

1 **Title: Exercise intensity independently modulates thermal behavior during exercise recovery, but**
2 **not during exercise**
3

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21 **Abstract:**

22 We tested the hypothesis that thermal behavior is greater during and following high compared to
23 moderate intensity exercise. In a 27°C, 20% relative humidity environment, 20 participants (10 females)
24 cycled for 30 min at moderate ($53\pm 6\%$ VO_{2peak}) or high ($78\pm 6\%$ VO_{2peak}) intensity, followed by 120
25 min recovery. Mean skin and core temperatures and mean skin wettedness were recorded continuously.
26 Participants maintained thermally comfortable neck temperatures using a custom-made neck device.
27 Neck device temperature provided an index of thermal behavior. The weighted average of mean skin
28 and core temperatures, and mean skin wettedness provided an indication of the afferent stimulus to
29 thermally behave. Mean skin and core temperatures were greater at end-exercise in high intensity
30 ($P<0.01$). Core temperature remained elevated in high until 70 min recovery ($P=0.03$). Mean skin
31 wettedness and the afferent stimulus were greater at 10-20 min of exercise in high ($P\leq 0.03$), and
32 remained elevated until 60 min recovery ($P<0.01$). Neck device temperature was lower during exercise
33 in high versus moderate intensity ($P\leq 0.02$). There was a strong relation between the afferent stimulus
34 and neck device temperature during exercise (High: $R^2=0.82$, $P<0.01$; Moderate: $R^2=0.95$, $P<0.01$) and
35 recovery (High: $R^2=0.97$, $P<0.01$; Moderate: $R^2=0.93$, $P<0.01$). During exercise, the slope ($P=0.49$) and
36 y-intercept ($P=0.91$) did not differ between intensities. In contrast, the slope was steeper ($P<0.01$) and y-
37 intercept was higher ($P<0.01$) during recovery from high intensity exercise. Thermal behavior is greater
38 during high intensity exercise because of the greater stimulus to behave. The withdrawal of thermal
39 behavior is augmented following high intensity exercise.

40

41 **Keywords:** Thermoafferent feedback, thermoregulation, thermoregulatory behavior, exercise, recovery

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43

44 **New and Noteworthy**

45 This is the first study to determine the effects of exercise intensity on thermal behavior. We show that
46 exercise intensity does not independently modulate thermal behavior during exercise, but is dependent
47 on the magnitude of afferent stimuli. In contrast, the withdrawal of thermal behavior after high intensity
48 exercise is augmented. This may be a consequence of an attenuated perceptual response to afferent
49 stimuli, which may be due to processes underlying post-exercise hypoalgesia.

50 **Introduction**

51 Exercise intensity influences the extent by which autonomic thermoeffectors (i.e. skin blood
52 flow and sweating) are recruited, such that larger elevations in metabolic heat production require
53 proportionately greater heat loss (9). Behavioral responses that promote heat loss are initiated alongside
54 autonomic heat loss thermoeffectors during exercise (37). Thermal behavior is driven by the perception
55 of thermal discomfort (34). At moderate exercise intensities, thermal behavior is influenced primarily by
56 skin wettedness, with a smaller influence from core and skin temperatures (36). Changes in core and
57 skin temperature initiate thermal behavior secondary to activation of thermoreceptors (34). Humans,
58 however, do not possess hygroreceptors to sense skin wettedness. Rather, skin wettedness contributes to
59 the initiation of thermal behavior via both thermal (i.e., evaporation of sweat that cools the skin and
60 signals thermoreceptors) and non-thermal (i.e., movement of perspiration or fluid on the skin that results
61 in a tactile stimulus and mechanoreceptor signaling) neurophysiological pathways (11).

62 It is not known if the intensity of exercise influences the magnitude of thermal behavioral
63 response. Metabolic heat production is greater at higher exercise intensities. This results in larger
64 increases in core and skin temperatures, and a larger sweating response, thereby eliciting greater skin
65 wettedness (9). Thus, it could be expected that thermal behavior will be engaged in proportion to
66 exercise intensity because the afferent stimulus to behave is a function of metabolic heat production. On
67 the other hand, higher intensities can induce hypoalgesia both during and after exercise, such that
68 thresholds to noxious and innocuous stimuli are increased (21, 28, 31) and thermal perceptual responses
69 to cutaneous stimulation are attenuated (14, 30). It would follow then, that higher exercise intensities
70 would require a greater stimulus to generate a level of thermal discomfort sufficient to motivate a
71 behavioral response. Thus, for a given increase in skin and core temperatures and skin wettedness (i.e.,
72 afferent stimuli), thermal behavior during and following high intensity exercise could be blunted
73 compared to lower intensity exercise.

74 Following exercise, autonomic thermoeffectors rapidly return to pre-exercise levels despite

75 continued elevations in core temperature (37). It is likely that high intensity exercise results in elevated
76 core temperature for longer into recovery compared to moderate intensity exercise. Furthermore, the
77 greater accumulation of sweat on the skin may remain for extended periods of time in high compared to
78 moderate intensities. Thus, it is plausible that thermal behavior would be greater during recovery from
79 high intensity exercise compared to moderate intensity exercise.

80 To our knowledge, the effect of exercise intensity on thermal behavior during and following
81 exercise is unknown. Thus, the purpose of the present study was to test the hypothesis that a higher
82 exercise intensity would stimulate a greater thermal behavioral response compared to a moderate
83 exercise intensity both during and following exercise.

84

85 **Methods**

86 *Participants*

87 Twenty young healthy adults (10 females, age: 24 ± 3 y, height: 170 ± 7 cm, weight: 73 ± 13 kg,
88 BSA: 1.8 ± 0.2 m², body fat: $16.4 \pm 7.1\%$, peak oxygen uptake (VO₂peak): 42.1 ± 7.1 ml·kg⁻¹·min⁻¹)
89 participated in this study. All participants were physically active, normotensive, non-smokers, not taking
90 medications, free of any overt cognitive impairments and from any known cardiovascular, metabolic,
91 neurologic or psychological diseases. Female participants were not pregnant, which was confirmed via a
92 urine pregnancy test, and self-reported to be normally menstruating. To control for menstrual cycle
93 hormones, all trials for females were performed during the first 10 days following self-identified
94 menstruation or during the placebo phase of their oral contraceptives (n=4), a period in which estrogen
95 and progesterone are at their lowest levels. Each subject was fully informed of the experimental
96 procedures and possible risks before giving informed written consent. The study was approved by the
97 Institutional Review Board at the University at Buffalo, and performed in accordance with the standards
98 set by the latest revision of the declaration of Helsinki. Participants visited the laboratory on three
99 occasions. Visit one was a screening and familiarization visit and visits two and three were experimental

100 trials. It should be noted that a subset of the present data has been published previously in a study that
101 tested a unique hypothesis (36).

102

103 *Instrumentation and measurements*

104 Height and weight was measured with a stadiometer and scale (Sartorius Corp. Bohemia, NY,
105 USA), and body surface area was calculated accordingly (3). Skinfold thickness was measured in
106 triplicate at the chest, axilla, triceps, sub scapula, abdomen, suprailiac, and thigh (Harpenden, Baty
107 International, UK), and percent body fat was estimated from body density (35), which was calculated
108 from the sum of skinfold measurements for males (17) and females (18). Cognitive ability was measured
109 using the Montreal Cognitive Assessment (27). Urine specific gravity was measured in duplicate using a
110 refractometer (Atago USA, Inc., Bellevue, WA, USA) to test that participants were euhydrated prior to
111 performing the trials.

112 A 3-lead ECG (DA100C, Biopac Systems, Inc. Goleta, CA, USA) was used for monitoring heart
113 rate. Blood pressure was measured using manual sphygmomanometry every 10 min throughout the
114 protocol. Skin blood flow was measured continually on the dorsal aspect of the left forearm via laser
115 Doppler flowmetry (Periflux System 5010, Perimed, Stockholm, Sweden).

116 Metabolic data were obtained via a mouthpiece with a one-way non-rebreathing valve (Hans
117 Rudolph, Inc. Shawnee, KS, USA) at the end of 10 min pre-exercise time point, at 15 and 30 minutes
118 during exercise and every 30 minutes during post-exercise. Minute ventilation was calculated from
119 expired airflow measured via a heated pneumotachometer (Hans Rudolph, Inc. Shawnee, KS, USA),
120 which was continuously integrated over 1 min and corrected to standard temperature, pressure, dry
121 (STPD). The fractions of expired oxygen and carbon dioxide (VacuMed, Ventura, CA, USA) were
122 continuously measured from a 3 L mixing chamber. Oxygen uptake and carbon dioxide production were
123 calculated using the Haldane Transformation. The rate of metabolic heat production was calculated from
124 oxygen uptake and the respiratory exchange ratio (RER) using a standard equation (9). These data are

125 presented normalized to body surface area (W/m^2). The external workload was calculated by multiplying
126 the cadence by the resistance load applied to the ergometer. The rate of evaporation required for heat
127 balance was also determined relative to body surface area (W/m^2) during exercise and recovery using a
128 standard equation (8).

129 Approximately 60 min prior to any experimental testing, participants swallowed a telemetry pill
130 (HQ Inc., Palmetto, FL, USA) for the measurement of core temperature. Following ingestion of the pill,
131 participants were not permitted to eat or drink anything until the end of the testing. In the event that a
132 subject had contraindications to swallowing a core temperature pill, a rectal thermistor (Mon-a-therm;
133 Mallinckrodt Medical, Inc., St Louis, MO, USA) was inserted by the subject, 10 cm beyond the anal
134 sphincter (n=1). Mean skin temperature was measured as the equally weighted average of ten
135 thermochron iButtons (Maxim Integrated Products Inc., San Jose, CA, USA) attached to the left side of
136 the body on the lower shin, posterior calf, posterior thigh, anterior thigh, abdomen, chest, scapula, hand,
137 triceps and forehead (23). This 10 site, unweighted average was used based on current evidence that this
138 method is best for studies related to thermal comfort (23).

139 Local sweat rate was measured by securing a capsule that covered $3.9cm^2$ of the skin 3-5 cm
140 below the axilla, on the mid-axillary line, and posterior shoulder on the left side of the body. The
141 capsule was taped tightly to the skin to prevent any air from escaping or entering the chamber
142 throughout the protocol. Both areas represent regions of the body that possess eccrine sweat glands,
143 were under the participant's shirt so as to provide an indication of sweat under clothed areas, and were
144 in accessible areas that are not rapidly moving during cycling exercise. Dry nitrogen was perfused
145 through the capsule at a rate of 0.5 L/min, allowing for measurement of the water vapor exiting the gas
146 capsules to be continuously measured by capacitance hygrometry (HMT130, Vaisala, Woburn, WA,
147 USA). Local sweat rate was calculated by multiplying the humidity output by the flow rate of the dry
148 nitrogen and dividing that value by the surface area of the capsule. The local sweat rates are reported as
149 an average of both areas.

150 Relative humidity of the skin was measured via 8 hydrochron iButtons (Maxim Integrated
151 Products Inc., San Jose, CA, USA) placed directly adjacent to a thermochron iButton at the forehead,
152 chest, upper arm, forearm, sub-scapula, abdomen, anterior thigh and calf. At each location, the iButton
153 was raised ~6 mm off the skin using a custom-made capsule that allowed airflow to pass through
154 naturally. The distance of 6 mm was chosen because it ensured that the humidity sensor of the iButton
155 would not become artificially supersaturated due to a droplet of sweat entering the hygrosensor (36).
156 Additionally, 6 mm was deemed acceptable based on pilot testing performed in our laboratory that
157 revealed no differences between 2 mm and 6 mm in the measured relative humidity or calculated partial
158 pressure of water on the mat (see Appendix A). Relative humidity from the iButtons placed on each site
159 were used to determine the water vapor pressure of the skin using standard calculations as previously
160 reported by Filingeri et al. (10). Local skin wettedness was calculated according to the methods of
161 Gagge (13). Whole body mean skin wettedness was calculated as the equally weighted average of all 8
162 local skin wettedness sites.

163 Thermal behavior was measured using a technique modified by those of Cabanac et al. (5, 6).
164 This technique requires participants to control the temperature of the dorsal aspect of their neck so that it
165 is thermally comfortable throughout the experiment (2, 33, 36). The neck is the only skin area known to
166 be equally and highly sensitive to both cooling and heating (26). Thus, neck skin and neck device
167 temperatures provide objective and continuous measures of thermal behavior (5, 6). Neck temperature
168 was controlled using a dual tubing system (effective contact area: 20 x 10 cm) that was in constant
169 contact with the posterior aspect of the subject's neck, secured using a Velcro strap. This tubing system
170 contains two unique series of tubing. One series was continually perfused with thermoneutral (34°C)
171 water. The other series was perfused by a cold fluid (-20°C), and the flow of this fluid was directly
172 controlled by the subject using a two-way ball valve. This permitted a range of neck skin temperatures
173 (~20 to ~35°C) that were rapidly changed (within ~15 s). The temperature of the effluent fluid
174 immediately following contact with the neck was measured using a single thermocouple embedded in

175 the tubing of the neck device. This neck device temperature provided a precise indication of when, and
176 the extent by which, participants behaviorally thermoregulated (37). Neck skin temperature was
177 measured using a single thermocouple taped to the dorsal aspect of the neck directly underneath the neck
178 device. Participants were specifically instructed to use the device to keep their neck at a thermally
179 comfortable temperature throughout the protocol and were allowed to turn the device on and off as
180 necessary to do so.

181 Perceptual measures for the whole-body and neck were taken every 10 min to the nearest 0.5
182 units using the following standard visual analogue scales: thermal sensation (1=cold, 4=neutral, 7=hot
183 (12)); thermal comfort (1=comfortable, 4=very uncomfortable (12)); and skin wettedness (+3=very wet,
184 +2=wet, +1=slightly wet, 0=neutral, -1=slightly dry, -2=dry, -3=very dry (10)).

185

186 *Familiarization Protocol*

187 At least 48 h prior to experimental testing, participants reported to the laboratory to perform a
188 VO_2 peak test and were familiarized with the neck device and perceptual questionnaires. The VO_2 peak
189 test was used to determine the relative cycling intensity that would elicit a high (~75% VO_2 peak) and
190 moderate (~50% VO_2 peak) relative exercise intensity. The high exercise intensity was chosen because
191 relative exercise intensities of greater than 70% of VO_2 peak have been shown to elicit perceptual
192 hypoalgesia (16). The moderate exercise intensity is similar to what we used previously in our initial
193 investigation into the control of thermal behavior during and following exercise (37). Participants
194 completed a 5 min warm up on the cycle ergometer at a resistance of their choice, followed by 2 min of
195 rest, after which 2 min of baseline measures were collected. The first stage of the VO_2 peak protocol
196 began immediately following baseline measures. Participants chose a cadence between 70-80 rpm. The
197 actual cadence was maintained throughout the duration of the test and during the subsequent
198 experimental trials. The first stage began at 0.5 kp for females and 1.0 kp for males, and increased by
199 0.25 kp every minute thereafter until volitional exhaustion, defined as the inability to maintain their

200 cadence within 10 rpm of the required cadence. $\text{VO}_{2\text{peak}}$ was identified as the highest oxygen
201 consumption value (per minute) measured during the test.

202

203 *Experimental protocol*

204 Participants arrived at the laboratory for their experimental trials euhydrated, confirmed via urine
205 specific gravity <1.020 (actual urine specific gravity – high: 1.009 ± 0.006 ; moderate: 1.010 ± 0.007),
206 and having refrained from strenuous exercise, alcohol and caffeine for 12 h, and food for 2 h. All
207 experimental testing was conducted during the winter months in Buffalo, NY (outside temperature on
208 experimental days – high: $-2 \pm 5^{\circ}\text{C}$; moderate: $-1 \pm 5^{\circ}\text{C}$). Participants wore a standard short sleeved
209 crew t-shirt and running shorts (lululemon, men or women’s cut), and their own socks and athletic shoes
210 (~ 0.4 clo). Females also wore the same sports bra of their choosing for both trials.

211 The experimental trials took place in a moderate thermal environment (high: $27.0 \pm 1.0^{\circ}\text{C}$, $21 \pm$
212 2% relative humidity, moderate: $27.0 \pm 0.5^{\circ}\text{C}$, $22 \pm 4\%$ relative humidity). Following instrumentation,
213 participants sat on a mesh chair behind a standard upright cycle ergometer (Monark 828E, Sweden) for
214 10 min while baseline measures were collected. Participants were then carefully transferred to the cycle
215 ergometer for 30 min of high intensity ($78 \pm 6\% \text{VO}_{2\text{peak}}$, metabolic heat production: $396 \pm 69 \text{ W/m}^2$)
216 or moderate intensity cycling ($53 \pm 6\% \text{VO}_{2\text{peak}}$, $275 \pm 50 \text{ W/m}^2$). The moderate intensity was
217 chosen to simulate an earlier study that we have performed, while the high intensity trial was chosen
218 because $75\% \text{VO}_{2\text{peak}}$ has been shown to be above the threshold of exercise induced hypoalgesia (16,
219 21). This was followed by 120 min seated recovery on the aforementioned mesh chair. Participants
220 were allowed to watch non-stimulating documentaries (i.e., Planet Earth, BBC Natural History Unit)
221 throughout the entire protocol.

222

223 *Data and statistical analyses*

224 Data were continuously recorded at 100 Hz via a data acquisition system and binned as 60 s
225 averages every 10 min (Biopac MP160, Goleta, CA, USA). The mean afferent stimulus is thought to be
226 a measure of thermal stimuli (mean skin and core temperatures, and skin wettedness) that can contribute
227 to thermal behavior (36). The mean afferent stimulus was calculated for minute data using the sum of
228 the following weightings: core x 0.22; mean skin temperature x 0.26, mean skin wettedness x 0.52 (36).
229 This derivation provided an index of the afferent stimulus for thermal behavior (36). Temporal data were
230 analyzed for changes over time using a two-way (time x condition) repeated measures ANOVA. For the
231 temporal data, when a significant F test was identified, a priori Sidak post hoc comparisons were made
232 between pre-exercise (i.e., 10 min pre-exercise) and end-exercise (i.e., 30 min exercise) time points.
233 Segmental regression analyses were initially employed to determine the threshold mean afferent
234 stimulus at which thermal behavior was engaged and the gain of the response after activation. However,
235 inspection of the data revealed a linear response with no clear threshold. Therefore, linear regression
236 analyses were performed on minute data for exercise and recovery to determine the relationships
237 between the mean afferent stimulus (independent variable) and neck device temperature (i.e., thermal
238 behavior, dependent variable) during high and moderate intensity exercise. These linear regression
239 analyses were carried out on the mean data and not on a per subject basis because the linear regression
240 analyses on the individual data revealed that some models were not statistically significant ($P > 0.05$)
241 during recovery. Specifically, four participants did not engage in thermal behavior following exercise in
242 the moderate intensity trial. Removal of these subjects from the analysis was deemed unacceptable
243 because it would have biased the results (i.e., the subjects who chose not to behaviorally thermoregulate
244 did so willingly). Independent sample t-tests were used to determine differences in the slope of the line
245 and the y-intercept obtained from the linear regression models between exercise intensities during
246 exercise and recovery (1). No comparisons were made between exercise and recovery because these
247 comparisons were not necessary to test our hypothesis. All analyses were carried out using Prism

248 (Version 7, GraphPad Software Inc., La Jolla, CA). For all analyses, *a priori* statistical significance was
249 set at $P \leq 0.05$ and actual P-values are reported where possible.

250

251 **Results**

252 *Body temperatures, mean skin wettedness and the mean afferent stimulus*

253 Mean skin temperature increased and was greater by the end of exercise in the high intensity trial
254 compared to moderate intensity ($P \leq 0.01$) (Figure 1A). Core temperature also peaked at the end of
255 exercise and was elevated in the high compared to moderate intensity trials and remained elevated in
256 high intensity through 90 min of recovery ($P \leq 0.01$) (Figure 1B). Due to technical difficulties, skin
257 wettedness data were not collected for 5 participants, resulting in $n=15$ (8 females). The increase in
258 mean skin wettedness was greater in high compared to moderate intensity at 10 and 20 min ($P \leq 0.03$),
259 but was not different at the end of exercise ($P=0.43$). However, mean skin wettedness remained elevated
260 through 60 min of recovery in high compared to moderate intensity ($P < 0.01$) (Figure 1C). The mean
261 afferent stimulus followed a similar trajectory with elevations in high compared to moderate intensity in
262 the first 10-20 min ($P \leq 0.02$), but was not different at end of exercise ($P=0.25$). The mean afferent
263 stimulus also remained elevated in the high intensity compared to moderate intensity condition through
264 60 min of recovery ($P < 0.01$) (Figure 1D).

265

266 *Thermoeffectors*

267 Neck device temperature was lower (i.e., thermal behavior was greater) in high compared to
268 moderate intensity at 10 and 20 min of exercise ($P \leq 0.02$). Neck device temperature was not different
269 between intensities during recovery ($P \geq 0.60$) (Figure 2A). There were no differences in temporal
270 analyses between high and moderate intensity for neck skin temperature during exercise or recovery
271 ($P \geq 0.41$) (Figure 2B). Average local sweat rate (Figure 2C) and forearm skin blood flow (Figure 2D)
272 were greater in high compared to moderate intensity within the first 10 min of exercise, and remained

273 elevated throughout the first 10 min of recovery ($P \leq 0.03$). During recovery, there were no temporal
274 differences for average local sweat rate ($P \geq 0.90$) or forearm skin blood flow ($P \geq 0.65$) between
275 intensities.

276

277 *Thermal perceptions*

278 Neck thermal sensation was perceived to be warmer in high compared to moderate intensity
279 exercise only at 30 min during exercise ($P < 0.01$) (Figure 3A). The thermal comfort of the neck was
280 perceived to be more uncomfortable at 20 and 30 min of exercise ($P < 0.01$) (Figure 3C), while neck skin
281 wettedness was perceived to be greater during all of high intensity exercise compared to moderate
282 intensity ($P \leq 0.05$) (Figure 3E). Whole body thermal sensation ($P < 0.01$) (Figure 3B), thermal comfort
283 ($P \leq 0.01$) (Figure 3D) and skin wettedness ($P < 0.01$) (Figure 3F) were perceived to be greater in high
284 compared to moderate intensity throughout the entire exercise period. Only whole body skin wettedness
285 remained elevated in high compared to moderate intensity exercise until 20 min into recovery ($P < 0.01$),
286 after which they were not different from each other ($P \geq 0.93$).

287

288 *Relationships between the mean afferent stimulus and thermal behavior*

289 Linear regression analyses for the mean afferent stimulus and neck device temperature revealed a
290 strong relation during exercise for high ($R^2 = 0.824$, $P < 0.01$) and moderate ($R^2 = 0.953$, $P < 0.01$)
291 intensities. Likewise, there was a strong relation between the two variables during recovery for high
292 ($R^2 = 0.966$, $P < 0.01$) and moderate ($R^2 = 0.926$, $P < 0.01$) intensities. There were no differences between
293 intensities for the slope of the line (High: $-0.93 \pm 0.31^\circ\text{C}/\text{a.u.}$; Moderate: $-0.87 \pm 0.14^\circ\text{C}/\text{a.u.}$, $P = 0.49$) or
294 the y-intercept (High: $43.43 \pm 11.56^\circ\text{C}$; Moderate: $43.76 \pm 4.86^\circ\text{C}$, $P = 0.92$) during exercise. However,
295 during recovery, high intensity exercise had a greater slope (High: $-0.94 \pm 0.06^\circ\text{C}/\text{a.u.}$; Moderate: -0.77
296 $\pm 0.07^\circ\text{C}/\text{a.u.}$; $P < 0.01$), and y-intercept (High: $49.33 \pm 2.05^\circ\text{C}$; Moderate: $41.77 \pm 2.35^\circ\text{C}$, $P < 0.01$)
297 (Figure 4).

298

299 **Discussion**

300 The present study tested the hypothesis that thermal behavior would be utilized to a greater
301 extent during and following high intensity exercise compared to moderate intensity exercise. Our data
302 during exercise support this hypothesis, revealing that thermal behavior was greater in high compared to
303 moderate intensity exercise (Figure 2). That is, neck device temperature was reduced to a greater extent
304 during high intensity exercise. However, linear regression analyses between thermal behavior and the
305 mean afferent stimulus revealed no differences in the slope of the line or y-intercept during exercise
306 (Figure 4). Therefore, thermal behavior was engaged to a greater extent during high intensity exercise,
307 but this was likely due to the greater level of afferent stimuli. In contrast to our hypothesis, however,
308 thermal behavior did not differ during recovery between high and moderate intensity exercise (Figure 2).
309 Despite this, the slope of the linear regression was steeper and the y-intercept was higher during
310 recovery from high intensity exercise (Figure 4). Thus, during recovery from high intensity exercise, the
311 withdrawal of thermal behavior for a given reduction in the afferent stimulus back towards pre-exercise
312 levels was augmented, compared to moderate intensity exercise. Contrary to what occurs during
313 exercise, this suggests that exercise intensity independently modulates thermal behavior during post-
314 exercise recovery.

315

316 *Thermal behavior during different intensities of exercise*

317 We have previously shown that thermal behavior is engaged during moderate intensity exercise
318 alongside activation of the other heat loss thermoeffectors including sweat rate and increases in skin
319 blood flow (37). To our knowledge, the present study is the first to determine whether the intensity of
320 exercise affects the engagement of thermal behavior. It has been shown that skin wettedness and core
321 and mean skin temperatures are all important contributors to thermal behavior (36). These variables all
322 increase in proportion to exercise intensity and the rate of metabolic heat production (8). Hence, it

323 follows that because high intensity exercise induces greater elevations in body temperatures and skin
324 wettedness, the desire to engage in thermal behavior would also be greater. Indeed, the data in the
325 present study reveal that the mean afferent stimulus for thermal behavior was elevated in high compared
326 to moderate intensity exercise (Figure 1), and that this coincided with a greater thermal behavioral
327 response, defined as a greater magnitude of neck cooling (i.e., lower neck device temperature) (Figure
328 2).

329 Exercise has been shown to attenuate the perceptual response to thermal stimuli (15, 30). These
330 observations have been attributed to exercise induced hypoalgesia, whereby thresholds to pain and
331 innocuous stimuli are increased during and following exercise (16). This response is particularly marked
332 with exercise intensities exceeding 70% of maximal oxygen uptake (16, 20). Theoretically, exercise
333 induced hypoalgesia could attenuate the magnitude of thermal behavior during high intensity exercise.
334 For instance, a given increase in the afferent stimulus to behaviorally thermoregulate could translate to a
335 lower level of thermal discomfort during high intensity exercise compared to moderate intensity
336 exercise. Because thermal behavior is dependent on the magnitude of thermal discomfort (34), this could
337 result in a blunted thermal behavioral response. Importantly, the findings from the present study indicate
338 that this scenario is unlikely because the slope and y-intercept of the relation between neck device
339 temperature and the mean afferent stimulus did not differ between high and moderate exercise intensities
340 (Figure 4). Collectively, this supports that exercise intensity is not an independent modulator of thermal
341 behavior during exercise. Rather, thermal behavior is engaged in proportion to the magnitude of afferent
342 stimulation, which is dependent on exercise intensity.

343 Importantly, the neck device did not fully alleviate neck thermal discomfort throughout high
344 intensity exercise. This is evidenced by the average neck thermal discomfort being slightly elevated
345 during high intensity exercise (Figure 3). It is possible that despite a drop in neck skin temperature by
346 $\sim 7^{\circ}\text{C}$, subjects required even greater reductions in neck skin temperature to maintain neck thermal
347 comfort than our neck device permitted during high intensity exercise. Therefore, our data indicating a

348 greater decrease in neck device temperature during high intensity exercise may be underestimating the
349 magnitude of this effect. To further explore this possibility, we normalized neck device temperature to
350 neck thermal comfort. This post hoc analysis (data not shown) revealed similar results to those formally
351 presented herein, such that reductions in these normalized data were greater during high intensity
352 exercise. Although performing linear regression analyses on these normalized data may provide further
353 insight, we were unable to accurately complete this analysis due to the limited time points in which neck
354 thermal comfort was assessed during exercise (i.e., 3 data points). Nevertheless, we believe that these
355 normalized data further support that the magnitude of thermal behavior during exercise is dependent on
356 the magnitude of the afferent stimulus and not exercise intensity.

357

358 *Thermal behavior during recovery from different intensities of exercise*

359 During recovery from moderate intensity exercise, thermal behavior remains engaged, likely in
360 an effort to maximize heat loss at a time when autonomic thermoeffectors are effectively withdrawn
361 (37). In the present study, local sweat rate and forearm skin blood flow remained elevated in high
362 compared to moderate intensity exercise in the first 10 min of recovery. However, in both trials these
363 autonomic thermoeffectors had returned to pre-exercise levels 20 min into recovery (Figure 2), despite
364 continued elevations in core temperature (Figure 1). In accordance with our previous findings (37), neck
365 device temperature was depressed compared to pre-exercise levels for almost an hour into recovery
366 (Figure 2). Notably, neck device temperature was not different between high and moderate exercise
367 intensities during recovery (Figure 2). This occurred despite a greater afferent stimulus to continue to
368 thermally behave following high intensity exercise (Figure 1). Thus, compared to the recovery during
369 moderate intensity exercise, during recovery from high intensity exercise, subjects withdrew thermal
370 behavior at a rate that was disproportionately high relative to the magnitude of changes in the afferent
371 stimulus to continue behaving. In line with this conclusion, our linear regression analyses indicated that
372 the slope was steeper and the y-intercept was higher following high intensity exercise, compared to

373 moderate intensity exercise (Figure 4). Hence, for a given change in the mean afferent stimulus back
374 towards pre-exercise levels, the withdrawal of thermal behavior was greater following high intensity
375 exercise. We interpret these findings to suggest a blunted thermal behavioral sensitivity following high
376 intensity exercise. To illustrate this point, we have calculated the mean afferent stimulus that would be
377 expected at the same neck device temperature as occurs pre-exercise (i.e., when thermal behavior is not
378 engaged) from the regression equations obtained for recovery in the high and moderate exercise
379 intensity trials. This analysis might provide insight into the threshold mean afferent stimulus upon which
380 thermal behavior would be engaged. In doing so, we found that the mean afferent stimulus for high
381 intensity exercise was higher than that obtained for moderate intensity exercise (24.1 a.u. vs. 19.8 a.u.).
382 Thus, there is likely a shift in the activation threshold towards a greater afferent stimulus after which
383 thermal behavior will be engaged following high intensity exercise compared to following moderate
384 intensity exercise. We believe that this observation might be explained by post-exercise hypoalgesia,
385 which typically occurs following higher intensity exercise (16, 20). The mechanisms underlying post-
386 exercise hypoalgesia are not fully understood. However, the increased perceptual threshold sensitivity
387 following higher intensity exercise may be related to exercise induced opioid release, inhibition of
388 central perceptual circuitry, the release of factors that bind to pain and/or thermal receptor sites, and/or
389 simply distraction from pain or discomfort (16). Unfortunately, we do not have any measures of
390 endogenous opioid release or other related factors contributing to hypoalgesia following exercise.
391 However, we speculate that decisions to withdraw thermal behavior following exercise are influenced by
392 factors contributing to post-exercise hypoalgesia and that these factors contribute to a greater extent
393 following high intensity exercise.

394

395 *Considerations*

396 Some considerations should be discussed regarding the present study. Firstly, it is worth noting
397 that the results presented herein are constrained to the specific exercise protocols and intensities that

398 were used in the study. Thus, it is possible that the results may vary in different environmental
399 conditions or protocols (i.e., increased or decreased temperatures and/or relative humidity, or using
400 different modes of exercise). Further to this, the individual weightings for the variables used to calculate
401 the mean afferent stimulus for thermal behavior were determined using only moderate intensity exercise.
402 Notably, when we calculated the individual weightings for the variables during the high intensity
403 exercise trial of the current study, they were not statistically different from the moderate intensity
404 exercise trial from our previous study ($P \geq 0.60$, skin temperature: 0.18 ± 0.20 ; core temperature: $0.29 \pm$
405 0.14 ; skin wettedness: 0.53 ± 0.22). Thus, we believe it is appropriate to apply the same weightings for
406 both moderate and high intensity exercise.

407 It is also important to acknowledge that the relation between thermal behavior and the mean
408 afferent stimulus for high intensity exercise may not be linear. We explored numerous regression
409 models, and concluded that linear regression was the best option. This decision was at least partially due
410 to the other three relations that were clearly linear (e.g., Figures 4B, 4C, and 4D). Thus, using linear
411 regression for all four situations permitted formal comparisons between high and moderate intensity
412 exercise. Despite this decision, however, it is possible that thermal behavior was stimulated prior to
413 changes in the afferent stimulus during high intensity exercise, as exemplified by a drop in neck device
414 temperature without an increase in the mean afferent stimulus (Figure 4A). It may be that there was an
415 anticipatory reaction in which subjects employed thermal behavior early to ensure thermal comfort.
416 However, this is speculative. These results highlight the need for further investigation into other thermal
417 and non-thermal factors (i.e., not changes in core temperature, skin temperature or skin wettedness)
418 capable of stimulating thermal behavior during high intensity exercise (24).

419 Additionally, we ensured our females were screened for normal menstruation, were not pregnant,
420 and were tested in the first 10 days of their menstrual cycle. However, we did not confirm their
421 menstrual cycle phase through hormonal analyses. We are confident that our results are representative of
422 females when estrogen and progesterone are at their lowest levels. Nevertheless, it remains important to

423 test females during different stages of their menstrual cycle, especially considering the differences in
424 temperature regulation and perceptions that can occur (22, 32). We also acknowledge that the use of a
425 wireless telemetry pill as an index of core temperature that was ingested only 60 min prior to exercise
426 comes with some limitations, most notably is the reduced temporal sensitivity compared to measures of
427 esophageal temperature (25). However, ingestion of the telemetry pill only 60 min prior to exercise
428 limits the transit time it has to enter the GI tract and thus, may be a more accurate measure than rectal
429 temperature, another index of core temperature with a relatively sluggish temporal resolution (4).

430 Another important consideration is skin wettedness. Skin wettedness is an important contributor
431 to the stimulus for thermal behavior (36). Hence, it was included in our estimate of the mean afferent
432 stimulus to behaviorally thermoregulate. That said, humans do not possess hygrosensors that transmit
433 skin wettedness information to the brain (7). Thus, it is difficult to know whether it is actual skin
434 wettedness or the perception of skin wettedness that is the main driver of thermal behavior (36). This is
435 an important question that remains to be answered. Finally, we note that there were not significant
436 differences in neck skin temperatures, despite differences in neck device temperature. The reason for
437 this discrepancy is not inherently clear. However, it may be due to differences in heat production and the
438 resulting greater elevations in skin blood flow that occurred with high intensity exercise. Theoretically,
439 this could have elevated neck skin temperature to a greater extent, which may have prevented the
440 observation of greater reductions in neck skin temperature in the high intensity exercise trial, despite
441 lower neck device temperatures.

442

443 *Perspectives*

444 Behavioral thermoregulation is an important heat loss effector that will be increasingly relied
445 upon both in sporting events, occupational settings, and in the general population in the face of rising
446 global temperatures. Recreational and professional athletes, individuals performing specific
447 occupational duties (i.e., firefighting or agriculture work), and clinical populations (e.g., multiple

448 sclerosis, the elderly) alike, could benefit from employing behavioral thermoregulation during different
449 intensities of exercise. The present study provides novel insights into the mechanisms by which thermal
450 behavior might be engaged both during and following moderate and high intensity exercise. While
451 numerous factors play a role in the likelihood that an individual will employ thermal behavior whilst
452 performing exercise and/or physical activity, our data indicate that it is not the intensity, but rather the
453 combination of afferent stimuli that provokes an individual to behaviorally thermoregulate. In contrast,
454 following high intensity exercise, the employment of thermal behavior is blunted despite similar levels
455 of afferent stimuli. This could theoretically increase the duration following exercise by which a person
456 might be rendered hyperthermic, which may have implications for safety, fatigue or performance
457 following a bout of exercise. Nevertheless, further research is warranted to examine whether or not
458 altered environmental (19), biophysical (9, 29), and clothing characteristics (10) could modify thermal
459 behavior in different intensities of exercise and if specific recovery modalities are warranted following
460 higher intensities of exercise.

461

462 *Conclusions*

463 To our knowledge, the present study is the first to investigate whether thermal behavior differs as
464 a function of exercise intensity. Our data reveal that the magnitude of thermal behavior during exercise
465 is not affected by exercise intensity per se. Rather, thermal behavior during exercise occurs in proportion
466 to the overall stimulus to behaviorally thermoregulate, which is a function of skin wettedness, core
467 temperature, and skin temperature. After exercise, however, thermal behavioral sensitivity is blunted
468 following high intensity exercise. That is, for a given change in the stimulus to behaviorally
469 thermoregulate back towards pre-exercise levels the withdrawal of thermal behavior was greater
470 following high intensity exercise. Collectively, the present study provides novel insights into the
471 mechanisms by which exercise intensity might modulate thermal behavior during and following
472 exercise.

473

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482 report.

483

484 **Appendix A. iButton Pilot Data**

485 Pilot testing was performed to determine if there were differences between raising our humidity
486 sensors 2 mm and 6 mm off a surface for calculating relative humidity and the partial pressure of water
487 on the mat. Following a 5 min baseline on a dry surface, two humidity sensors were placed on a paper
488 towel saturated with water for 25 min. The paper towel was placed on a water perfused mat set at a
489 temperature of $32.1 \pm 0.4^{\circ}\text{C}$ to mimic skin temperature during low intensity exercise. During each
490 testing period, two humidity sensors were placed at a distance of 2 mm or 6 mm above the mat. For a
491 given humidity sensor, the assignment to a height was tested 5 times. All testing was done in a $27.1 \pm$
492 1.2°C , $25.4 \pm 6.0\%$ relative humidity environment. The relative humidity measured by the sensors and
493 the temperature of the surface (obtained via the average of two thermocouples taped to it) were
494 converted to the partial pressure of water post hoc. Data are presented as mean \pm SD.

495 There were no differences in relative humidity between 2 mm and 6 mm heights at any time
496 point ($P=0.86$) (Figure 5A). There were also no differences in the partial pressure of water on the mat at
497 any time point ($P=0.76$) (Figure 5B). We therefore determined 6 mm to be an appropriate height for

498 measuring skin wettedness, especially during high intensity exercise where the possibility of
499 supersaturation of the iButton is possible.

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586 autonomic thermoeffector withdrawal. *Physiol Behav* 188: 94–102, 2018.
- 587

588 **Table 1** The exercise stimulus (mean \pm SD). External work rates, metabolic heat production, the
589 evaporative heat loss requirement, heart rate, percent maximal oxygen consumption and mean arterial
590 pressure during pre-exercise, exercise and post-exercise (n=20, 10 females).

591

592 **Figure 1** Mean skin temperature (A), core temperature (B), mean skin wettedness (C) and the mean
593 afferent stimulus (D) during exercise and recovery (A&B, n=20, 10 females; C&D, n=15, 8 females;
594 mean \pm SD). *High intensity greater than moderate intensity ($P \leq 0.03$).

595

596 **Figure 2** Neck device temperature (A), neck skin temperature (B), average local sweat rate (C) and
597 forearm skin blood flow (D) during exercise and recovery (n=20, 10 females, mean \pm SD). *High
598 intensity different to moderate intensity ($P \leq 0.03$). #High intensity different to moderate intensity
599 ($P = 0.06$). ^PDifferent from pre-exercise ($P \leq 0.02$). ^EDifferent from end-exercise ($P \leq 0.05$).

600

601 **Figure 3** Neck thermal comfort (A), whole body thermal comfort (B), neck thermal sensation (C), whole
602 body thermal sensation (D), neck skin wettedness (E) and whole-body skin wettedness (F) during
603 exercise and recovery (n=20, 10 females, mean \pm SD). *High intensity different to moderate intensity
604 ($P \leq 0.05$).

605

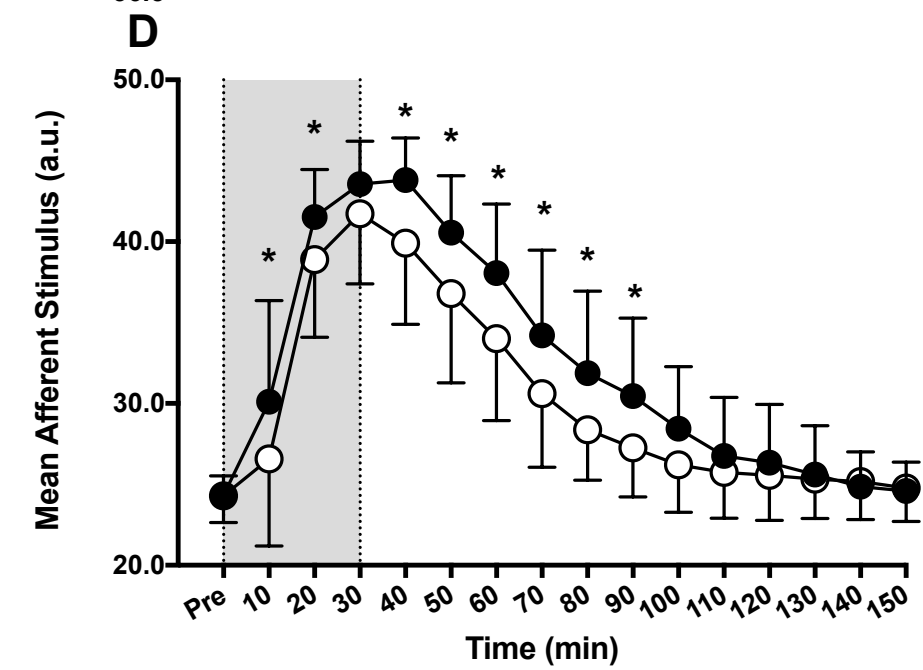
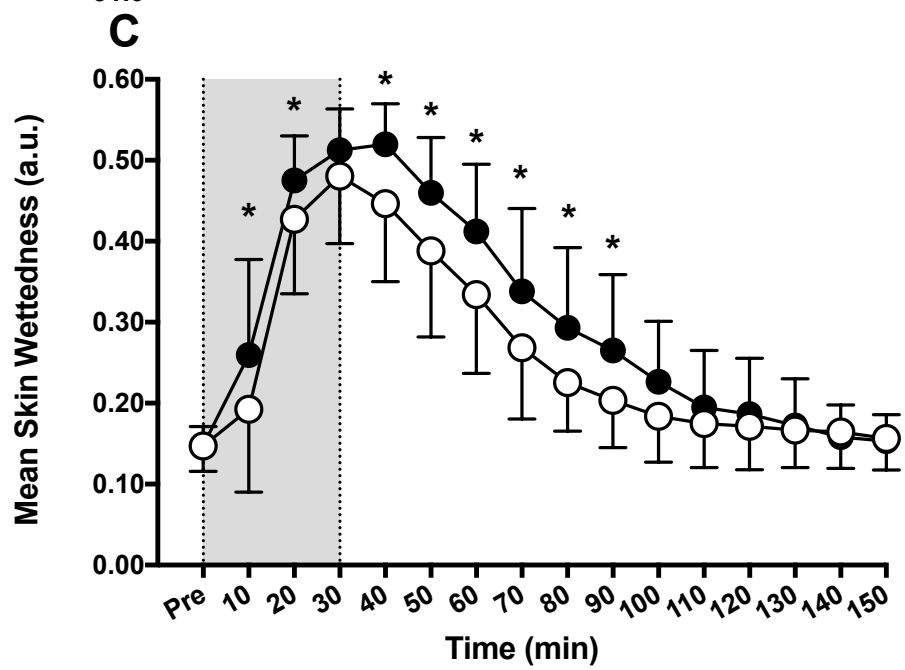
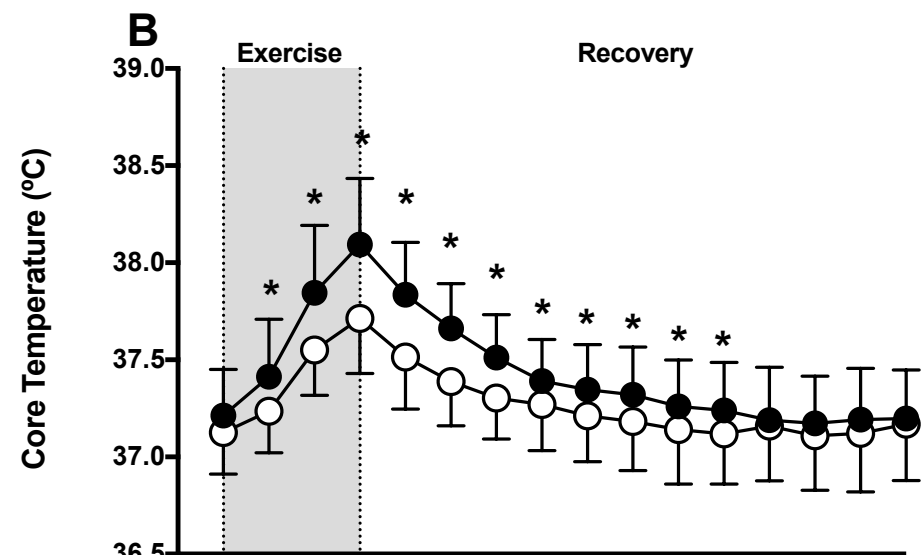
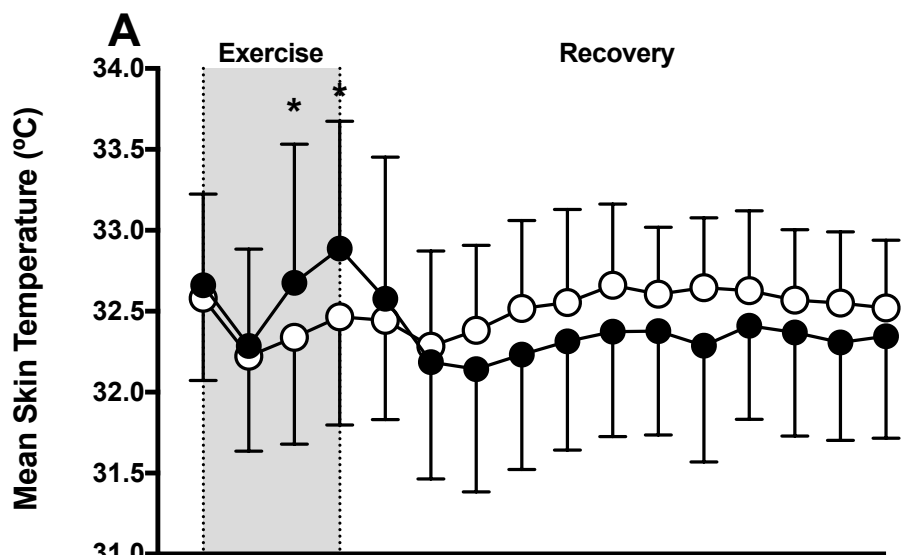
606 **Figure 4** Linear regression analyses (mean \pm SD) between the mean afferent stimulus and neck device
607 temperature (i.e., thermal behavior) during exercise (A, B) and recovery (C, D) (n=15, 8 females). *High
608 intensity different to moderate intensity during recovery ($P < 0.01$).

609

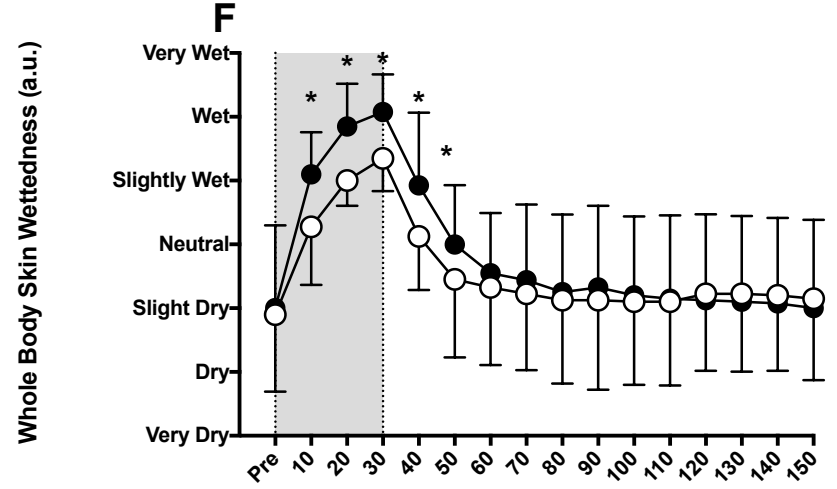
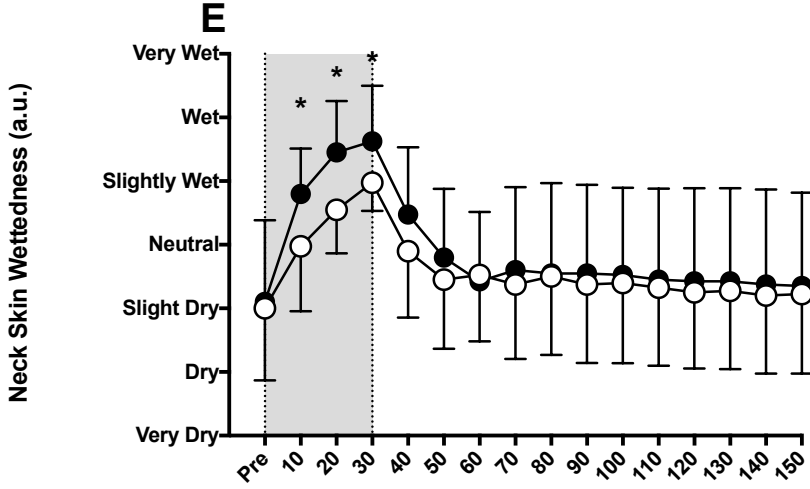
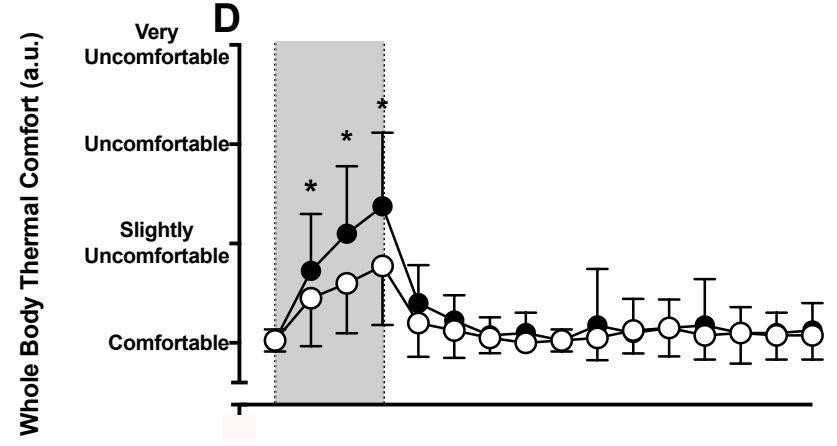
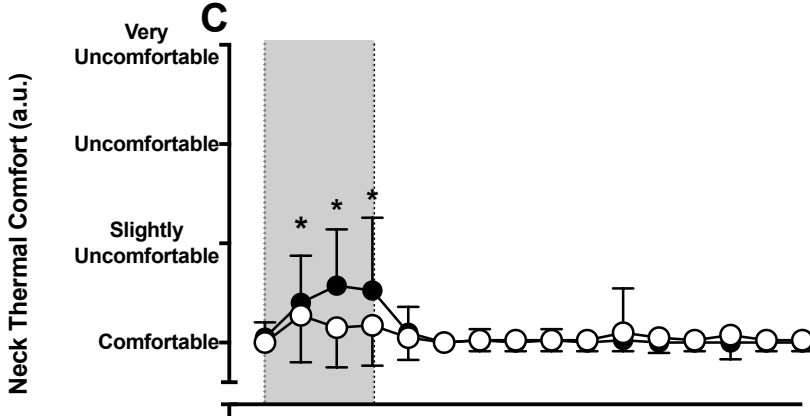
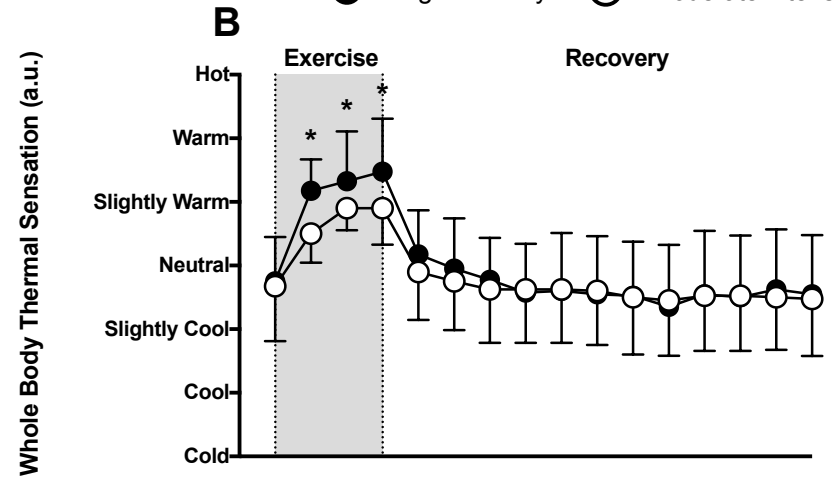
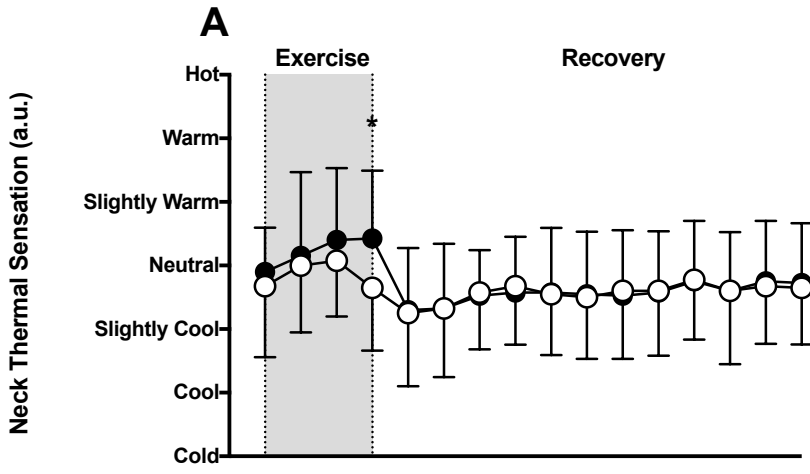
610 **Figure 5** Pilot data (mean \pm SD) between 2 mm and 6 mm humidity sensors for relative humidity (A)
611 and partial pressure of water on the mat (B).

Variables		Pre-Exercise (min)	Exercise (min)		Recovery Time (min)	
		10	15	30	60	120
External work rate (W·m ⁻²)	High	0 ± 0	70 ± 13 ^{P*}	68 ± 13 ^{P*}	0 ± 0 ^E	0 ± 0 ^E
	Moderate	0 ± 0	46 ± 10 ^P	46 ± 10 ^P	0 ± 0 ^E	0 ± 0 ^E
Metabolic heat production (W·m ⁻²)	High	64 ± 8	396 ± 58 ^{P*}	396 ± 79 ^{P*}	66 ± 8 ^E	65 ± 9 ^E
	Moderate	59 ± 10	270 ± 43 ^{PE}	280 ± 57 ^{PE}	62 ± 7 ^E	57 ± 15 ^E
Evaporative heat loss requirement (W·m ⁻²)	High	37 ± 9	311 ± 59 ^{P*}	315 ± 76 ^{P*}	40 ± 10 ^E	37 ± 9 ^E
	Moderate	34 ± 10	209 ± 53 ^P	227 ± 55 ^P	38 ± 8 ^E	35 ± 6 ^E
Heart rate (beats·min ⁻¹)	High	71 ± 10	157 ± 11 ^{P*}	160 ± 13 ^{P*}	77 ± 11 ^{PE*}	73 ± 10 ^{E*}
	Moderate	68 ± 11	124 ± 11 ^P	126 ± 14 ^P	69 ± 10 ^E	67 ± 10 ^E
Peak Oxygen Consumption (%)	High	11 ± 2	78 ± 7 ^{P*}	78 ± 7 ^{P*}	12 ± 2 ^E	11 ± 3 ^E
	Moderate	10 ± 2	53 ± 5 ^P	54 ± 7 ^P	11 ± 2 ^E	10 ± 3 ^E
Mean Arterial Pressure (mmHg)	High	87 ± 8	104 ± 11 ^{P*}	105 ± 12 ^{P*}	85 ± 7 ^E	86 ± 8 ^E
	Moderate	84 ± 8	95 ± 11 ^P	95 ± 11 ^P	83 ± 8 ^E	83 ± 9 ^E

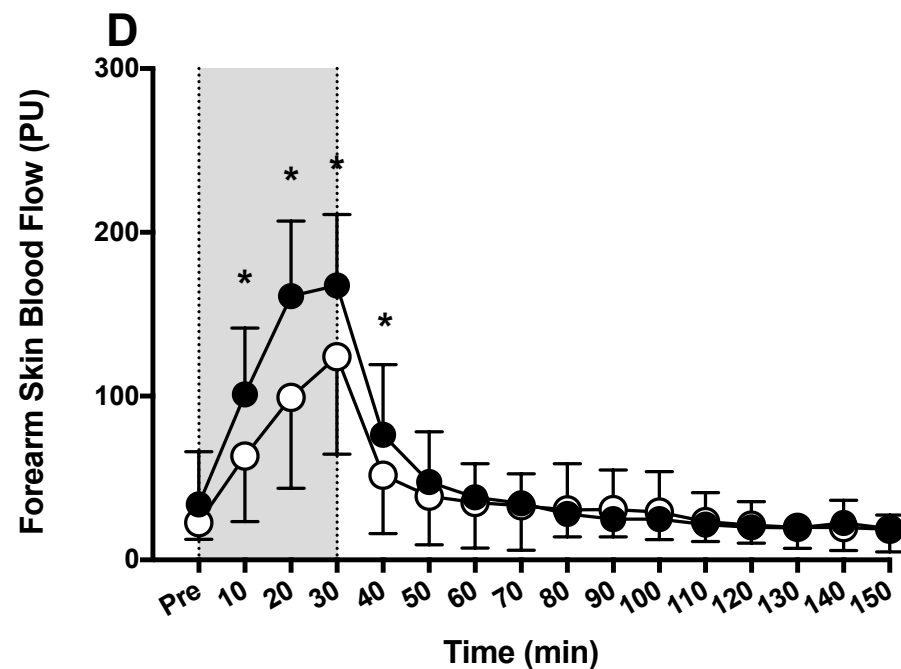
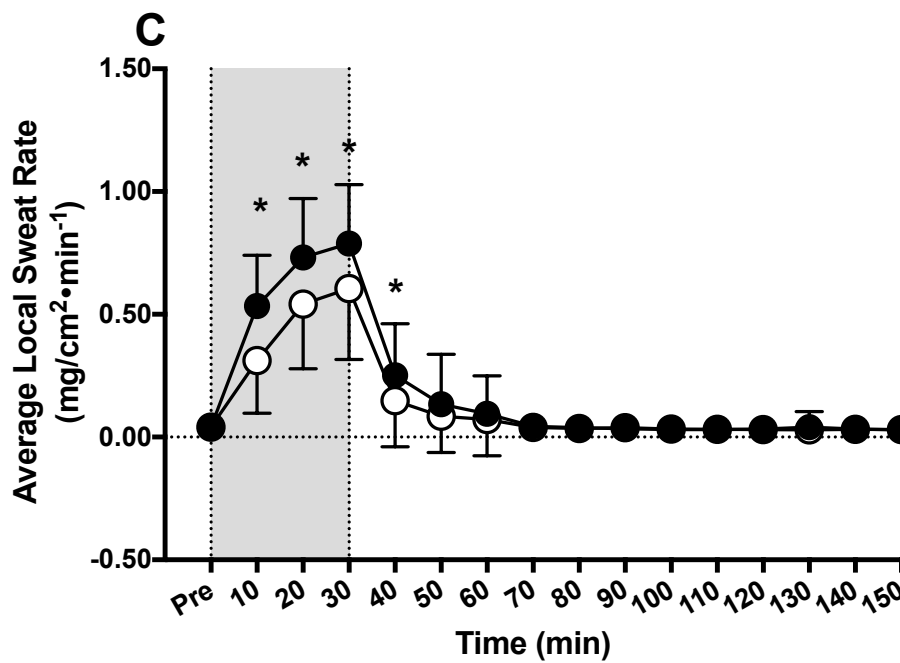
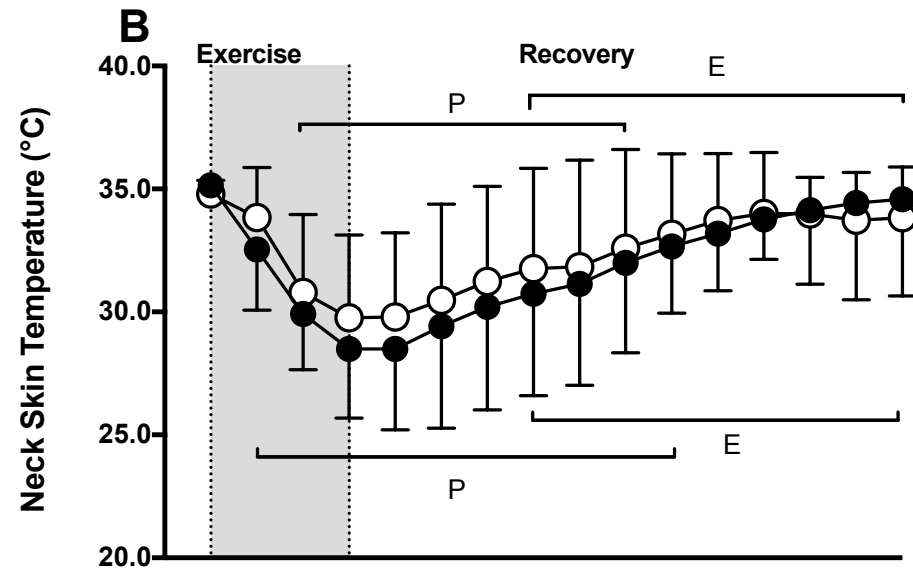
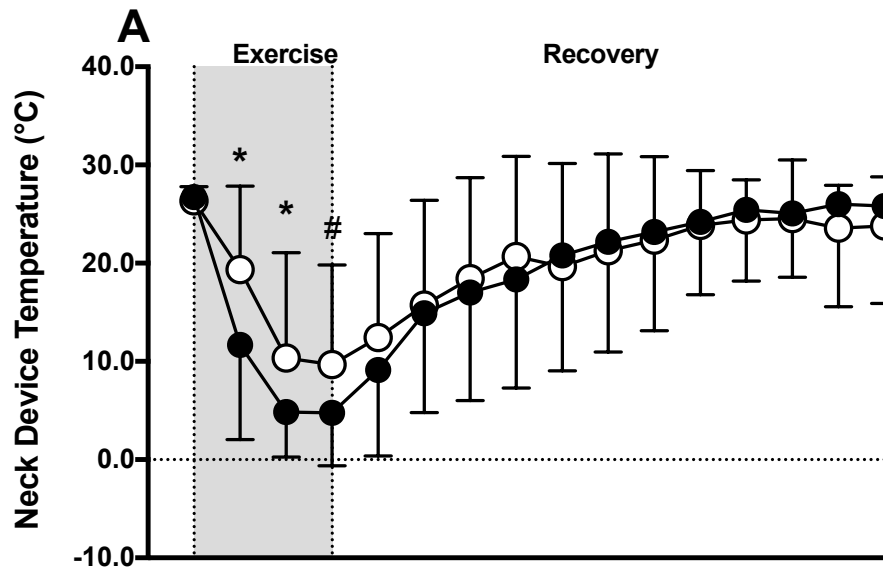
● High Intensity ○ Moderate Intensity



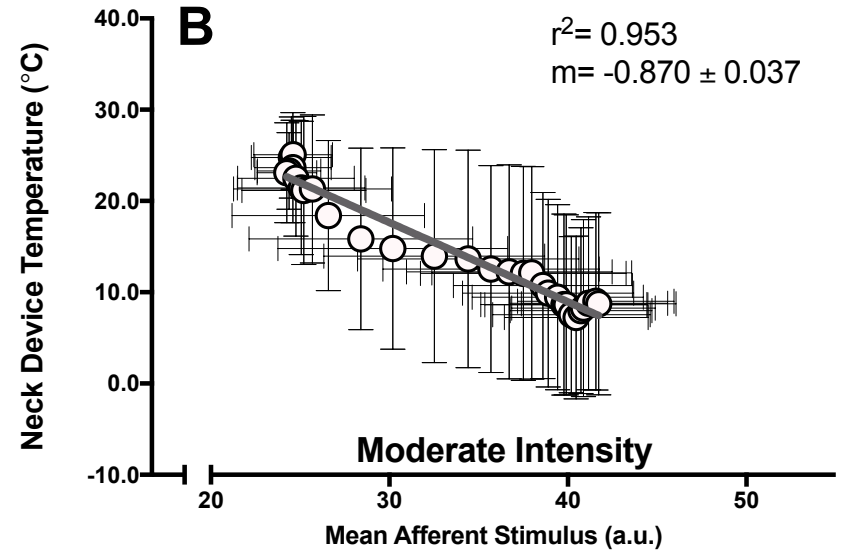
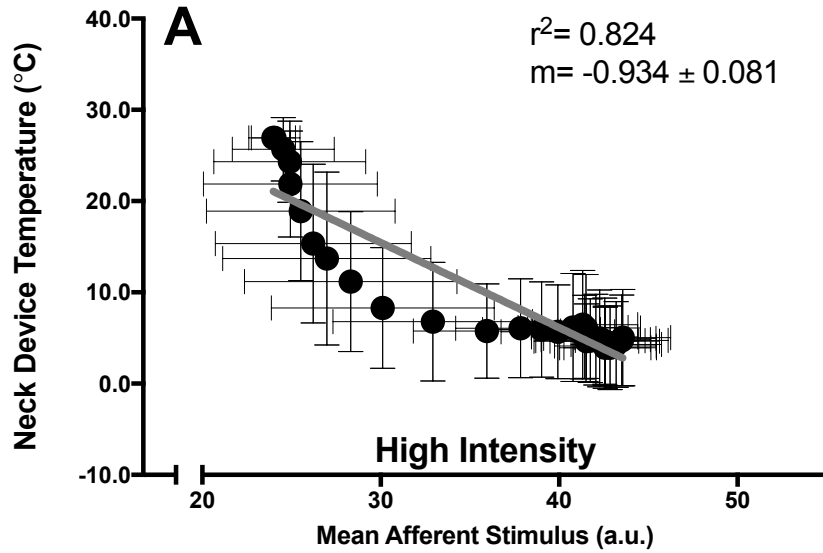
● High Intensity ○ Moderate Intensity



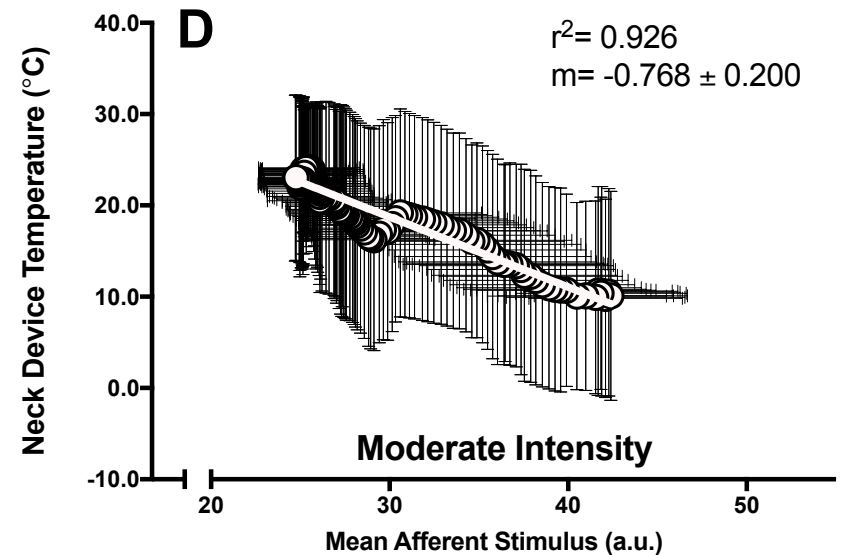
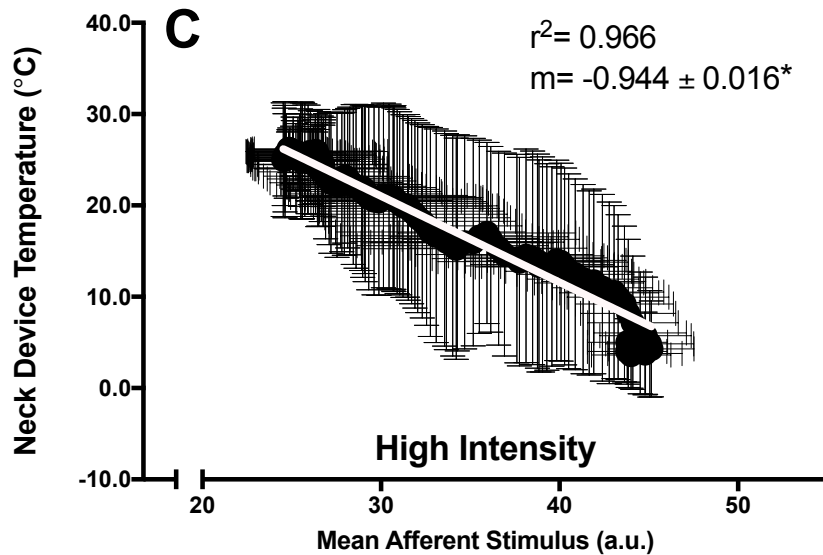
● High Intensity ○ Moderate Intensity



Exercise



Recovery



● 2mm

○ 6mm

