

### LJMU Research Online

Thomas, S, Carter, HH, Jones, H, Thijssen, DHJ and Lowe, D

Effects of acute exercise on cutaneous thermal sensation

http://researchonline.ljmu.ac.uk/id/eprint/12642/

Article

**Citation** (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Thomas, S, Carter, HH, Jones, H, Thijssen, DHJ and Lowe, D Effects of acute exercise on cutaneous thermal sensation. International Journal of Environmental Research and Public Health. ISSN 1660-4601 (Accepted)

LJMU has developed LJMU Research Online for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact researchonline@ljmu.ac.uk

http://researchonline.ljmu.ac.uk/



International Journal of Environmental Research and Public Health



# Article Effects of acute exercise on cutaneous thermal sensation

4 Thomas, S., D.<sup>1</sup>; Carter, H.H<sup>1</sup>, Jones, H.<sup>1</sup>; Thijssen, D.<sup>1,2</sup>; Low, D. A.<sup>1,\*</sup>

- Research Institute of Sports & Exercise Sciences, Liverpool John Moores University; <u>s.d.thomas@ljmu.ac.uk</u>
   (S.T.), <u>howard.carter@uwa.edu.au</u> (H.C.), <u>h.jones@ljmu.ac.uk</u> (H.J.), <u>d.thijssen@ljmu.ac.uk</u> (D.T.)
- 7 <sup>2</sup> Radboud University Nijmegen Medical Centre, Nijmegen, the Netherlands
- 8 \* Correspondence: d.a.low@ljmu.ac.uk; Tel.: 0151 904 6244
- 9 Received: date; Accepted: date; Published: date

10 Abstract: The aim of this study was to assess the effect of exercise intensity on thermal sensory 11 function of active and inactive limbs. In a randomised and counterbalanced manner 13 healthy 12 young male participants (25±6 yr, 1.8±0.1 m, 77±6 kg) conducted; 1) 30 minutes low (50% heart rate 13 maximum, HRmax; LOW) intensity, 2) 30 minutes high (80% HRmax; HIGH) intensity cycling 14 exercise and 3) 30 minutes seated rest (CONTROL). Before, immediately and 1-hour after each 15 intervention thermal sensory function of the non-dominant dorsal forearm and posterior calf were 16 examined by increasing local skin temperature (1°C/s) to assess perceptual heat sensitivity and pain 17 thresholds. Relative to pre-exercise, forearm heat sensitivity thresholds were increased immediately 18 and 1-hr after HIGH but there were no changes after LOW exercise or during CONTROL (main 19 effect of trial; P=0.017). Relative to pre-exercise, calf heat sensitivity thresholds were not changed 20 after LOW or HIGH exercise or during CONTROL (main effect of trial; P=0.629). There were no 21 changes in calf (main effect of trial; P=0.528) or forearm (main effect of trial; P=0.088) heat pain 22 thresholds after exercise in either LOW or HIGH or CONTROL. These results suggest that 23 cutaneous thermal sensitivity function of an inactive limb is only reduced after higher intensity 24 exercise but is not changed in a previously active limb after exercise. Exercise does not affect heat 25 pain sensitivity in either active or inactive limbs.

- 26 Keywords: acute exercise; skin; sensory function; heat
- 27

### 28 1. Introduction

The skin is a vital organ of regulation, helping maintain optimal cardiovascular, autonomic and sensory function, amongst others, through its vast array of neural and morphological structures. Cutaneous thermal sensation plays a critical role in behavioural thermoregulation, which is the first line of defence against thermal disturbances [1]. Thermal sensation provides immediate feedback about the thermal state of the body and a level of thermal discomfort (the reciprocal of thermal comfort) is determined and, if necessary, a set of desired actions, e.g., behaviour, are initiated to correct thermal imbalance/discomfort [2].

36 Exercise results in various responses to ensure optimal metabolic, cardiovascular and 37 thermoregulatory function. For example, as heat production from active musculature increases, 38 various neurally-mediated skin blood flow and sweating reflexes occur in order to facilitate heat 39 dissipation [3]. Despite these autonomic adjustments in order to serve cardiovascular and 40 thermoregulatory function, behavioural thermoregulation is still active during exercise and plays an 41 important role in exercise intensity and local microclimate (e.g., seeking cooling and/or removing 42 clothing) selection during exercise, ultimately to help limit thermal discomfort and avoid heat-related 43 illness [4]. Furthermore, behavioural thermoregulation remains engaged after the cessation of exercise, which is particularly important due to the withdrawal of autonomic thermoeffectors [5] andthe extended elevation of internal temperature and thermal discomfort post-exercise [6].

46 During and after exercise sensory perceptions to a variety of different stimuli can be altered, 47 including a reduction in pain sensation [7]; or exercise-induced analgesia. The effect of exercise on 48 thermal sensation is not entirely clear, however. Any changes in thermal sensation during or after 49 exercise would have implications for behavioural thermoregulation and associated strategies. 50 Minimal previous research has suggested a similar phenomenon to exercise-induced analgesia 51 whereby arm and leg warmth sensation thresholds are increased, e.g., a higher skin temperature is 52 required to generate the sensation of warmth, during exercise [8], and the perceptual sensations of 53 local cold (20 °C) and warmth (40 °C) stimuli are reduced, e.g., the same cold/heat applications are 54 rated as less cold or hot, respectively, during low-intensity exercise [9-11]. With regards to thermal 55 sensation post-exercise recent work has shown that compared with recovery after moderate-intensity 56 exercise, during recovery from high-intensity exercise thermal behavior is withdrawn at a rate that is 57 disproportionately high relative to the magnitude of changes in the afferent stimulus (e.g., core and 58 skin temperatures) to continue behaving [12]. These findings are indicative of blunted thermal 59 behavior following high-intensity exercise and could be a result of attenuated perception of thermal 60 afferent stimuli, e.g., thermal sensation, due to exercise-induced analgesia, which is more prevalent 61 during/after high-intensities [7] and a carryover of reduced thermal sensation during exercise [8-11]. 62 Thermal sensation after exercise, and any effect of the preceding exercise intensity, is relatively 63 unknown however [13]. Moreover, whether there is a regional variation in any changes in thermal 64 sensation after exercise is also unknown. Regional variation in thermal sensation is evident under 65 resting conditions [14, 15] but whether thermal sensation is affected differently in previously active 66 vs. inactive limbs is not known. The aim of this study was to therefore assess the effect of exercise 67 intensity on thermal sensory function of previously active and inactive limbs. The hypotheses are 68 that 1) thermal sensory function would be impaired after high-intensity exercise but not after low-69 intensity exercise and 2) the thermal sensory function responses to exercise would not be different in

70 the previously active leg and inactive forearm.

### 71 2. Materials and Methods

72 Participants: Participants (n=13 males) who were recreationally active (as assessed by short 73 IPAQ physical activity questionnaire, <4 sessions per week, VO<sub>2peak</sub> 3.5±0.5 L.min<sup>-1</sup>), healthy (as 74 assessed by PARQ health screening form), young (age <45 years, mean = 25±6 years), and non-75 smokers were recruited. Individuals with cardiovascular disease, local infections, limitations of 76 physical activity, smokers or persons taking medication were excluded. Participants were informed 77 of the procedures prior to participation and provided written and verbal informed consent. This 78 study was approved by the Liverpool John Moores University Research Ethics Committee in 79 accordance with the Declaration of Helsinki (ref: 17SPS010). Height and weight measurements were 80 collected as well as the assessment of VO<sub>2peak</sub> were conducted at the first laboratory visit (mean height 81 1.8±0.1 m, weight 77±6 kg). The protocol for the VO<sub>2peak</sub> involved an incremental cycling (Lode Corival 82 CPET, Lode B. V., Groningen, NL) protocol to volitional exhaustion (30 watt increments every 2 min) 83 while heart rate (Polar FT1 and T31, Polar UK) and expired air (Jaeger Oxycon Pro, Wuerzburg, 84 Germany) were continuously collected.

85 Experimental design: Participants attended the laboratories on 3 occasions for 2 bouts of 30 86 minutes of exercise on a cycle ergometer (Lode Corival CPET, Lode B. V., Groningen, NL) at 50% 87 (low-intensity exercise, LOW) or 80% (high-intensity exercise, HIGH) maximum heart rate (cadence 88 of ~70-90 rpm) or a control (CONTROL) no exercise session session when participants sat quietly for 89 30 min. Prior to (PRE), immediately following (IMM), and 1 hour following the cessation of exercise 90 (1HR), thermal sensory function of the non-dominant dorsal forearm and posterior calf were 91 examined by increasing local skin temperature (1°C/s) to assess heat sensitivity (detection of a change 92 in skin temperature) and pain (detection of discomfort) thresholds. The order of the visits was 93 randomised and counterbalanced, separated by 4-7 days, and were performed at the same time of 94 day to minimise circadian variation [16]. Participants reported to the laboratories having fasted from

95 food for 4hrs, abstained from alcohol and caffeine for 16 hours, and refrained from exercise 24 hours 96 prior to testing. Participants were advised to ingest 500ml of water prior to testing to avoid 97 dehydration. All testing visits took place in the same temperature controlled room (23.3±0.28°C, 98 42±7% relative humidity).

99 Thermal sensory function assessment: Participants were positioned semi-recumbent for baseline 100 stabilisation and thermal sensory function assessment. After instrumentation resting baseline 101 measurements were collected for 5 minutes. Non-dominant dorsal forearm and posterior calf were 102 examined by increasing local skin temperature (1°C/s) to assess heat sensitivity (detection of a warm 103 sensation) and heat pain (detection of heat discomfort) thresholds (TSA II NeuroSensory Analyser, 104 Medoc) according to international consensus guidelines [17]. Five consecutive measurements was 105 conducted for both warmth detection and heat pain detection thresholds. All thresholds were 106 obtained with ramped stimuli (1 °C/s) that were terminated when the subject pressed a button. The 107 contact area of the thermode was 7.84 cm<sup>2</sup>. The measurements for warmth and heat pain detection 108 thresholds were not made in the same place during each set of 5 consecutive measurements to avoid 109 any carryover effect of a previous stimuli affecting a subsequent detection threshold.

110 *Cardiovascular and local thermoregulatory assessment:* Intermittent systolic and diastolic 111 blood pressure and heart rate were measured using an automated sphygmomanometer (Dinamap 112 Procare 100, GE Medical Systems Ltd., Buckinghamshire, UK). Intra-exercise heart rate was 113 continuously monitored using short-range telemetry (Polar FT1 and T31, Polar UK). Local forearm 114 and calf skin temperatures were recorded using thermocouples (Grant Instruments, Sheppreth, 115 Cambridge, U.K). Whole body thermal discomfort (0-9 scale) [18] and Ratings of Perceived Exertion 116 (6-20 scale) [19] were assessed during the last 5 minutes of exercise.

117 Statistical analysis: The median 3 results of the 5 trials at each stage were averaged for analyses 118 of the warmth and heat pain thresholds. Separate two factor Linear Mixed Modelling with stage (2 119 levels: IMM vs. 1HR) and intensity (3 levels: LOW vs. HIGH vs. CONTROL) as factors were used to 120 compare the changes in warmth and heat pain thresholds from baseline during the 3 trials at the 121 forearm and calf. Haemodynamics and local skin temperature data were compared using linear 122 mixed models, with main effects of stage and intensity. Baseline warmth and heat pain thresholds 123 were compared using Linear Mixed Modelling with intensity (3 levels: LOW vs. HIGH vs. 124 CONTROL) as the single factor. Thermal discomfort and Ratings of Perceived Exertion (RPE) data 125 were compared between LOW and HIGH using Paired T-Tests. The normality of data distribution 126 and homogeneity of variance were checked prior to statistical analyses, which were performed using 127 SPSS (IBM SPSS Statistical Package 24). Statistical significance was set at p<0.05 and data are 128 expressed as mean  $\pm 1$  standard deviation (SD).

129

### 130 **3. Results**

132 By design, exercise work rate was significantly higher during HIGH compared to LOW (157±28 133 vs. 82±17 watts, P<0.001). Exercise induced significant changes to all haemodynamic and local skin 134 temperature variables whereas there were no changes during the CONTROL trial (Table 1). Exercise 135 increased heart rate in an intensity dependent manner (P<0.001). Systolic and diastolic blood pressure 136 increased during exercise (P<0.001) with a higher systolic blood pressure during HIGH vs. LOW 137 (P=0.006) but no difference in diastolic blood pressure between HIGH and LOW (P=0.633). Forearm 138 skin temperature decreased during LOW exercise but was maintained during HIGH (P=0.014). Calf 139 skin temperature was higher during LOW and HIGH relative to CONTROL (P<0.001) due to slight 140 increases during and after exercise (P=0.174). Ratings of perceived exertion were 10±2 and 14±2 for 141 LOW and HIGH, respectively (P<0.001). Thermal discomfort ratings were 5±1 and 6±1 for LOW and 142 HIGH, respectively (P=0.002).



International Journal of Environmental Research and Public Health



 Table 1: Cardiovascular and local skin temperature responses before (PRE), during (Ex) and immediately (IMM) and 1 hr (1HR) after 30 minutes of low and high intensity exercise and control rest. Data are mean ± 1 SD.

	CONTROL				LOW				HIGH				P values		
	PRE	Ex	IMM	1HR	PRE	Ex	IMM	1HR	PRE	Ex	IMM	1HR	Stage	Intensity	Stage*Intensity
Heart rate (beats/min)	64±9	59±10	59±10	57±8	61±7	101±4	65±8	60±9	58±7	147±7	86±14	64±11	<0.001	< 0.001	< 0.001
Skin temperature (°C)															
Forearm	32.3±0.8	32.3±1.0	32.4±1.0	32.2±1.0	32.3±0.7	31.0±0.9	31.3±1.0	$32.8 \pm 1.1$	32.2±0.8	32.0±0.8	31.9±1.1	32.4±1.1	0.006	0.050	0.014
Calf	31.0±0.7	31.2±1.0	31.2±0.9	30.9±0.9	31.1±0.7	31.4±1.5	31.8±1.3	31.6±1.0	31.5±1.4	32.2±0.9	32.0±1.2	31.8±0.9	0.174	< 0.001	0.778
Blood pressure (mmHg)															
Systolic	122±8	118±9	119±9	121±8	118±6	137±11	124±5	116±9	121±8	142±17	124±8	116±8	< 0.001	0.006	< 0.001
Diastolic	67±7	69±7	68±8	69±8	65±8	80±12	67±9	68±9	66±8	78±11	67±7	63±6	< 0.001	0.633	0.026

145

143

144





### 146 3.2. Thermal sensation function

147 Baseline forearm thermal sensation was not different between trials (CONTROL 35.0±1.2°C; 148 LOW 34.3±0.6°C; HIGH 34.5±0.5°C; P=0.073). There was a main effect of intensity for the change in 149 forearm heat sensitivity threshold (P=0.017) with an elevation immediately and 60 min after HIGH 150 but no change after LOW or during CONTROL (Figure 1; stage\*intensity effect; P=0.210). Baseline 151 calf thermal sensation was not different between trials (CONTROL 37.0±1.3°C; LOW 37.5±1.7°C; 152 HIGH 37.1±2.0°C; P=0.629). There was no main effect of stage (P=0.840), intensity (P=0.783) or 153 stage\*intensity interaction effect (P=0.849) for the changes in calf heat sensitivity thresholds (Figure 154 1).



## Figure 1. Changes in forearm and calf skin warm thermal sensitivity immediately and 1 hr after LOW and HIGH exercise and CONTROL \*P<0.05 vs. LOW and CONTROL.</li>

#### 157 3.3. *Thermal pain function*

Baseline forearm heat pain threshold was not different between trials (CONTROL 45.0 $\pm$ 3.0°C; LOW 46.1 $\pm$ 2.2°C; HIGH 45.7 $\pm$ 1.9°C; P=0.393). There was no main effect of stage (P=0.551), intensity (P=0.088) or stage\*intensity interaction effect (P=0.764) for the changes in forearm heat pain thresholds (Figure 2). Baseline calf thermal sensation was not different between trials (CONTROL 47.2 $\pm$ 1.6°C; LOW 47.8 $\pm$ 1.8°C; HIGH 47.4 $\pm$ 1.4°C; P=0.558). There was no main effect of stage (P=0.683), intensity (P=0.528) or stage\*intensity interaction effect (P=0.551) for the changes in calf heat sensitivity thresholds (Figure 2).



## Figure 2. Changes in forearm and calf skin heat pain thresholds immediately and 1 hr after LOW andHIGH exercise and CONTROL.

#### 167 4. Discussion

168 The aim of this study was to assess the effect of exercise intensity on thermal sensory function 169 of previously active and inactive limbs. Cutaneous thermal sensory function responses of a lower leg 170 (calf) and a forearm were assessed before, immediately and 1 hr after 30 min of low or high-intensity 171 continuous cycling exercise. The main findings were 1) cutaneous thermal sensitivity of the forearm, e.g., a previously inactive limb, is reduced after high intensity exercise consistent with previous
findings during exercise [8]; 2) cutaneous thermal sensitivity of the lower leg, e.g., a previously active
limb, is not changed after exercise in contrast to previous findings during exercise [8, 9]; 3) exercise
does not affect heat pain sensitivity in either previously active or inactive limbs consistent with
previous studies of heat pain sensitivity after exercise [13] but not other metrics of pain sensitivity
after exercise [7].

178 Thermal sensation provides immediate feedback about the thermal state of the body and plays 179 a critical role in behavioural thermoregulation, which is the first line of defence against exogenous 180 thermal disturbances [1]. During thermal stress, despite intricate autonomic control of 181 thermoeffectors, e.g., sweating and skin blood flow, that facilitate heat loss or gain in order to 182 maintain internal temperature within safe limits, changes in levels of thermal discomfort [3] can 183 initiate behaviour, e.g., finding shade or removing clothing, in order to also correct the thermal 184 imbalance/discomfort [2]. The importance of effective thermal sensation and behavioural 185 thermoregulation is particularly significant after exercise when autonomic thermoeffectors are 186 withdrawn despite the elevation of internal temperature post-exercise [6]. A collection of previous 187 studies suggest that thermal sensation might be altered after exercise however. During exercise 188 sensory perceptions of pain are reduced (exercise-induced analgesia) [7] and thermal sensation is 189 impaired [8-11], which may carry over into the post-exercise period. Furthermore, recent work has 190 suggested an attenuated perception of thermal afferent stimuli following high-intensity exercise due 191 to a disproportionately high withdrawal of thermal behavior [12]. In the present study, we showed 192 that, using the warmth threshold detection limits during a local skin heating stimulus, cutaneous 193 thermal sensitivity of the forearm was reduced immediately and 1 hour after high intensity exercise, 194 e.g., a higher skin temperature was required to generate the sensation of warmth. Such a 195 phenomenon has been ascribed to exercise-induced activation of opioids [7, 20], proprioceptive and 196 muscle afferents that inhibit central pain circuitry that may involve modulation of descending 197 inhibitory pathways [21], the binding of released factors to pain and/or thermal receptors [22], and/or 198 distraction from pain or discomfort [23].

In the present study, cutaneous thermal sensitivity of the forearm was not different after the low intensity exercise bout. Similar findings have also been demonstrated during low intensity cycling (~30% VO<sub>2peak</sub>) [9]. It has been demonstrated that an exercise intensity of ~ $\geq$ 75% VO<sub>2peak</sub> is required to induce exercise-induced analgesia [7]. Given that the intensity of the LOW exercise in the current study was 50% of maximum heart rate then it is not surprising that thermal sensitivity in that condition was unchanged after exercise.

205 Interestingly, the thermal sensitivity of the calf was also not different after both low and high 206 intensity exercise in the present study. Whether the thermal sensation of a limb that has been 207 previously exercised, relative to an inactive limb, is affected is not clear. Several substances released 208 by exercising muscles (e.g., potassium, hydrogen, prostaglandins) can activate or sensitize muscle 209 nociceptors [22]. Whether any of these substances could also sensitize cutaneous nociceptors in active 210 limbs and offset the reductions in thermal sensation observed in the non-active limbs is not known. 211 An alternative explanation for the differing responses in the calf compared to the forearm in the 212 present study could be regional variation in thermal sensitivity at rest and in response to exercise 213 stimuli [14, 15]. Previous research has demonstrated an exercise-induced reduction in calf cutaneous 214 thermal sensitivity during exercise [9]. Differences in findings of this previous and the present study 215 could be due to differences in the assessment method of thermal sensation; in the previous study 216 participants were asked to rate their thermal sensation after 10s of 40 °C local heat application, e.g., 217 magnitude estimation, rather than indicate the sensation of warmth during an increasing local heat 218 stimulus, e.g., detection threshold; as well as differences in the timing (during vs. post-exercise) of 219 thermal sensation assessments in both studies.

Exercise of low and high intensity did not affect heat pain sensitivity in either previously active or inactive limbs in the present study consistent with previous research that reported a lack of change in heat pain thresholds after 30 min of moderate exercise in young participants [13] but not research that has demonstrated a reduction in other metrics of pain during and after exercise [7]. Exerciseinduced analgesia is more consistently evident for methods that assess pain using tactile or electrical
stimuli in comparison to equivocal findings for heat pain [7]. A lack of change in heat pain sensitivity
(as well as calf heat sensitivity) in the present study may also be a result of the exercise intensity not
being high enough and/or the exercise not being long enough.

The findings of this study have a range of implications, including, individuals exposed to heat exposure after periods of exercise/physical activity. If thermal sensation and, subsequently, thermal behavior are impaired after exercise then the risk of heat-related illness may be elevated if an individual is subsequently exposed to heat stress because they may not engage in optimal thermal behavior to alleviate thermal discomfort. Furthermore, the findings could help inform clothing design that counteracts impaired thermal sensation of individuals exercising or working and exposed to heat stress.

235 There are some limitations to this study that are worthy of consideration. Given the regional 236 variation in thermal sensation across the body [14, 15], assessment of thermal sensation at additional 237 sites, particularly on the torso or head, may have provided contrasting findings. Although local skin 238 temperature at the sensation assessment sites was monitored, an index of core temperature was not 239 recorded. It is highly likely that core temperature would have been elevated in the HIGH relative to 240 the LOW trial and remained elevated for some time into the recovery period. Whether a higher 241 exercise intensity would have further accentuated the changes in forearm thermal sensation and/or 242 unmasked any changes in calf thermal sensation is also relevant. Finally, we chose to assess thermal 243 sensation using a standard and commonly used method of thermal detection thresholds. Alternative

means of assessing thermal sensation, such as magnitude estimation via perceptual ratings of

245 constant local heat stimuli, could have revealed complementary findings.

### 246 5. Conclusions

In conclusion, the findings of the present study indicate that cutaneous thermal sensitivity of an
 inactive limb is elevated only after higher intensity exercise, suggesting impaired sensory afferent
 function post-exercise, whereas thermal sensitivity of a previously active limb is not changed after

- 250 exercise. Exercise does not affect heat pain sensitivity in either previously active or inactive limbs.
- 251

- Author Contributions: Conceptualization, D.A.L., H.J., D.H.J.T. and H.H.C.; methodology, D.A.L., H.J. S.D.T.
- and H.H.C.; formal analysis, D.A.L. and S.D.T.; investigation, D.A.L. and S.D.T.; data curation, S.D.T. and D.A.L.; writing—original draft preparation, S.D.T. and D.A.L.; writing—review and editing, D.A.L., S.D.T., H.J.,
- D.A.L.; writing original draft preparation, S.D.T. and D.A.L.; writing review and editing, D.A.L., S.D.T., H.J.,
   H.H.C., D.H.J.T.; visualization, S.D.T. and D.A.L.; supervision, D.A.L.; project administration, S.D.T. and D.A.L.
- 256 All authors have read and agreed to the published version of the manuscript.
- 257 **Funding:** This research received no external funding
- 258 Acknowledgments: We wish to acknowledge support for data collection provided by Mr Yuvo Kuco.
- 259 Conflicts of Interest: The authors declare no conflict of interest.
- 260 References
- 261 1. Schlader ZJ, Stannard SR, Mundel T. Human thermoregulatory behavior during rest and
- 262 exercise a prospective review. *Physiol Behav.* 2010;99(3):269-75.
- 263 2. Flouris AD. Functional architecture of behavioural thermoregulation. *Eur J Appl Physiol*.
- 264 2011;111(1):1-8.
- 265 3. Smith CJ, Johnson JM. Responses to hyperthermia. Optimizing heat dissipation by convection
- and evaporation: Neural control of skin blood flow and sweating in humans. *Auton Neurosci.*2016;196:25-36.
- 268 4. Vargas NT, Chapman CL, Johnson BD, Gathercole R, Cramer MN, Schlader ZJ. Thermal
- 269 behavior alleviates thermal discomfort during steady-state exercise without affecting whole body
- 270 heat loss. J Appl Physiol. 2019;127(4):984-94.
- 271 5. Kenny GP, McGinn R. Restoration of thermoregulation after exercise. *J Appl Physiol*.
- 272 2017;122(4):933-44.
- 273 6. Vargas NT, Chapman CL, Sackett JR, Abdul-Rashed J, McBryde M, Johnson BD, Gathercole R,
- 274 Schlader ZJ. Thermal behavior remains engaged following exercise despite autonomic
- thermoeffector withdrawal. *Physiol Behav.* 2018;188:94-102.
- 276 7. Koltyn KF. Analgesia following exercise: a review. *Sports Med.* 2000;29(2):85-98.
- 8. Kemppainen P, Pertovaara A, Huopaniemi T, Johansson G, Karonen SL. Modification of dental
- pain and cutaneous thermal sensitivity by physical exercise in man. *Brain Res.* 1985;360(1-2):33-40.
- 9. Gerrett N, Ouzzahra Y, Redortier B, Voelcker T, Havenith G. Female thermal sensitivity to hot
- and cold during rest and exercise. *Physiol Behav.* 2015;152(Pt A):11-9.
- 281 10. Ouzzahra Y, Havenith G, Redortier B. Regional distribution of thermal sensitivity to cold at
- rest and during mild exercise in males. *J Therm Biol*. 2012;37(7):517-23.
- 283 11. Gerrett N, Ouzzahra Y, Coleby S, Hobbs S, Redortier B, Voelcker T, Havenith G. Thermal
- sensitivity to warmth during rest and exercise: a sex comparison. *Eur J Appl Physiol*.
- 285 2014;114(7):1451-62.
- 286 12. Vargas NT, Chapman CL, Johnson BD, Gathercole R, Schlader ZJ. Exercise intensity
- independently modulates thermal behavior during exercise recovery but not during exercise. *J Appl Physiol.* 2019;126(4):1150-9.
- 289 13. Ruble SB, Hoffman MD, Shepanski MA, Valic Z, Buckwalter JB, Clifford PS. Thermal pain
- 290 perception after aerobic exercise. *Arch Phys Med Rehabil*. 2005;86(5):1019-23.
- 291 14. Stevens JC, Marks LE, Simonson DC. Regional sensitivity and spatial summation in the
- 292 warmth sense. *Physiol Behav.* 1974;13(6):825-36.
- 293 15. Nadel ER, Mitchell JW, Stolwijk JA. Differential thermal sensitivity in the human skin. *Pflugers*
- 294 Arch. 1973;340(1):71-6.

- 295 16. Jones H, Green DJ, George K, Atkinson G. Intermittent exercise abolishes the diurnal variation
- in endothelial-dependent flow-mediated dilation in humans. *Am J Physiol Regul Integr Comp Physiol*.
  2010;298(2):R427-32.
- 298 17. Rolke R, Magerl W, Campbell KA, Schalber C, Caspari S, Birklein F, Treede RD. Quantitative
- sensory testing: a comprehensive protocol for clinical trials. *Eur J Pain*. 2006;10(1):77-88.
- 300 18. Toner MM, Drolet LL, Pandolf KB. Perceptual and physiological responses during exercise in
- 301 cool and cold water. *Percept Mot Skills*. 1986;62(1):211-20.
- 302 19. Borg GA. Psychophysical bases of perceived exertion. *Med Sci Sports Exerc.* 1982;14(5):377-81.
- 303 20. Beaumont A, Hughes J. Biology of opioid peptides. *Annu Rev Pharmacol Toxicol*. 1979;19:245-67.
- 304 21. Farrell PA, Gustafson AB, Morgan WP, Pert CB. Enkephalins, catecholamines, and
- psychological mood alterations: effects of prolonged exercise. *Med Sci Sports Exerc.* 1987;19(4):347 53.
- 307 22. O'Connor PJ, Cook DB. Exercise and pain: the neurobiology, measurement, and laboratory
- 308 study of pain in relation to exercise in humans. *Exerc Sport Sci Rev.* 1999;27:119-66.
- 309 23. Bushnell MC, Duncan GH, Dubner R, Jones RL, Maixner W. Attentional influences on noxious
- 310 and innocuous cutaneous heat detection in humans and monkeys. *J Neurosci.* 1985;5(5):1103-10.
- 311



© 2020 by the authors. Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).

312