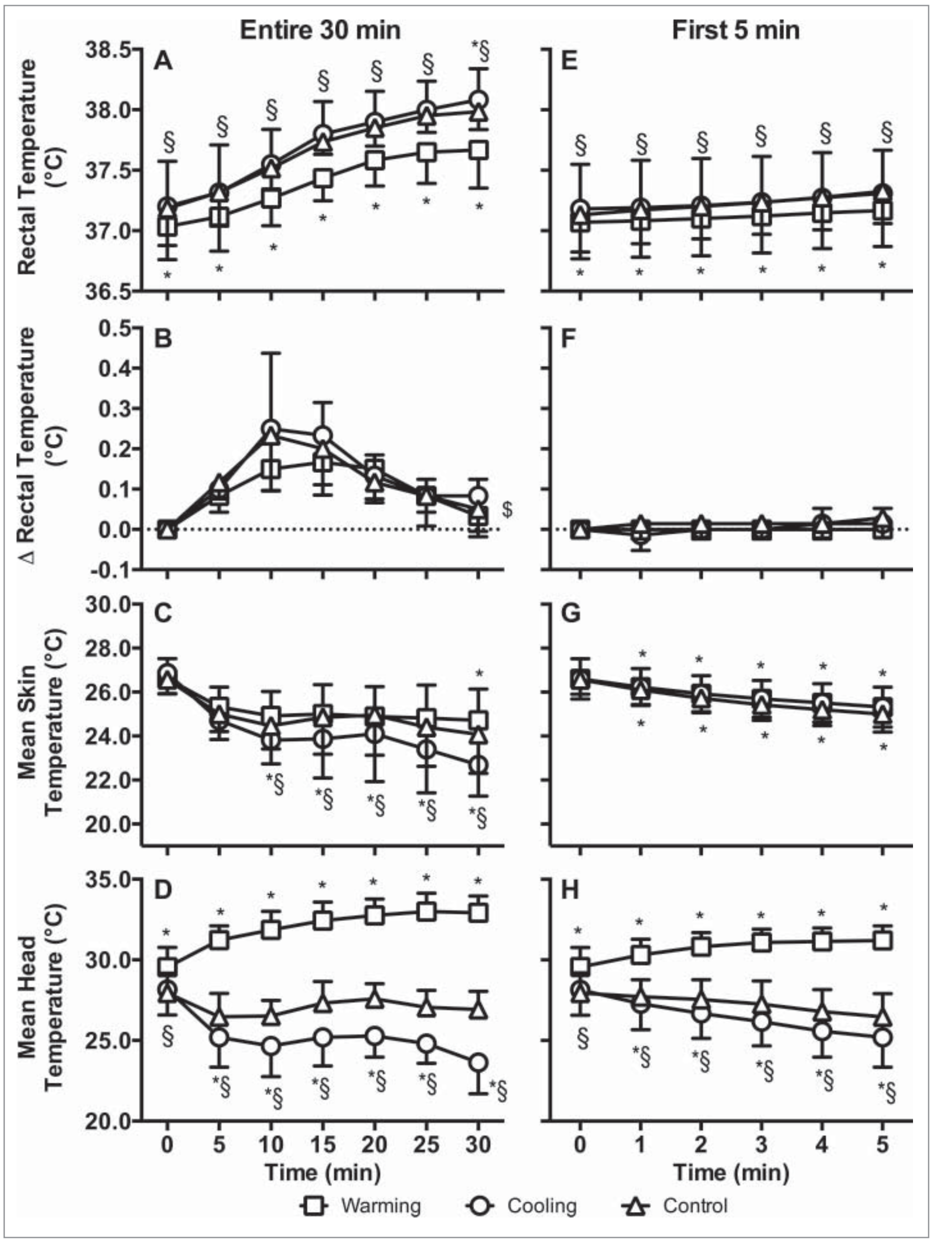

Figure 3. Rectal temperature (A, E), the change (Δ) in rectal temperature from the preceding time point (B, F), mean skin temperature (C, G), and mean head temperature (D, H) every 5 min during exercise (on left) and every minute during the first 5 min of exercise (on right) during the Warming, Cooling, and Control trials. * Different from Control trial (P≤0.04), § Different from Warming trial (P≤0.01), $ Main effect of time (P<0.01).

Fig. 4A). Pre-exercise head thermal discomfort was greatest in the Cooling trial (P < 0.01), and lowest in the Warming trial (P < 0.01, Fig. 4C). These differences persisted through the first 5 min of exercise (P ≤ 0.05), after which head thermal discomfort was not different between the Control and Warming trials (P ≥ 0.13), both of which were generally more comfortable than that occurring during the Cooling trial (Fig. 4C). Pre-exercise whole-body thermal sensation was cooler in the Cooling and Control trials, compared to the Warming trial (P < 0.01, Fig. 4B). However, during exercise whole-body thermal sensation was not different between the Warming and Control trials (P ≥ 0.08), both of which were generally perceived as warmer than during the Cooling trial (Fig. 4B). Head thermal sensation was different between trials pre- and throughout exercise (P<0.01, Fig. 4D).

Discussion

The main findings of the current study are that exercise behavior in the cold: i) is primarily initiated and maintained by low peripheral (skin) temperatures and negative thermal perception, while central (core) temperature remains within the normothermic or even hyperthermic range, ii) can be modulated by head-warming and -cooling as early as the first and second minutes, respectively, at a time when central (core) temperature is not different and unchanged. This behavior is most likely driven through an effect on thermal perception.

Can peripheral temperatures modulate behavior?

When placed into a cold (∼6°C) environment wearing only shorts, body heat will be lost to the environment, autonomic cold-defense responses will be initiated as hypothermia develops, and thermal discomfort will increase.[28] However, when allowed to behave – in this study voluntarily producing endogenous heat – it allows an individual to prevent hypothermia and permits the maintenance of thermal comfort. It has been demonstrated that exercise can be a thermal behavior[7,8] as it establishes a preferred condition for heat exchange and optimizes thermal comfort.[1,5] The initiation of this behavior has been shown to be primarily driven by changes in skin temperature both at rest[29-31] and during exercise,[15,16,32] although this notion has been challenged during exercise in the cold.[8]

The present results demonstrate that the temperature of the skin is an important input for the initiation of thermal behavior during exercise in the cold. At rest our participants were 'normothermic' (≥ 37.0°C)

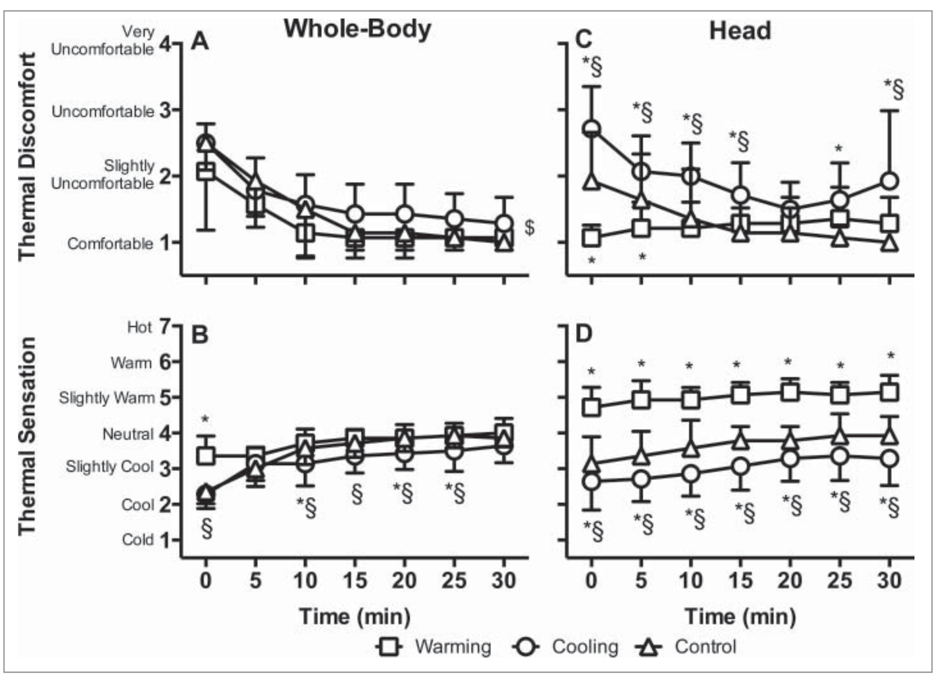

Figure 4. Thermal discomfort (A, C), and thermal sensation (B, D) of the whole-body (on left) and head (on right) every 5 min during exercise during the Warming, Cooling, and Control trials. * Different from Control trial (P≤0.05), § Different from Warming trial (P≤0.05), $ Main effect of time (P<0.01).

yet in response to cool skin temperatures (<27°C) (Fig. 3C) they began cycling to increase their rate of metabolic heat production (Fig. 2A), in an attempt at restoring thermal comfort (Fig. 4A). Moreover, participants had achieved thermal comfort by 10 ± 7 min (i.e. <2 = slightly uncomfortable, Fig. 4A) yet they continued to exercise for the 30 min duration despite a relative hyperthermia (i.e., T_{Rec} approaching 38.0°C and ΔT_{Rec} of +1.0°C), while skin temperatures remained below 26°C, a finding that adds further support to the importance of peripheral temperatures.

Can head temperatures modulate behavior?

When compared with the control condition, participants decreased (with head-warming) and increased (with head-cooling) their work rate after only 1 and 2 minutes of exercise, respectively (Fig. 1C), differences that persisted for the first 10 min (Fig. 1A). However, it appears that this initial behavior (≤ 5 min) to augment or reduce metabolic heat production was important as changes over time in work completed (Fig. 1B), metabolic heat production (Fig. 2B) and core temperature (Fig. 3B) were not different between trials. This observation that the thermal status of the body upon commencement of exercise strongly influences behavior supports our previous work.[15,16] This finding also suggests that the head region is capable of driving thermal behavior, translating observations made by Nakamura and colleagues,[18,19] which demonstrated that the head region plays a relatively large role in dictating thermal perceptions. These findings also support our previous work that head heating and cooling is capable of modulating thermal behavior during exercise in the heat.[16]

Does comfort drive thermal behavior?

Thermal discomfort is often considered to provide the motivation for thermal behavior.[27,33] We have experimentally confirmed this during an exercise in the heat model of thermal behavior in humans.[16] The present study extends these findings by highlighting the importance of local thermal discomfort as a modulator of thermal behavior during exercise in the cold. For instance, whole-body thermal discomfort was not different between the trials (Fig. 4A), while head thermal discomfort differed during the early stages of exercise (Fig. 4C). At this time exercise work rate (Fig. 1C), and thus the rate of metabolic heat production (Fig. 2A), was elevated in proportion to the magnitude of head thermal discomfort. The mechanism for this remains unclear. However, it is likely that in the present experimental paradigm TRP channel-activated cool-specific thermoreceptors projected the intensity of whole-body cold (Figs. 3C and 4B) to the posterior insula that was then conveyed as a state of whole-body thermal discomfort (Fig. 4A). This likely occurred in parallel with inputs from the head, as evidenced by the ability to discriminate thermal sensation of the whole-body versus the head region (Fig. 4B vs. 4D). Interestingly, the anterior insula, where emotional whole-body homeostatic behaviors, including thermal behavior, are controlled[34] appears to have weighted signals from the head region more strongly when thermal behavior was initiated. As introduced above, this conclusion is supported by data indicating the head region is more perceptually sensitive to changes in temperature than other regions.[18-20]

Considerations

While many of our results are in agreement with those previously of Caputa and Cabanac,[8] our interpretation remains different as these authors concluded that "increased motivation for muscular activity in a cold environment appears to be governed chiefly by brain temperature." However, this was based on the premise that they were comparing whether it was trunk (esophageal) or brain (tympanic) temperatures being more strongly related to self-selected work rate (thereby ignoring peripheral/skin temperatures). Notably, this proposition arose during their series of experiments[35,36] fundamentally devoted to selective brain-cooling, a topic that is beyond the current discussion (see ref. 38), as is whether tympanic temperature is a valid index of brain temperature (see ref. 39). While it is acknowledged that our use of rectal temperature to approximate the body's core temperature is not without limitation,[40] in the absence of a direct measure of hypothalamic temperature our conclusions likely hold true no matter which index of core temperature one wishes to choose.

It is noteworthy that contrary to our expectations, mean skin temperature was altered by our head-cooling (−0.6±0.5°C) and -warming (+0.3±0.4°C) interventions when compared to Control. Conceivably these differences could have contributed to the behaviors observed, however the magnitude of change for

T_{Head} (−1.5±1.3°C and +3.1±1.1°C, respectively) was considerably greater and is further supported by local (head) thermal perceptions (Figs. 4C and D). Nevertheless, both measures can be classed as peripheral signals, and therefore the contention remains that in the present study the peripheral (skin) temperatures represented both the feedforward and feedback signal for motivated and regulated behavior.[13]

Conclusions

The present study has shown that in order to achieve and maintain thermal comfort in the cold, low peripheral (skin) temperatures and associated thermal perceptions are the primary input signal to motivate behavior (exercise), despite a normothermic central (core) temperature, and this behavior - to continue generating metabolic heat - is maintained despite a relative hyperthermia even once thermal comfort is attained. Moreover, the rate of metabolic heat production can be modulated by manipulating head temperature and related alliesthesia.

Abbreviations

ANOVA	Analysis of variance
BSA	Body surface area
M	Rate of metabolic heat production
RER	Respiratory exchange ratio
SD	standard deviation
STPD	Standard temperature pressure dry
T_{Rec}	Rectal temperature
VO_2	Oxygen uptake
Δ	Change

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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