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Do greater rates of body heat storage precede the accelerated reduction of self-paced exercise intensity in the heat?

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Abstract

Aim: To re-evaluate the previous hypothesis that greater reductions in self-paced exercise intensity in the heat are mediated by early differences in the rate of body heat storage (S).
Methods: Eight trained volunteers cycled in 19˚C/1.8kPa (COOL), 25˚C/1.2kPa (NORM), and 34˚C/1.6kPa (HOT), while maintaining an RPE of 16. Potential differences in S following the onset of exercise were assessed by comparing rates of esophageal temperature change ($\Delta T_{es}/\Delta t$); a traditional two-compartment thermometric model (S_{therm}) of changes in rectal (T_{re}) and skin (T_{sk}) temperature; and partitional calorimetry (S_{cal}).
Results: After 15-min of exercise, workload decreased more (*P*=0.03) in HOT vs. COOL, resulting in a shorter time (HOT:40.7±14.9-min; COOL:53.5±18.7-min; *P*=0.04) to 70% of initial workload. However, there were no preceding differences (P=0.18) in $\Delta T_{es}/\Delta t$ between conditions. S_{therm} values were different (P<0.05) between HOT and COOL during the first 5-min of exercise, primarily due to negative S_{therm} values (-32±15kJ·min^{-1}) in COOL, which according to partitional calorimetric measurements, required improbably high (~56kJ·min^{-1}) rates of evaporation when no sweating on the back or thigh was observed until after 7.6±1.5-min and 4.8±1.7-min of exercise, respectively. S_{cal} values in the first 5-min of exercise confirmed S were actually positive in COOL (+21±8kJ·min^{-1}) and not negative. Different S_{therm} values following the onset of exercise at different environmental temperatures are simply due to transient differences in the rate of change in T_{sk}.
Conclusion: Reductions in self-paced exercise intensity in the heat are not mediated by early differences in S following the onset of exercise.

Keywords: Core temperature; Exercise performance; Partitional calorimetry; Rate of perceived exertion; Thermoregulation

Abbreviations

A_r/A_D: Effective radiant surface area (ND)
BF: biceps femoris
A_D: Body surface area (m^2)
C: Convective heat exchange (W/m^2)
C_{res}: Convective heat exchange via respiration (W/m^2)
E_{sk}: Evaporative heat loss from the skin (W/m^2)
E_{res}: Evaporative heat loss via respiration (W/m^2)
E_C: Caloric equivalent of carbohydrates (kJ/LO^2)
E_F: Caloric equivalent of lipids (kJ/LO^2)
EMG: Electromyography (% of initial EMG)
ε: Area-weighted emissivity of the skin (ND)
f_{cl}: Area-weighted clothing factor (ND)
GM: Gluteus maximus
h: Combined heat transfer coefficient (W·m^{-2}·°C^{-1})
h_c: Convective heat transfer coefficient (W·m^{-2}·°C^{-1})
h_r: Radiative heat transfer coefficient (W·m^{-2}·°C^{-1})
H_{prod}: Rate of metabolic heat production (W/m^2)
iEMG: Integrated electromyography (% of initial iEMG)
LG: Lateral gastrocnemius
LSR_{back}: Local sweat rate on the lower back (mg·cm^{-2}·min^{-1})
LSR_{thigh}: Local sweat rate on the thigh (mg·cm^{-2}·min^{-1})
M: Metabolic energy expenditure (W/m^2)
PAR-Q: Physical Activity Readiness Questionnaire
P_a: Ambient water vapor pressure (kPa)
R: Radiant Heat exchange (W/m^2)
R_{cl}: Thermal resistance of clothing (m^2·°C·W^{-1})
RER: Respiratory exchange ratio (ND)
RPE: Rating of perceived exertion
S: Rate of body heat storage (kJ/min)
S_{cal}: Rate of body heat storage measured with partitional calorimetry (kJ/min)
S_{therm}: Rate of body heat storage estimated with a traditional 2-compartment thermometry model (kJ/min)
σ: Stefan-Boltzmann constant (5.67·10^{-8}W·m^{-2}·°C^{-4})
T_a: Ambient air temperature (°C)
ΔT_b: Change in mean body temperature (°C)
T_{cl}: Temperature of the clothing (°C)

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T_{es}:	Esophageal temperature (°C)
$\Delta T_{es}/\Delta t$:	Rate of esophageal temperature change (°C/min)
T_o:	Operative temperature (°C)
T_r:	Mean radiant temperature (°C)
T_{re}:	Rectal temperature (°C)
T_{sk}:	Mean skin temperature (°C)
VO_{2peak}:	Peak rate of oxygen consumption (L/min)
VO_2:	Rate of oxygen consumption (L/min)
v:	Air velocity (m/s)
VL:	vastus lateralis
W:	Rate of external work (W/m^2)
W_{peak}:	Peak rate of external work (Watts)

Introduction

In a highly cited study, Tucker et al. (2006) reported that catastrophic levels of hyperthermia are avoided during self-paced exercise in the heat via an anticipatory (i.e. feed-forward) reduction of power output, motor unit recruitment (and therefore metabolic heat production), which is subconsciously mediated by the rate of body heat storage (S) during the first 4 min of exercise. In a later article, we argued against this interpretation, since a theoretical heat balance assessment demonstrated that their reported S values following the onset of exercise were not possible (Jay and Kenny, 2009). We proposed that these values were a result of the erroneous nature of the two-compartment thermometric model employed that uses minute-by-minute changes in rectal temperature (T_{re}) and mean skin temperature (T_{sk}) to estimate S (Stolwijk and Hardy 1966; Horstman and Horvath 1972; Vallerand 1992; Snellen 2000; Jay et al. 2007). Specifically, it is possible that early changes in T_{sk}, which represents the body "shell", may exaggerate any potential differences in S during the early stages of exercise between hot and cold environments; and changes in T_{re}, which represent the body "core," may not accurately reflect any changes in S following the start of exercise due to its well documented time lag (Jay and Kenny 2009). If this is the case, then the conclusion presented in the original study by Tucker et al. (2006) - that differences in S between hot and cool conditions only occur during the first 4 min of exercise, with no differences observed thereafter (when changes in self-regulated power output then occur) - may be the result of erroneous "core" to "shell" weightings used to estimate S.

In the absence of whole-body direct calorimetry, a different thermometric approach is required to re-evaluate whether S plays a potential role in a feedforward regulatory model of self-paced exercise. Firstly, any early changes in T_{sk} can likely be discounted since they do not contribute to the description of changes in heat storage during the first 10 min of exercise (Jay et al. 2007). Secondly, a temperature probe placed in the esophagus (T_{es}) should provide a more responsive indicator of early changes in S than T_{re}. Since the tissue temperature changes occurring in the body as a consequence of the large rates of initial heat storage will primarily be centralized around the active musculature, which is the main source of exercise-induced thermogenesis (Jay et al. 2007), temperature of out-flowing blood from active muscle and returning to the heart should therefore closely resemble T_{es} - a measure that has been shown to approach aortic blood temperature with only a minor lag of 80 to 160 s during high rates of changing blood temperature (Cooper and Kenyon 1957; Shiraki et al. 1986). Therefore, while replacing T_{re} with T_{es} as a representative of the body "core" in the conventional two-compartment thermometry model probably does not yield precise absolute values for S during the early stages of exercise, it stands to reason that different rates of change of T_{es} ($\Delta T_{es}/\Delta t$) will occur in parallel to proportional physiologically significant differences in S with a minimal time delay.

The primary purpose of the present study was to re-evaluate the potential role of early changes in S in an anticipatory feedforward regulatory model of self-paced exercise (Tucker et al. 2006). Previous procedures were replicated and S was assessed using a range of methods in subjects self-regulating their cycling power output at a fixed rating of perceived exertion (RPE) (Borg 1982) in a cool, neutral and warm environment. Specifically we sought to determine if subjects only show different $\Delta T_{es}/\Delta t$ during the early stages of exercise, indicative of different S, with similar $\Delta T_{es}/\Delta t$ occurring thereafter irrespective of environmental conditions due to a reduction in power output that is greatest in the hottest environment. A secondary purpose of the present study was to assess whether previous conclusions related to role of S were dependent upon the weighting coefficients of the "core" and "shell" components of the two-compartment thermometry model used to estimate S, and to determine how the S values previously reported in cooler environments using thermometry during the early stages of exercise compare to S values measured using partitional calorimetry. It was hypothesized that: 1) $\Delta T_{es}/\Delta t$ would be similar between cool, neutral and hot conditions throughout self-regulated exercise at a fixed RPE; 2) different "core" and "shell" weighting coefficients employed in the two-compartment thermometry model alter the conclusion of different S values between conditions during the early stages of exercise; and 3) S values measured with partitional calorimetry during the early stages of self-regulated exercise in cooler environments are positive and not negative.

Methods

Participants

A power calculation using esophageal temperature data from pilot studies was performed using the calculated effect size of 1.2, an $\alpha = 0.05$, and a $\beta = 0.2$ which determined that eight participants were required demonstrate a difference in ΔTes/Δt. Therefore, 8 endurance-trained

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volunteers (seven males, one female) participated in this study (VO_2peak: 59.3±6.3 mL·kg^{-1}·min^{-1}; Wpeak: 355±49 W, 5.0±0.6 W·kg^{-1}; Age: 26.0±5.5 y; Mass: 72.0±7.3 kg; Height: 1.88±0.12 m^2). Prior to experimentation, all participants provided written informed consent, and completed a Physical Activity Readiness Questionnaire (PAR-Q) as well as an American Heart Association/American College of Sports Medicine Health/Fitness Facility Pre-participation Screening Questionnaire. The experimental protocol was approved by the University of Ottawa Research Ethics Committee, and conformed to the guidelines set forth in the Declaration of Helsinki.

Preliminary trials

During the first visit to the laboratory, each participant performed an incremental exercise test to exhaustion on an upright cycle ergometer in order to determine their peak rate of oxygen consumption (VO_2peak) and peak external workload (W_{peak}): Following a 10-min warm-up the incremental protocol began at an external workload of 80 W, which was then increased by 20 W/min until volitional exhaustion. This test was conducted in accordance with the guidelines of the Canadian Society for Exercise Physiology (CSEP 1996). The second visit involved familiarization with the fixed RPE protocol: In the familiarization trial, participants commenced cycling at a workload of 100 W, which was subsequently increased by 10 W every 5 min until an RPE of 16 (corresponding to a rating between 'hard' and 'very hard' on the Borg scale) was reached. The participants were then instructed to adjust their workload to maintain this sensation for an additional 10 min. This approach allowed the participants to become familiar with the Borg scale and the sensation associated with the target RPE. Thus for each participant the initial workload for each experimental trial was established as the average workload during the final 10 min of the familiarization trial.

Experimental protocol

In separate sessions, experimental trials were performed in hot (HOT: 33.7±0.8°C, 1.6±0.5 kPa), thermoneutral (NORM: 25.2±0.7°C, 1.2±0.5 kPa), and cool (COOL: 19.3±1.4°C, 1.8±0.5 kPa) conditions, with trial order counterbalanced across participants. Levels of humidity were chosen to elicit a similar absolute skin-air vapor pressure gradient at each ambient air temperature, and to thereby produce a similar capacity for evaporation. In the 24 h prior to each experimental trial, participants were asked to avoid alcohol, caffeine, and strenuous exercise. Additionally, they were asked to consume a light meal and 500 ml of water ~2 h prior to arrival at the laboratory. Upon arrival, the participants voided their bladders providing a urine sample to ensure hydration and changed into a standardized clothing ensemble consisting of cotton shorts, cotton socks, and cycling shoes. Trials would be postponed and rescheduled if urine specific gravity measured using a clinical refractometer (Reichert TS 400, Depew, NY, USA) was greater than 1.020. Following a 45-min instrumentation period, a 10-min warm-up with the cycle ergometer set at 125 W was performed. Following this, the participants entered the laboratory and rested quietly in a seated position on the ergometer while instrumentation was completed. A 20-min baseline data collection period preceded exercise, during which time a body mass measurement was taken 5 min before exercise with a platform scale accurate to the nearest ± 2 g (Combics 2; Sartorius, Mississauga, ON, Canada) with sensor cables taped off to a nearby equipment cart. Immediately prior to the start of exercise participants were reminded to maintain a RPE of 16 by adjusting the workload. The ergometer was set to a cadence-independent mode, so that a preferred cadence could be maintained for any self-selected workload. The participants then began cycling, facing a mechanized fan providing an air velocity of 1.7±0.4 m/s. Participants were blinded to physiological and performance feedback throughout all trials. Exercise continued until workload declined to <70% of the initial 5-min average. A final body mass measurement was taken immediately upon the completion of exercise, prior to subjects drying off, and with sensor cables secured to an adjacent table at exactly the same point as during the pre-exercise body mass measurement.

Measurements

Ambient conditions: Dry-bulb temperature and absolute humidity were measured every 5 s using a dew point mirror (473 RH Systems, Albuquerque, NM, USA). Air velocity was measured with a hot wire anemometer (HHF42, Omega Engineering, Stamford, CT, USA).

Indirect calorimetry: Participants were equipped with a mouthpiece and nose clip, and were instructed to breathe normally at all times. Expired gases were analyzed breath-by-breath throughout exercise using a metabolic cart (Vmax Encore, CareFusion, Yorba Linda, CA, USA).

Thermometry: Core temperature was measured continuously in the rectum and the esophagus using general purpose pediatric T-type (copper/constantan) thermocouple probes (Mon-a-therm®, Mallinckrodt Medical, St. Louis, MO, USA). Rectal temperature (Tre) was measured at a depth of 12 cm beyond the anal sphincter. Esophageal temperature (T_{es}) was measured at a maximum depth of 40 cm, estimated to be at the level of the left ventricle (Mekjavic and Rempel 1990). Skin temperature was measured at four sites on the left side of the body (chest, triceps, thigh, and calf) using T-type thermocouples integrated into heat flux sensors (Concept Engineering, Old Saybrook, CT, USA), which were secured to the skin with surgical tape (Transpore®, 3M, London, ON, Canada). Mean skin temperature (T_{sk}) was estimated using a weighted average of four sites in accordance with

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Ramanathan (1964): chest 30%, triceps 30%, thigh 20%, and calf 20%. Thermometric measurements were sampled every 5 s (NI cDAQ-91722 module, National Instruments, Austin, TX, USA) and displayed in real-time on a desktop computer using customized LabView software (v7.0, National Instruments, Austin, TX, USA).

Local sweat rates: were measured on the lower back (LSR_{back}) and thigh (LSR_{thigh}) on the right side of the body using the ventilated capsule technique. These sites were chosen as they demonstrate the relatively early onset times for thermoregulatory sweating (Cotter and Taylor, 2005). Anhydrous air was supplied to each 4.1-cm^2 capsule at a constant flow rate of 1.80 L min^{-1} (Omega FMA-A2307, Omega Engineering, Stamford, CT, USA). Capsules were secured to the skin using skin glue (Collodion USP MD0002, Mavidon, Lake Worth, FL, USA) and surgical tape. The temperature and humidity of effluent air were measured every 5 s using factory-calibrated capacitance hygrometers (HMT333, Vaisala, Vantaa, Finland). Local sweat rate was then calculated as the product of absolute humidity and flow rate, and expressed relative to the area under the capsule in milligrams per square centimeter per minute ($mg \cdot cm^{-2} \cdot min^{-1}$).

Electromyography (EMG): Surface EMG data were collected from the right vastus lateralis (VL), gluteus maximus (GM), biceps femoris (BF), and lateral gastrocnemius (LG) using bipolar, preamplified surface electrodes connected to an external amplifier system (Delsys Bagnoli-8, Natick, MA, USA). The recording sites were prepared and the electrodes were attached using double-sided adhesive strips, and secured using surgical tape. A grounding electrode (Kendall Q-Trace 5400, Covidien Inc., Mansfield, MA, USA) was placed over the participant's right anterior superior iliac spine.

Unfiltered raw EMG were digitally sampled at 1 kHz (National Instruments PCI-6052E, Austin, TX, USA) for the first 10 s of each minute during cycling and EMG values for all four muscles were calculated from a time window corresponding to 10 cycles within each 10-s time block irrespective of cadence. The magnitude of the integrated EMG (iEMG) was calculated for each muscle by numerically integrating the rectified EMG signal within the 10-cycle window on each trial. In order to quantify muscle output for the whole-leg (LEG) in a more holistic manner, LEG weighted average iEMG was calculated from the normalized iEMG and expressed as a percentage of initial LEG. The weightings used were: VL, 41%; GM, 28%; BF, 10%; LG, 21% (Ericson 1986). To normalize between testing sessions, iEMG was expressed as a value per unit of work (W) by dividing iEMG by the cycle ergometer power output observed at minute 5 in each session (see above). Initial iEMG was then calculated as the mean of iEMG at minutes 4, 5, and 6. For minutes 10, 15 and 20, iEMG values were calculated as the mean iEMG values from the preceding 5 minutes (i.e., 6-10, 11-15, 16-20), and expressed as a percentage of initial iEMG.

Calculations

Rate of heat storage (partitional calorimetry):

Calorimetric estimates of the rates of heat storage (S_{cal}) were calculated for NORM and COOL conditions according to the conceptual heat balance equation:

$$Scal = M - W - (C + R + E_{sk} + C_{res} + E_{res}) \; [W\,m^{-2}]$$

Metabolic rate (M) was calculated as:

$$M = VO_2 \bullet ((RER - 0.7 /0.3)\, e_c) + ((1.0 - RER / 0.3)\, e_f) / ((60)\, (A_D)) \bullet 1000 \; [W\,m^{-2}]$$

Where: VO_2 is the rate of oxygen consumption (L min^{-1}) ; RER is the non-dimensional respiratory exchange ratio; e_c and e_f are the energetic equivalents of carbohydrate (21.13 kJ L^{-1} O_2) and fat (19.62 kJ L^{-1} O_2), respectively; A_D is body surface area in m^2, estimated using the equation of DuBois and Dubois (1916). External workload (W) was measured using an electromagnetically-braked upright cycle ergometer (Ergo Race, Kettler, Ense-Parsit, Germany). The rate of metabolic heat production (H_{prod}) was calculated as the difference between metabolic rate and external workload (in W m^{-2}).

Combined respiratory heat exchange (H_{res}) via convection (C_{res}) and evaporation (E_{res}) was calculated as:

$$Cres + Eres = [0.0014 \bullet (H_{prod}) \bullet (34 - T_a)] + [0.0173 \bullet (Hprod) \bullet (5.87 - P_a)] \; [W\,m^{-2}]$$

Where: P_a is the ambient vapor pressure in kilopascals (kPa).

Heat exchange via convection (C) and radiation (R) was calculated as:

$$C + R = ((T_{sk} - T_o)) / (R_{cl} + 1 / (f_{cl} \bullet {}^{h})) [W\,m^{-2}]$$

Where: R_{cl} is the thermal resistance of clothing ($m^2 \bullet °C \bullet W^{-1}$), but was assumed to be negligible in the present study due to a minimal clothing ensemble; f_{cl} is the non-dimensional area-weighted clothing factor (assumed to be 1.0 with minimal clothing); h is the combined heat transfer coefficient ($W\,m^{-2} \bullet °C^{-1}$), which is the sum of the convective (h_c) and radiant (h_r) heat transfer coefficients (see below).

Operative temperature (T_o) was estimated as:

$$T_o = ((h_c \bullet T_a) + (h_r \bullet T_r)) / (h_r + h_c) [°C]$$

Where: Ta is ambient temperature (°C) and T_r is the radiant temperature (°C), assumed to be equal to T_a.

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Values for h_c and h_r were calculated as:

$h_c = 8.3v^{0.6}$ [$W\ m^{-2} \bullet °C^{-1}$]

$h_r = 4\varepsilon\sigma\ (A_r / A_D)\ [273.15 + ((T_{cl} + T_r) / 2)]^3$ [$W\ m^{-2} \bullet °C^{-1}$]

Where: v is air velocity ($m \bullet s^{-1}$); ε is the area-weighted emissivity of the skin, taken as 0.95; σ is the Stefan-Boltzmann constant ($5.67 \bullet 10^{-8}$ $W\ m^{-2} \bullet °C^{-4}$); A_r/A_D is the effective radiant surface area (ND), estimated to be 0.7 for a seated individual (Fanger 1970); and T_{cl} is the temperature of the clothing (°C), assumed to be equal to T_{sk}.

Evaporative heat loss was assumed to be negligible in NORM and COOL conditions until the onset of sweating. No estimate of evaporative heat loss and therefore Scal was made in HOT since sweating was evident prior to exercise.

Although estimated in $W\ m^{-2}$, all heat balance parameters were converted to $kJ\ min^{-1}$ ($1\ W = 0.06\ kJ\ min^{-1}$) to compare the present results to those of previous studies.

Rate of heat storage (thermometry): Minute-by-minute changes in mean body temperature (ΔT_b) were estimated using four different two-compartment thermometric models: T_{re}/T_{sk} (A) 0.66/0.34, (B) 0.79/0.21, (C) 0.90/0.10, and (D) 1.00/0.00. Thermometric estimates of heat storage (Stherm) were calculated as the product of body mass, an estimated average specific heat capacity of $3.47\ kJ \bullet kg^{-1} \bullet °C^{-1}$ for body tissue (Gephart and DuBois 1915), and ΔT_b. Values of Stherm using T_{re}/T_{sk} weighting coefficients of 0.79/0.21 were compared directly to S_{cal} during the first 5 min of exercise in COOL and NORM.

Statistical analysis

All data are reported as the mean ± standard deviation (SD) for each variable. Mean trial duration was analyzed using a one-way analyses of variance (ANOVA) employing the independent variable of ambient temperature (three levels: HOT, NORM, COOL). Since trial duration varied between subjects, analyses were performed for the first 20 min of exercise, which was the minimum trial duration for all participants. A two-way repeated measures ANOVA, with the independent factors of ambient temperature and time (four levels: Baseline, 10, 15, 20 min) were used to analyze the independent variables of percentage change in workload, $\Delta T_{es}/\Delta t$, $\Delta T_{sk}/\Delta t$, H_{prod}, S_{therm}, LSR_{back}, LSR_{thigh}, individual muscle iEMG, and whole-leg iEMG. S_{cal} values in each of the first 5-min of exercise were compared between NORM and COOL using a two-way ANOVA. A Greenhouse-Geisser correction was applied if assumptions of sphericity were not met. When a significant main effect was detected, individual differences were compared using the Holm-Bonferonni method. The probability of a Type I error was set at the 0.05 level. All statistical analyses were performed with SPSS 19.0 (SPSS Inc., Chicago, IL, USA).

Results

Trial duration

Mean trial duration was 53.5±18.7 min, 54.5±18.5 min, and 40.7±14.9 min for COOL, NORM, and HOT, respectively (Fig. 1A). Mean trial duration was significantly shorter in the HOT compared to the NORM and COOL condition ($P < 0.05$).

External workload

Changes in workload expressed as a percentage of the initial workload (i.e., at 5 min) are depicted in Fig. 1B. Initial workloads were not different between the COOL, NORM, and HOT (219±27 W, 224±35 W, and 219±35 W, respectively; $P>0.05$). However the reduction in workload was significantly greater in HOT compared to COOL after 15 min ($P<0.05$; Fig. 1B).

Rates of change of Esophageal and Skin temperatures

The rate of change of esophageal temperature ($\Delta T_{es}/\Delta t$) is shown in Fig. 2. $\Delta T_{es}/\Delta t$ changed significantly with exercise time ($P<0.001$), however, there was no difference between HOT, NORM and COOL ($P=0.18$) (Fig.2).

The rates of change of rectal temperature ($\Delta T_{re}/\Delta t$) and mean skin temperature ($\Delta T_{sk}/\Delta t$) are shown in Fig. 3A-B. No differences were observed between conditions for $\Delta T_{re}/\Delta t$ during the first 20 min of exercise. $\Delta T_{sk}/\Delta t$ declined rapidly following the onset of exercise, with the highest rates of skin cooling observed at 2 min in all conditions. While $\Delta T_{sk}/\Delta t$ changed significantly with exercise time ($P<0.001$), there was also a significant interaction between time and environmental temperature ($P<0.001$) showing that the change in $\Delta T_{sk}/\Delta t$ with exercise time was most negative and greatest in magnitude in the COOL (Fig. 3B).

Differences in absolute T_{sk} were evident between conditions ($P<0.001$), with the highest values observed in HOT (33.89±0.20˚C) and the lowest values in COOL (28.30±0.57˚C) during the first 20 min.

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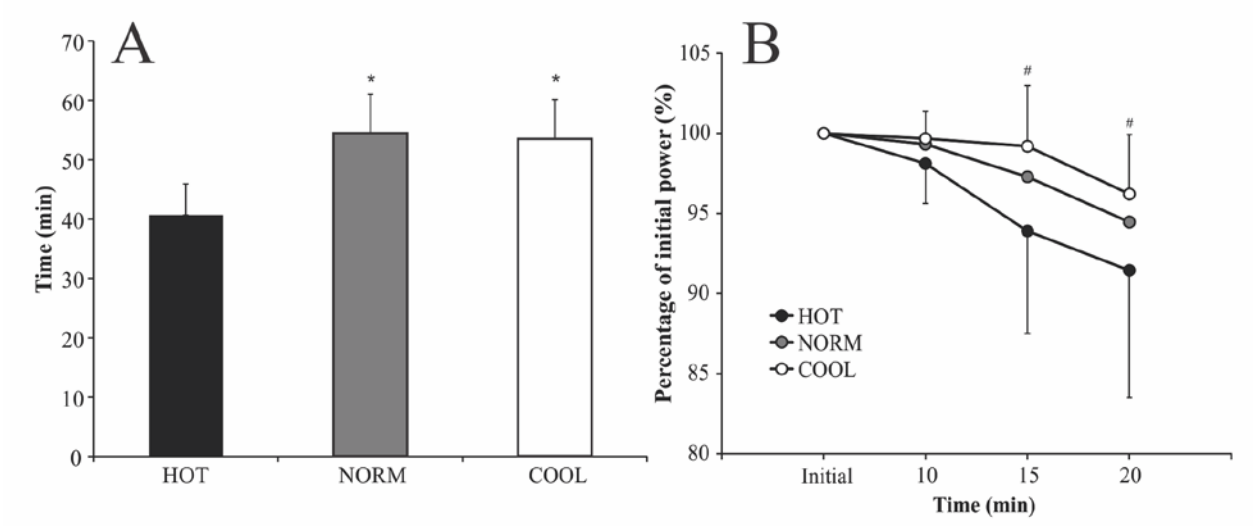

Figure 1. Mean trial duration (A) and self-selected power output expressed as a percentage of the absolute workload at 5 min of exercise (B) for HOT, NORM, and COOL.*Significantly higher than HOT (P< 0.05). #Significantly lower in HOT compared to COOL (P< 0.05)

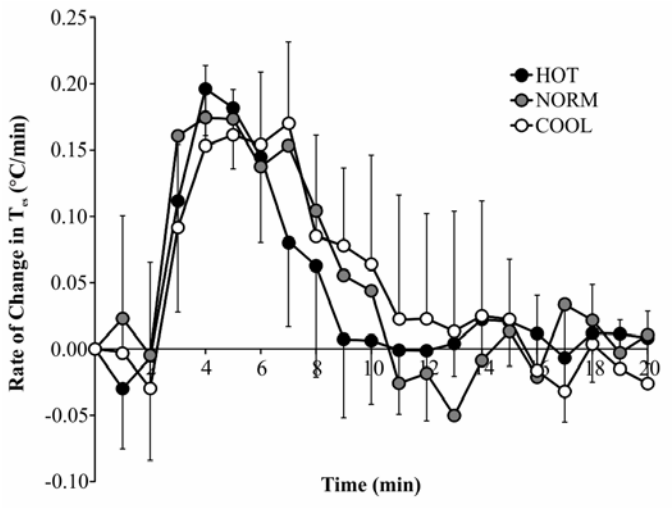

Figure 2. Rate of change in T_{es} during the first 20 min of exercise.

Rate of heat storage estimated using thermometry (S_{therm})

Compared to HOT, S_{therm} in NORM and COOL was negative and significantly lower during the first 4-min of exercise using model A (core/shell: 0.66/0.34) and B (core/shell: 0.79/0.21), and between 2-4 min of exercise using model C (core/shell: 0.90/0.10). In models A, B, and C, S_{therm} reached a nadir after 2 min (Fig.4A-C). However, as the proportion of "shell" compartment became progressive smaller (from 0.34 to 0.10), the estimated values of S_{therm} became less negative in the COOL and NORM conditions and became increasingly similar to the HOT condition. When the "shell" compartment was completely eliminated in model D (core/shell: 1.00/0.00) (Fig. 4D), no difference in S_{therm} was observed between conditions.

Rate of heat storage estimated in COOL and NORM conditions using partitional calorimetry (S_{cal})

S_{cal} in the HOT condition could not be estimated using partitional calorimetry because sweating had already begun and minute-by-minute rates of evaporation could not be measured (see Methods). The average of the first 5 minutes of exercise heat balance parameters for NORM and COOL condition are detailed in Fig. 5. While H_{prod} increased significantly with exercise time (P<0.001), this change was not altered by environmental temperature (P=0.98). In both COOL and NORM, S_{cal} was positive (i.e. heat energy was stored in the body), and increased during the first 5 min of exercise while the first 5-minute average was negative and significantly lower for S_{therm} (P<0.001). While the rate of evaporation could not be measured, when compared to the values estimated in the COOL and NORM using thermometry (S_{therm}), rates of evaporation needed for these S_{therm} values to be correct would have been between 30 to 56 kJ·min^{-1} respectively.

Local sweat rates

Significantly greater LSR_{back} were observed in the HOT compared to the COOL during the first 20 min (P<0.05), while LSR_{thigh} was significantly greater in the HOT compared to the COOL during the first 11 min (P<0.05). The onset of sweating at LSR_{back} and LSR_{thigh} in COOL and NORM occurred after 7.6±1.5 and 4.8±1.7 min of exercise respectively. Both LSR_{back} and LSR_{thigh} had already initiated prior to the onset of exercise in the HOT condition.

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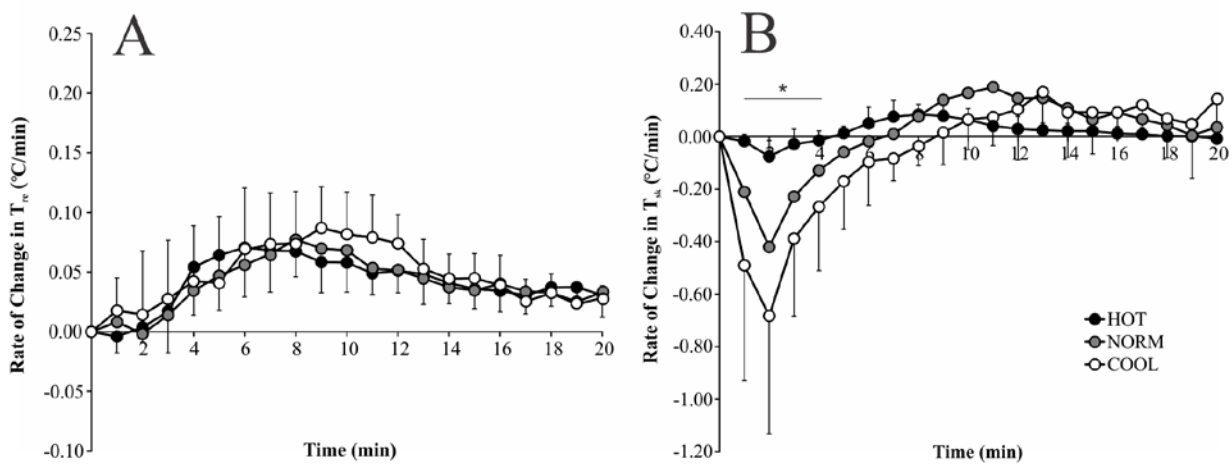

Figure 3. Rate of change in T_{re} (A) and T_{sk} (B) during the first 20 min of exercise. *Significantly greater in HOT compared to NORM and COOL ($P<0.05$).

Integrated EMG (iEMG)

For iEMG values, a main effect of time was found for all four muscles (Fig.6; $P<0.05$). There were no other main effects or interactions. Preplanned comparisons showed that for BF and GM, iEMG was significantly lower than initial iEMG at 10, 15, and 20min ($P<0.05$). For VL, iEMG was significantly lower than initial iEMG at the 15 and 20min ($P<0.05$), and for LG, iEMG was only significantly lower than initial iEMG at 20 min ($P<0.05$).

LEG weighted average iEMG data are presented in Fig.6. Similar to the individual muscles, for LEG there was a main effect of time on iEMG ($P=0.001$).Preplanned comparisons showed that for LEG, iEMG was significantly lower at all time points compared to initial iEMG ($P<0.05$). There was no main effect for temperature ($P=0.387$) and no interaction between the variables ($P=0.497$).

Discussion

In the present study an ambient temperature-dependent reduction in power output occurred after 15 to 20 min of self-paced fixed-RPE exercise, a result similar to that reported by Tucker et al. (2006). However, in contrast to their conclusions, we did not observe any difference in $\Delta T_{es}/\Delta t$ between COOL, NORM and HOT conditions in advance of these changes in power output, or thereafter, suggesting a similar S in all conditions. The negative S estimated by Tucker et al. (2006) during the first 4-min of exercise using the traditional two-compartment thermometry model in the COOL and NORM conditions, were also obtained with the same thermometry model in the present study, but it is clear that these negative values are simply the result of a disproportionate influence of negative rates of skin temperature change during the first 5-min of exercise arising from an increased self-generated air velocity across the legs (Nishi and Gagge 1970). Taken together our findings do not support the hypothesis that S during the early minutes of exercise mediates subsequent changes in self-selected exercise intensity.

It has been previously argued that T_{es} may not provide an accurate absolute estimation of changes in body heat content when incorporated within a two-compartment thermometry model (Jay et al. 2007). However, while an accurate absolute S value can probably not be derived, considering the responsiveness of this core temperature measurement to changes in arterial blood temperature, it stands to reason that physiologically significant differences in the rate of body heat storage will be paralleled by different rates of change of T_{es}. Theoretically, differences in S will be best detected by measuring rates of temperature change at a site that is well-perfused with blood, and serves as a major conduit for heat transfer from the working muscles to the skin. Despite its close proximity to the working muscles, the pelvic region has a high tissue density and relatively low blood perfusion, therefore the rate of change in rectal temperature is unsuitable to assess rapid changes in S such as those seen during the early stages of exercise (Blight 1957; Jay and Kenny 2009). In contrast, T_{es} is measured at the level of the right atrium/aorta (Mekjavić and Rempel 1990); therefore, rapid changes in blood temperature due to changes in heat storage are adequately reflected in the change in T_{es} (Cooper and Kenyon 1957; Molnar and Read 1974; Shiraki et al. 1986). Indeed, heat production within the muscle begins almost immediately at the onset of dynamic exercise, followed by heat transfer to the blood (with a rise in blood temperature) and a rise in T_{es} (González-Alonso et al. 2000). Therefore, based on the time course for heat exchange between muscle and blood, as well as the regional differences between the

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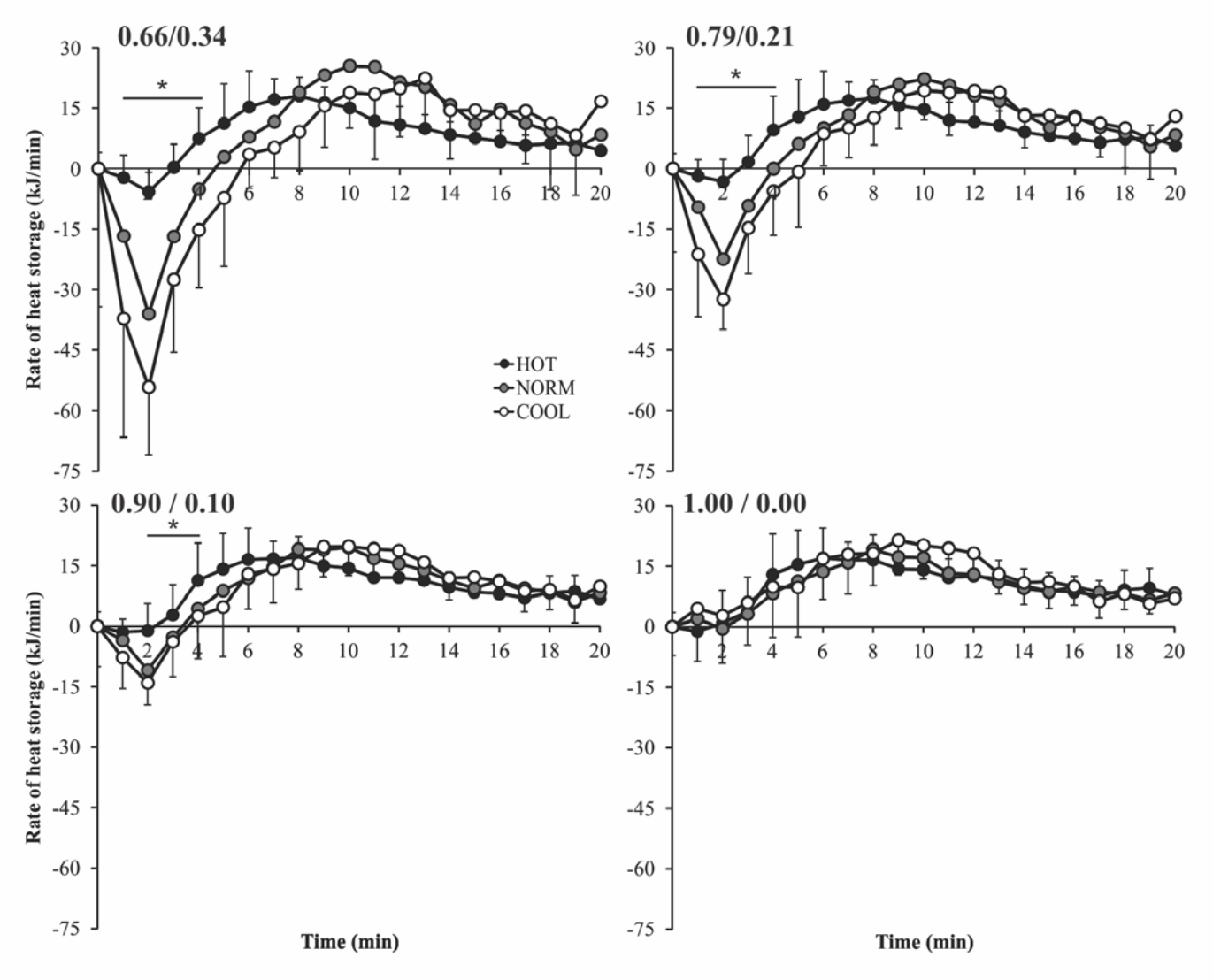

Figure 4. Thermometric estimates of the rate of heat storage, using 4 different T_{re}/T_{sk} weighting coefficients for T_b: (A) 0.66/0.34, (B) 0.79/0.21, (C) 0.90/0.10 and (D) 1.00/0.00. *Significantly greater in HOT compared to NORM and COOL (P<0.05).

esophagus and rectum, it would be expected that only a slight delay between the rise in H_{prod} and $\Delta T_{es}/\Delta t$ should be observed, while $\Delta T_{re}/\Delta t$ would be delayed. Accordingly, H_{prod} reached its peak between 2 and 4-min into exercise; meanwhile T_{es} and T_{re} reached their peak after 4-min and 8-min of exercise, respectively (Fig. 2 and Fig. 3A).

Large differences in S_{therm} between conditions during the first 5 min of exercise are clearly the result of a disproportionate influence of early and marked differences in the rate of skin temperature change ($\Delta T_{sk}/\Delta t$) (Fig. 3B). In both COOL and NORM conditions, the greatest $\Delta T_{sk}/\Delta t$ occurred after 2 min, coinciding with the most negative S_{therm} values when T_{sk} was included in the thermometry model (Fig. 4A-C). Moreover, the thermometry models with the greatest weighting of T_{sk} yielded the most negative S_{therm} values during the first 5 min of exercise. Notably, when T_{sk} was eliminated from the thermometry model, no differences in S_{therm} were observed between COOL, NORM and HOT conditions (Fig. 4).

While the rate of metabolic heat production rises rapidly at the start of exercise, the increase in the rate of total heat dissipation lags considerably, resulting in heat imbalance and a positive S. Based on this well-established pattern of thermogenesis and thermolysis, Jay and Kenny (2009) argued that the negative S values estimated using the traditional two-compartment thermometric model in cold environments, such as those reported by Tucker et al. (2006), would require rates of heat dissipation that were impossible based on the characteristics of the environment (i.e., ambient temperature, humidity, air velocity) and the lag in thermoeffector onset (i.e., thermoregulatory sweating). Indeed, given the H_{prod}, C+R, and $E_{res}+C_{res}$

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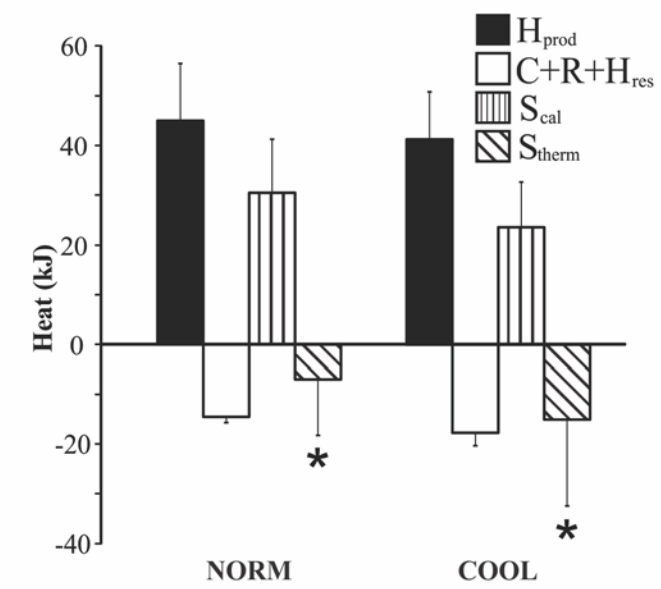

Figure 5. Heat balance parameters averaged over the first 5 minutes of exersice for COOL and NORM conditions. H_{prod}, rate of metabolic heat production (i.e. M-W); $C+R+H_{res}$, rates of convective, radiant, and respiratory heat exchange, respectively; S_{cal}, rate of heat storage estimated via partitional calorimetry; S_{therm}, core/shell weighting of 0.79/0.21 respectively. * Significantly lower in S_{therm} compared to S_{cal} ($P<0.001$).

values measured in the present study, for the S_{therm} values estimated in the COOL and NORM conditions after 2 min of exercise to be correct, rates of whole-body sweating (and subsequent evaporation) equivalent to 1.39 and 1.31 L h^{-1} respectively would have been required when in fact local sweat rate on the back and thigh had not changed from baseline pre-exercise levels. Assuming no evaporation from the skin was occurring, S_{cal} in COOL and NORM conditions actually increased rapidly in a positive direction during the first 3 min of exercise, as would be expected (Jay and Kenny 2009), suggesting early whole-body heat storage– which is also supported by the positive change in T_{es} by ~0.4°C from rest to 5 min. Since H_{prod} and $\Delta T_{es}/dt$ (Fig. 2) were similar throughout this period in all conditions, it is likely that S_{cal} was also similar in the HOT compared to COOL and NORM conditions even though it could not be measured in the present study because sweating had already begun prior to the start of exercise in the HOT condition, and we had no means of measuring the dynamic rate of whole-body evaporation. However, such a scenario would have elicited an evaporation rate that counterbalanced the smaller dry heat loss via convection and radiation.

A unique feature of the fixed-RPE protocol is the ability to isolate the physiological factor(s) that affect RPE-mediated changes in work rate, and therefore performance (Tucker 2009). As in previous studies, exercise duration (i.e., the time to reach 70% of initial work rate) was shorter in HOT compared to NORM and COOL (Fig. 1A) with similar variability as previously reported (Tucker et al. 2006; Crewe et al. 2008) due to an accelerated decline in self-selected work rate (Fig. 1B), suggesting some factor related to a high ambient temperature influenced the selection of work rate for a RPE of 16. The present findings do not support any influence of S on the decline in exercise performance; however, this does not discount the possibility of other thermally-mediated effects. While a reduction in force production has been shown following hyperthermia (Nybo and Nielsen 2001), absolute core temperature responses were not different between conditions. However, large differences in skin temperature were observed. A high T_{sk}, or thermal sensation, alters RPE and performance (Schlader et al. 2011*a*, 2011*c*, 2011*b*; Flouris 2011), and therefore may have been the primary stimulus for the reduction in work rate during the early minutes of exercise in the present study. Yet, since a high T_{sk} was present before the onset of exercise, one might expect that the initial self-selected workload would have been lower in the HOT condition due to a higher T_{sk}. Although this was not the case, a high T_{sk} coupled with a rising core temperature may have precipitated the subsequent reduction in self-selected work rate (Ely et al. 2009). Future studies should investigate the independent role of T_{sk} on exercise performance through acute mean or local T_{sk} manipulations as recent work has suggested afferent feedback from skin thermoreceptors could mediate differences in self-paced work rate (Schlader et al. 2011*a*).

Another important unresolved issue regarding exercise performance is whether the accelerated decline in work rate during the HOT condition occurred in an anticipatory fashion. That is, it may be that neuromuscular activation (and therefore exercise intensity) was regulated to prevent deleterious homeostatic disturbances. However, it is unclear whether this was the case in the present study. Exercise performance in the HOT condition was impaired (Fig. 1), with a more accelerated decline in self-selected work rate resulting in a shorter time to reach 70% of the initial work rate (the condition for terminating exercise). An anticipatory reduction in exercise intensity is argued to be mediated through a non-consciously altered pattern of neuromuscular activation (Tucker et al. 2006). In the present study, iEMG declined similarly over the first 20 min of exercise in HOT, NORM, and COOL conditions (Fig. 6), yet the reduction in work rate was significantly greater in the HOT condition when expressed as a percentage of the initial work rate (Fig. 1). It is possible that greater reductions in work rate in the HOT condition, while significant relative to NORM and COOL condition, in terms of the percentage decline from the initial work rate, were not large enough in absolute terms to yield significantly different iEMG signals between conditions. These iEMG results are similar to those previously presented by Tucker et al. (2006), even though the methods for normalizing iEMG varied. In fact, our normalization method (averaging over the first 5 minutes of dynamic exercise) led to a decrease in variability compared to normalizing to MVC, a static contraction. Importantly,

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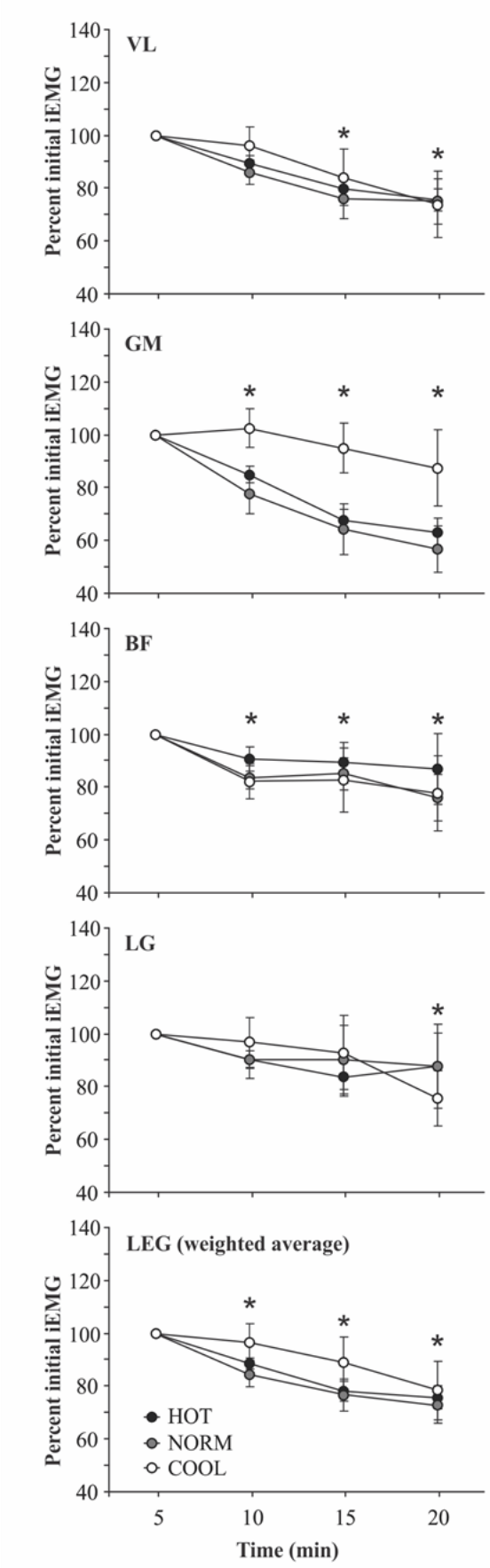

Figure 5. iEMG during the first 20 min of exercise. VL, vastus lateralis; GM, gluteus medius; BF, biceps femoris; LG, lateral gastrocnemius. *Significantly different from initial for all conditions (P<0.05).

however, in the present study the observed decrease in iEMG did not seem to occur in an anticipatory manner but rather *in response* to changes in core temperature.

The main limitation of the present study was the inability to measure S_{cal} in the HOT condition. The determination of S_{cal} depends on the ability to measure (i) the rate of metabolic heat production and (ii) the estimation of all avenues of heat exchange. This latter condition is complicated by the inability to measure minute-by-minute changes in evaporative heat loss from the skin (E_{sk}) that would have required a direct calorimeter or continuous body mass measurements while accounting for dripping sweat (if necessary). No evidence of sweating was evident until 3 and 5 min of exercise in NORM and COOL, respectively; therefore, there was no need to account for E_{sk} in the estimation of S_{cal} in those conditions (see Methods). However, sweating was apparent in the HOT condition during the baseline period, preventing an accurate determination of E_{sk} and S_{cal}. Nevertheless, since the rates of change of both T_{es} were similar in all conditions, it seems reasonable that a higher E_{sk} counterbalanced the negligible dry heat loss in the HOT condition to elicit similar S_{cal} values as the COOL and NORM conditions.

In conclusion, despite a greater decline in self-paced exercise intensity in the HOT condition after ~15-min of exercise as previously reported (Tucker et al. 2006), $\Delta T_{es}/\Delta t$ was similar in COOL, NORM and HOT conditions suggesting no early differences in the rate of body heat storage, thus apparently ruling this factor out as a potential mediator of the subsequent changes in power output. The accelerated decline in power output in the HOT condition occurred in parallel with a lower neuromuscular activation but in the absence of any evidence of neuromuscular fatigue, which may indicate an anticipatory regulation of exercise intensity based on factors unrelated to S, such as a high mean skin temperature.

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