Localized and systemic variations in central motor drive at different local skin and muscle temperatures

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Title: Localized and systemic variations in central motor drive at different local skin and muscle temperatures

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Running Head: Central motor drive at different muscle temperatures

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ABSTRACT

This study investigated the ability to sustain quadriceps central motor drive while subjected to localized heat and metaboreceptive feedback from the contralateral leg. Eight active males each completed two counter-balanced trials, in which muscle temperature ($T_m$) of a single-leg (TEMP-LEG) was altered to 29.4°C (COOL) or 37.6°C (WARM), while the contralateral leg (CL-LEG) remained thermoneutral; 35.3 and 35.2°C $T_m$ in COOL and WARM respectively. To activate metaboreceptive feedback, participants first performed one 120-s isometric maximal voluntary contraction (MVC) of the knee extensors in the TEMP-LEG, immediately followed by post-exercise muscle ischemia (PEMI) via femoral blood flow occlusion. To assess central motor drive of a remote muscle group immediately following PEMI, another 120-s MVC was subsequently performed in the CL-LEG. Voluntary muscle activation (VA) was assessed using the twitch interpolation method. Perceived mental effort and limb discomfort were also recorded. In a cooled muscle, a significant increase in mean force output and mean VA (force, $p<0.001$; VA, $p<0.05$) as well as a significant decrease in limb discomfort ($p<0.05$) occurred during the sustained MVC in the TEMP-LEG. However, no differences between $T_m$ were observed in mean force output, mean VA or limb discomfort during the sustained MVC in the CL-LEG (Force, $p=0.33$; VA, $p>0.68$, limb discomfort, $p=0.73$). The present findings suggest that elevated local $T_s$ and $T_m$ can increase limb discomfort and decrease central motor drive, but this does not limit systemic motor activation of a thermoneutral muscle group.

PERSPECTIVES AND SIGNIFICANCE

Previous research indicates that as local skin and muscle temperature increase, the capacity to maximally activate skeletal muscle is reduced. The present study aimed to examine the afferent, supracortical and efferent factors that contribute to this phenomenon. It was concluded that changes central motor drive at different local temperatures are unrelated to the co-variance in core temperature, whole-body mean skin temperature, and/or true mean body temperature. Herein it is proposed that the causative factors are most probably a direct effect of afferent nerve sensitization on conscious motor control, inefficient contractility leading to increased metabolite precipitation, and/or reduced efficiency of sarcolemmal action potential propagation. Further research required to elucidate the contribution of each to the failure in voluntary activation in heated skeletal muscle, with greater consideration given to the interrelationship between supracortical control and multimodal somatosensory feedback from active muscle.
INTRODUCTION

Thermal strain can reduce performance during prolonged physical work (11, 52). In the heat, this is partially attributed to lower maximum cardiac output which compromises oxygen delivery to active muscle, particularly during high-intensity or dehydrated exercise (29, 55, 64). Conversely, in the cold this is attributable to a lower biomechanical efficiency due to antagonist muscle co-activation and a higher joint resistance (11, 48, 78). In both the heat and the cold, the relative aerobic-mechanical efficiency of exercise is therefore reduced. This in turn limits performance through accelerated chemical metabolite accumulation in active muscle (30, 39, 42) due to an increase in the total muscle fiber recruitment required to sustain a given workload (1, 35, 75).

In addition to faster rates of peripheral fatigue development, a down-regulation in voluntary muscle activation (VA) has been observed as body temperature increases (10, 51, 59, 76). This has been attributed to hyperventilation, arterial hypocapnia, and reduced cerebral blood flow instigated by an increase in core temperature (Tcore). It is thought that this reduction in cerebral blood flow may limit central drive through altered cerebral metabolite and/or neurotransmitter concentrations (33, 69). However, Tcore as a variable is highly non-specific, encompassing as much as 90% of all bodily tissues during heat stress (14). Ultimately, this implicates the integration of a range of regional, spatial and specific organ temperatures in the regulation of central motor drive. Indeed, the impact of body temperature on central drive appears to be related to the relative mass of the heated tissue (40, 74), perhaps indicating a proportional response to true mean body temperature rather than Tcore per se.

Tcore is also often used to reflect the local temperature of the brain or hypothalamus (7, 33, 53). Yet the firing rate of temperature sensitive hypothalamic neurons are highly dependent on extra-hypothalamic, thermal and non-thermal, inputs (8, 9, 71). In line with this, previous observations indicate that both cutaneous-thermal and muscular-ergoreceptive feedback can initiate autonomic thermo-effectors such as sweating and vasodilation (5, 45), as well as behavioral thermoregulation through voluntary alterations in central motor drive (22, 40, 46, 51).
Despite its obvious role as an effector organ, active muscle is also highly innervated with neuro-sensory receptors (49, 73). At least one of these sensory pathways - metaboreceptive feedback via group III and IV afferents – has been suggested to be a critical stimulus for modulations in central drive to active muscle (2–4). Cardiovascular strain arises under heat stress, exacerbating the rate at which muscles fatigue (42, 55, 56). Thus, faster metaboreceptor activation is a likely consequence of exercise in the heat as well (51, 52). Compounding this, as active muscle temperature increases, both heat related and acid-base related increases in intramuscular TRPV1 receptor activation (6, 13, 19, 57), as well as more efficient transduction in peripheral afferent nerve fibers (34, 44, 60), may lead to upregulation in the sensitivity of the muscle to metabolites. As a result exercise with increasing body temperatures may be subject to sensory nerve sensitization, an increase in metaboreceptor activation, and an increased chemical metabolite accumulation caused by increased cardiovascular strain (see paragraph 1). The net result could be increased activation of the thermo-metabolic sensory pathways from the active muscle, intensifying any reductions in VA that occur with heat stress (28, 52).

To investigate the role of muscle temperature ($T_m$) on VA via metaboreceptive feedback, the present study sought to: a) examine the impact of $T_m$ on perceived limb discomfort in metabolite saturated muscle i.e. fatigued muscle; and b) examine whether elevated or reduced $T_m$ combined with metaboreceptive feedback inhibits motor drive to a remote (i.e. unaffected) muscle group.

To investigate the role of metaboreceptive feedback, post-exercise muscle ischemia (PEMI) in a temperature-manipulated leg was used. PEMI prevents the washout and circulatory distribution of intramuscular metabolites following exhaustive exercise, allowing the metaboreceptive signal to be explored independently of additional factors associated with fiber recruitment (4, 27, 47). Given the need for both a localized change in muscle temperature and minimal cardiovascular strain, the exercise chosen for this study was a 120-s maximal isometric voluntary contraction (MVC) of the knee extensors.

The first hypothesis for the present study was that warm local $T_{sk}$ and $T_m$ would reduce central motor drive in a temperature-manipulated leg. The second hypothesis was that a corresponding decrease in central motor drive of a remote muscle group (i.e. the contralateral- thermoneutral leg) would occur with an
increase in both local $T_{sk}$ and $T_m$ in the temperature manipulated leg, due to a combination of: a) thermal sensitization of metaboreceptive feedback in a warmer muscle; and b) higher integrated thermal afferent feedback from an increase in localized $T_{sk}$ and $T_m$, which leads to an increase in true mean body temperature (total mass normalized whole-body heat content).

**METHODS**

*Participants*

Eight healthy and physically active male participants were recruited for this study from Loughborough University’s Gymnasium (mean ± SD: age, 22 ± 3 yrs.; stature, 189 ± 1 cm; body mass, 93.4 ± 18.9 kg).

All participants were regularly performing moderate to vigorous physical activity (4.5 ± 1.4 exercises/week) as confirmed using self-assessment prior to the start of the familiarization session. Participants were right leg dominant with no history of cardiovascular, neuromuscular or metabolic debility. At least 24-hours prior to undertaking any trials, participants were requested to refrain from strenuous exercise, as well as caffeine and alcohol consumption. Participants were given an information sheet detailing the experimental protocol before completing both a health screening questionnaire and written informed consent. The experimental protocol was approved by the Loughborough University Ethical Advisory Committee, and all procedures were conducted by trained experimenters. The experiments were conducted in spring (UK) with the likely levels of heat acclimation low.

*Experimental design and overview*

Each participant visited the laboratory on three separate occasions to complete one preliminary, and two experimental trials. All trials were separated by a minimum of 2 days recovery. The experimental trial order was counter-balanced. All contractions during the experimental protocols were performed with femoral nerve stimulation using the twitch interpolation technique to ascertain changes in VA (50). Figure 1, Panel A outlines the general procedure for the main experimental sessions.
On arrival at the laboratory, participant’s baseline neuromuscular performance was assessed using three brief MVCs on each leg, in a random order, and each interspersed with 30-s rest. Participants were then prepared and instrumented with the temperature recording equipment and vastus lateralis \( T_m \) was assessed in both legs. Following this, the right leg was temperature manipulated in a water bath (hereafter referred to as the TEMP-LEG). The two experimental trials differed by water temperature (\( T_{\text{water}} \)) and consisted of either: a) 25 minutes immersion in 8°C \( T_{\text{water}} \) (COOL) changing vastus lateralis \( T_m \) to 29.4 ± 4.0°C at 2-cm depth; or b) 15 minutes immersion in 44°C \( T_{\text{water}} \) (WARM) changing vastus lateralis \( T_m \) to 37.6 ± 0.4°C at 2-cm depth. During immersion, the thermoneutral contralateral (left) leg was suspended out of the water by a support frame (hereafter referred to as the CL-LEG).

After single leg water-immersion, \( T_m \) was immediately reassessed in both legs. No \( T_m \) changes occurred in the CL-LEG. To check for influences on VA that could not be attributed to a change in TEMP-LEG \( T_m \), participants completed another three brief MVCs (each interspersed with 30-s rest) in their CL-LEG only (Figure 1).

To complete the trial, participants conducted a sustained 120-s MVC immediately followed by PEMI in their TEMP-LEG. With PEMI maintained in the TEMP-LEG, participants immediately sustained a 120-s MVC in their CL-LEG. This allowed the self-regulated distribution of VA to be assessed in a local temperature-manipulated muscle, shortly followed by an assessment of the systemic influence of \( T_m \) on VA, as assessed in a remote and unaffected muscle group.

**Experimental rationale**

The immersion times were chosen based on the COOL and WARM conditions used by Lloyd et al. (2015b), shown to induce minimal (≤ 0.1°C) variations in rectal temperature. Given the previously observed linearity between VA and \( T_m \) in the range of 22 to 38.5°C (40), it was assumed that including a condition that corresponds with resting \( T_m \) (e.g. ~34°C), would provide no additional value to the present study. Similarly, a brief contraction immediately following immersion was not deemed necessary in the TEMP-LEG for the following reasons: a) the force and VA relation during brief isometric contractions has already been characterized at different \( T_m \) (40); b) any influential factors other than \( T_m \) or local \( T_{\text{skin}} \) should
influence the CL-LEG and TEMP-LEG proportionally; c) any acute changes in force and VA would be apparent at the initiation of the sustained contraction in the TEMP-LEG; and d) the requirement for a localized change in Tm imposes strict time restraints.

It is important to note that due to changes in contractile efficiency during isometric exercise at different Tm (10, 20, 40, 70, 76), a submaximal isometric contraction would not have provided a viable method for inducing similar metabolite concentrations in the TEMP-LEG. The chosen self-regulated 120-s MVC circumvents this issue by allowing participants to alter recruitment patterns to maintain the maximum tolerable level of metabolite saturation independent of Tm.

**Preliminary session**

Prior to the main experiment, participants attended a preliminary session to complete training in the procedure and an initial assessment of neuromuscular function in both left and right legs. After a series of contractions to potentiate the quadriceps, participants were then asked to perform repeated MVCs with femoral nerve stimulation in each leg. The contractions were repeated until participants reached a coefficient of variation below 5% for three successive MVCs in each leg. During this session, the positioning of all stimulation electrodes were ascertained then marked with indelible ink for the following experimental sessions (see ‘neuromuscular assessment’ for details). The current necessary for supramaximal femoral nerve stimulation of each leg was also ascertained using progressive increases in current until a plateau in the mechanical response of the muscle was observed (2, 40, 59). After adding 25% to the stimulator current to ensure supramaximal depolarization of the femoral nerve, the same output was then used for the main experimental trials: 186 ± 26 and 184 ± 27 mA for TEMP-LEG and CL-LEG respectively. During the familiarization sessions, the maximum force output was 1067 ± 186 and 973 ± 252 N in the TEMP-LEG and CL-LEG, respectively. Resting potentiated twitch force (using doublet stimulation; details below) was 413 ± 71 and 409 ± 65 N in the TEMP-LEG and CL-LEG respectively.

**Muscle temperature manipulation**

The procedure to manipulate Tm (single leg water-immersion) has been discussed in detail previously (40). Briefly, participants sat in a water-immersion bath with their TEMP-LEG immersed, and the CL-LEG held
out of the water. To restrict the temperature changes to the TEMP-LEG, participants sat suspended in a sling to keep as much of their trunk and non-exercising leg out of the water as possible, while still fully immersing the TEMP-LEG up to the iliac crest. Seated immersion with the leg horizontal and water level just covering the leg was used to minimize hydrostatic pressure to the lower limb. $T_{\text{water}}$ was maintained using active circulation, and continuously measured using a Grant Squirrel SQ2010 data logger and calibrated thermistor (Grant Instruments Ltd., Cambridge, UK). Following an initial start-up dose of 20 mg/l, the water chlorine level was maintained within 3-5 mg/l.

Participants were supplied with two sixteen inch floor-standing, variable intensity (4 speed) electric fans. To promote behavioral thermoregulation and to minimize the change in $T_{\text{core}}$ across conditions, participants were permitted adjust the fan intensity, as well as add or upper body remove clothing, as required.

**Body temperature measurement**

$T_{sk}$ was continuously recorded (1/min) using six wireless thermistors (Maxim, San Jose, USA), secured to the skin using Transpore tape (3M, Loughborough, UK). The thermistors were placed over the forehead, upper left chest, left bicep, stomach, CL-LEG thigh, and CL-LEG calf. Mean $T_{sk}$ was calculated using equal weighting from each of the six measurement sites. The towel dried thigh $T_{sk}$ in the TEMP-LEG was recorded using an infra-red sensor (FLUKE 566, Fluke Corporation, USA) immediately after water-immersion.

$T_{\text{core}}$ was measured rectally, recorded via a Grant Squirrel SQ2010 data logger (Grant Instruments Ltd., Cambridge, UK) with a sample rate of 4/min. The rectal thermistor was inserted to a depth of 10-cm beyond the anal sphincter. During each experimental trial, heart rate (HR) was monitored using a Polar monitor (Polar Electro Oy, Kempele, Finland) at a sample rate of 12/min.

$T_{m}$ was assessed in the vastus lateralis muscle of both legs, at 1- 2- and 3-cm using a solid needle thermocouple (MKA08050A275T; Ellab, Copenhagen, Denmark). The probe was inserted to a depth of 3-cm, and allowed to stabilize for 3-s. The needle was then withdrawn to 2- and 1-cm, with each depth
recorded upon temperature stabilization (21). $T_m$ was recorded a total of three times in each leg, at three
time points: 1) pre-water-immersion; 2) post-water-immersion; and 3) on completion of the exercise
protocol (Figure 1). The three insertions were located in an equilateral triangle, with each insertion
separated by $\sim$5mm. In the subsequent trial, insertions were delivered $\sim$1cm proximal of the previous
insertion site. All needle thermocouples were sterilized before use using a vacuum autoclave (Little Sister
SES 225B, Eschmann, UK). All procedures were conducted by trained personnel and in accordance with a
strict sterility protocol. The insertion sites were towel dried and re-sterilized using iodine before each
insertion.

**Neuromuscular assessment**

The procedures and equipment used for neuromuscular assessment have been detailed previously (40).
Briefly, participants changed into a swimsuit and were secured into a bespoke knee extension
dynamometer using a waist and chest belt system. The dynamometer was adjusted for each individual’s
femoral and tibial lengths, as well as their popliteal to patella width, whereas the hip and knee joint angles
were set to 90 and 100° respectively. An adjustable, non-compliant harness was applied around the ankle
malleolus to secure the leg to the force transducer (2000N, Model 615, Tedea- Huntleigh, Vishay Precision
Group, California, USA). A thin (1-cm) layer of padding was also applied between the tibia and the
harness to prevent bruising. Knee-extension force output was visually displayed (line trace and numerical
value) to all participants during all contractions (DataLog software, Biometrics Ltd, UK). This was
achieved using a Bluetooth wireless, 8 channel data logger (Miniature DataLog MWX8, Biometrics Ltd,
UK) and PC interface.

To calculate the mechanical properties of the muscle (i.e. peripheral fatigue) (2, 40, 59) as well as VA (i.e.
central command, central motor drive, central fatigue), the twitch interpolation technique was used (26,
50). To this end, two superimposed twitches ($Q_{tw, sup}$) were evoked over the force plateau of each brief (3-s)
MVC (Figure 1, Panel B). In the case of the sustained 120-s MVCs, a single $Q_{tw, sup}$ was evoked at initial
peak force, then again every 10-s during the MVC (totaling 13 $Q_{tw, sup}$). All MVCs (sustained and brief)
were followed by two resting potentiated twitches ($Q_{tw, pot}$), 1-second and 3-seconds after full muscle
relaxation respectively (40) (Figure 1, Panel B).
To circumvent the thermal influence associated with the use of singlet twitches (26, 40, 42), the present
twitches were evoked by two 0.2-ms rectangular pulses spaced 10-ms apart (i.e. doublet twitch) using a
high voltage simulation of the femoral nerve (max voltage 400 V; Digitimer DS7AH, Hertfordshire, UK)
(23). All stimulations were delivered manually by the same experimenter. The stimulator anode was placed
in the femoral triangle and the cathode over the greater trochanter (40). To ensure potentiation prior to the
brief (3-s) MVCs, each assessment was conducted 20-s after a series of incremental practice contractions
(2-s at 50, 50, 50, 75 and 90% MVC). All participants received moderate encouragement during all MVCs.

Analysis of the neuromuscular variables

VA was calculated using the following two equations. VA1 is considered to be a more conservative
estimate of central drive than VA2, while VA2 provides an estimation of changes in voluntary activation
over time during a sustained isometric contraction. For a detailed discussion see ref: (40).

VA1 = (1- Qtw, sup/Qtw, pot) x 100   (1)

VA2 = MVC/(MVC+ Qtw, sup)   (2)

For completeness, both calculations were used in the calculation of VA during the brief contractions also.
In addition, Qtw, pot was used as an index of the mechanical (contractile) status of the muscle (2, 40, 59).
The mean rate of force development (RFD) and mean rate of force relaxation (RFR) were also calculated
for all Qtw, pot (2). For all contractions, for each set of two Qtw, pot, mean RFR, and mean RFD were averaged.

For all brief MVCs pre- and post-water-immersion, only the MVC with highest peak force was assessed;
the two remaining contractions were discarded from the analysis. Likewise, to analyze the maximum
attainable VA for the pre- and post-water-immersion brief MVCs, the Qtw, sup delivered closest in time to
peak force was also used. In contrast, for all 120-s MVCs mean VA1 was calculated using the mean Qtw, sup
(thirteen twitches total) and mean pre- and post- Qtw, pot (four twitches total), resulting in a conservative
index of average central motor drive to the quadriceps femoris (40).
Post-exercise muscle ischemia

PEMI was used in order to restrict femoral arterial and venous blood flow following the 120-s MVC in the TEMP-LEG; thereby trapping quadriceps intramuscular metabolites. Using PEMI prevents direct circulatory metabolite effects on the CL-LEG while maintaining metaboreceptive feedback from the TEMP-LEG. This was achieved by rapid inflation (180mmHg) of a vascular cuff (SC12L, Hokanson, Bellevue, WA, USA) applied to the TEMP-LEG upper thigh. Occlusion pressure is inversely related to the vascular cuff width; thus 180mmHg was selected, as this is approximately one SD above the mean arterial occlusion pressure for a wide cuff (13.5cm) (43). The cuff was positioned to avoid any interference with the femoral nerve stimulation equipment. Rapid inflation was initiated 10-s prior to the completion of the 120-s MVC in the TEMP-LEG (Figure 1).

Perceptual variables

Participants were asked to retrospectively rate (on completion of both sustained MVCs) their mental effort and limb discomfort for each sustained MVC using a modified Borg’s CR-10 scale (12, 32). To this end, participants were retrospectively asked: A) ‘what was your internal sense of mental effort, independent of all discomforts?’ and B) ‘what was your sense of active muscle discomfort?’ for both the TEMP-LEG and CL-LEG during the sustained 120-s MVCs.

Statistical analysis

To examine the main effect of Tm on neuromuscular function at time points pre- (TEMP-LEG and CL-LEG) and post-water- immersion (CL-LEG only), a one-way (COOL vs WARM) repeated measures ANOVA was used. The tested outcome variables for each brief (3-s) MVC were peak force, 1-s mean force (over the MVC force plateau, including both Qtw,wt), peak VA1, peak VA2, Qtw,pot, Qtw,sup, mean RFD and mean RFR. In circumstances where Mauchly's Test of Sphericity was significant, the Greenhouse-Geisser correction was applied.

For each 120-s sustained MVC in each leg, the main effect of force output and VA2 were assessed over time (i.e. for each Qtw,sup) using a two-way-repeated measures ANOVA (Tm x Time; 2 x 13). Subsequently,
peak force, mean force (whole 120-s), mean force (every 30-s), mean VA₁, mean VA₂, VA₂ (at each time point), as well as post-exercise Qtw/pot. mean RFR and mean RFD were then analyzed using a one-way repeated measures ANOVA. A one-way ANOVA was also used to test the thermal variables (Tcore, mean Tsk, and Tm in both legs at all measured depths), HR, mental effort (for each leg) and limb discomfort (for each leg) at the pertinent time points. Parametric testing has been shown to be robust against violations of normal distribution (68); as such non-normally distributed data, which included the perceptual data only, were also analyzed using one-way repeated measures ANOVA. All statistical tests were assessed to a 95% confidence level (p < 0.05). All data are displayed as mean ± SD.

RESULTS

Temperature responses

Table 1 shows Tcore, mean Tsk, and Tm at all depths (1-, 2- and 3-cm) and in both legs (TEMP-LEG & CL-LEG). In response to TEMP-LEG water-immersion, none of Tcore, non-immersed mean Tsk or Tm of the CL-LEG at any depth were affected by condition. Immediately (~10-s) post-water-immersion, a spot measurement of thigh Tsk in the TEMP-LEG was 13.8 ± 1.1 and 36.5 ± 1.2 °C in the COOL and the WARM conditions, respectively (p < 0.001). Thus, TEMP-LEG temperature was independently manipulated, with Tm significantly (p = 0.001) higher in WARM compared to COOL conditions, across all measured depths. By completion of the exercise protocol in the WARM condition, Tcore had become significantly (p = 0.02) elevated (0.34°C), while mean Tsk was significantly (p = 0.04) reduced (~2°C), likely due to increased convective (fan) and evaporative (sweating) cooling during muscle heating. Mean Tsk did not change during COOL, and while end Tcore was lower (~0.1°C) during COOL, the effect was not significant (p = 0.06). Tm in the CL-LEG remained unaffected by condition immediately post-exercise, while Tm in the TEMP-LEG remained significantly (p < 0.001) higher (~4.5°C) in the WARM compared to the COOL conditions, at all measured depths immediately post-exercise.

Heart rate responses

During single-leg water immersion, HR was significantly (p = 0.004) higher in the WARM (93.8 ± 15.3 b.min⁻¹) compared to the COOL (80.5 ±18.7 b.min⁻¹) conditions. Likewise, during the 120-s MVC in the TEMP-LEG, a trend (p = 0.07) for higher HR in WARM was observed (WARM = 136.1 ± 28.3, COOL =
131.7 ± 24.3 b.min⁻¹); however during the 120-s MVC in the CL-LEG there were no significant differences in HR (WARM = 143.2 ± 26.8, COOL = 139.5 ± 28.6 b.min⁻¹).

**Neuromuscular function before water-immersion**

Table 2 shows the neuromuscular characteristics before and after water-immersion. Prior to immersion, there were no significant differences between conditions in peak force, mean force (1-s plateau), VA₁, VA₂, Qtw,pot, Qtw,sup or mean RFD during the brief (3-s) MVC, in either TEMP-LEG or CL-LEG. In the TEMP-LEG, a significant (p = 0.04) difference in mean RFR was observed between conditions (faster in WARM by 0.3 N.ms⁻¹). This was not observed for mean RFR in the CL-LEG.

**Neuromuscular function after water-immersion**

After the water-immersion protocol, there were no significant differences for all neuromuscular outcome variables between conditions in the CL-LEG, during the brief MVCs. This indicates that water-immersion of the TEMP-LEG had no effect on the brief MVC characteristics of CL-LEG, immediately post-immersion (Table 2).

**Sustained central motor drive at different muscle temperatures**

Figure 2 shows both mean force output (Panel A) as well as a more conservative estimate of mean VA (VA₁; Panel B) for each 120-s MVC, in both legs, in COOL and WARM conditions. Figure 3 shows a more detailed (over time) representation of MVC force output (Panel A and B) as well as the corresponding change in VA₂ (Panel C and D) in each leg and between conditions.
At the start of the sustained (120-s) contractions, both peak force in absolute and relative (% pre) terms were not significantly different between conditions, during either contraction. This was reflected in starting (peak) VA_2. Together this indicates there were no central or peripheral alterations in maximal force production at the start of the 120-s MVC, in either the TEMP-LEG or CL-LEG (Figure 3). However over time, both TEMP-LEG force output (condition main effect over time p = 0.02) and TEMP-LEG VA_2 (condition main effect over time p = 0.01) were significantly reduced in the WARM compared to the COOL condition (Figure 3: A and C). This amounted to a significant reduction (p < 0.001) in mean force output across the whole contraction in WARM (Figure 2: A), as well as a significant (p = 0.04) reduction in the most conservative estimate of mean VA (i.e. VA_1) in WARM (Figure 2: B). While the sense of mental effort was near maximal in both conditions, limb discomfort was significantly (p < 0.05) higher in WARM; however, it should be noted that four of eight participants rated limb discomfort as maximal (i.e. 10) in both WARM and COOL conditions (Table 3).

Following the sustained MVC and subsequent PEMI in the TEMP-LEG, CL-LEG force output and VA_2 were unaffected by the change in condition (Figure 3: B, D). This was reflected in mean MVC force, mean VA_1 as well as the sensation of limb discomfort in the CL-LEG (Figure 2: A, B and Table 3, respectively).

Post-exercise twitch characteristics

There were no significant differences between conditions in post-exercise Q_{tw,pot}, Q_{tw,sup} or mean RFD, in either the TEMP-LEG or CL-LEG. However in the CL-LEG, a significant (p = 0.04) difference of 0.21 N.ms^{-1} was observed in post-exercise mean RFR between conditions. This was not observed for post-exercise mean RFR in the TEMP-LEG.

DISCUSSION

This study investigated whether thermo-metabolic feedback from a warm local skin and muscle temperature would have a larger impact on central motor drive to a remote and thermoneutral muscle...
group, compared to thermo-metabolic feedback from a cold local skin and muscle temperature. In order to
sustain metaboreceptive feedback from the temperature-manipulated and exercising muscle, as well as to
exclude a systemic effect of circulating metabolites on the remote muscle group, post-exercise venous
occlusion was used. It was hypothesized that an increase in local skin and muscle temperature would
augment metaboreceptive feedback, thereby reducing VA in both a temperature-manipulated leg and the
contralateral (thermoneutral) leg.

In the temperature-manipulated leg, the present study showed that during active central motor drive of a
muscle characterized by high levels of metaboreceptive feedback, both force output and VA were
significantly reduced in a warm limb compared to a cooled limb (Figure 2; Figure 3: A, C). Extending
previous findings (40), the present study showed that at the same perceived mental effort, peripheral limb
discomfort is significantly higher with increasing muscle temperature (Table 3). However, contrary to our
hypothesis, the present study also indicated that any influence of increased local skin and muscle
temperature on leg thermo-metabolic feedback does not appear to inhibit voluntary muscle activation of a
remote muscle group, as represented by an equal force output and central motor drive in the thermoneutral,
contralateral leg (Figure 3).

Research context
Aerobic-mechanical efficiency is considered a critical determinant of self-selected pacing strategy during
exercise in extreme environments (55, 56); however humans are not provided with specific receptors for
sensing oxygen consumption (24). On the contrary, peripheral fatigue development rates - a direct
consequence of reductions in aerobic-mechanical efficiency - can be centrally assimilated through two
modalities (42): a) progressive deactivation of mechanoreceptive muscle afferents for a given central
motor drive (58); and b) a progressive activation of metaboreceptive muscle afferents (3, 57). In turn, this
composite of ergoreceptive activity likely provides the necessary inputs on which humans can modulate
VA (or ‘pace’), without exposing specific organs to excessive or intolerable homeostatic disturbances (3,
4, 27). Despite the importance of mechano- and metabo-receptive sensory modalities, the impact of
thermal factors on ergoreceptive feedback during fatiguing exercise are not well understood (28, 46, 52).
The influence of heat on metaboreceptor activation and afferent signal transmission

As $T_m$ increases, a faster transduction velocity and higher discharge frequency in metaboreceptive afferent fibers occurs (34, 36, 44, 49). Based on evidence from small muscle groups in humans, cooling delays, while heating increases, muscle sympathetic nerve activity during sustained isometric contractions; the effect of which has been attributed to altered mechano- and/or metabo-receptive sensitivity at different $T_m$ (60, 61). TRPV1 receptors located at the terminal end of III-IV muscle afferents have also been implicated in evoking noxious sensations in response to both thermal factors e.g. heat (63) and non-thermal metabolites produced during fatiguing exercise e.g. lactate (37, 57). As such, decreases in the temperature threshold and/or increases in the thermal sensitivity of TRPV1 may occur in the presence of low pH (13, 19, 63). A net result could be increased noxious sensations in combined heated and lactate saturated muscle (31, 57, 77). Such a thermal sensitization of metaboreceptive afferents is partially indicated in the present study. The findings show that during a prolonged high-intensity and fatiguing contraction, warmer muscle results in both a higher perceived limb discomfort and a lower VA. However, a parallel impact on the contralateral leg was not observed (Figure 3). This suggests that the change in limb discomfort from the temperature-manipulated leg did not influence systemic (whole-body) modulations of VA. This may indicate limited impact of thermal factors on the sensitivity of metaboreceptive afferents during whole-body exercise performance.

Chemical metabolite accumulation under local and systemic thermal strain

The present increase in limb discomfort and decrease in VA in the temperature-manipulated leg may also arise as a direct response to an increase in metabolite production and accumulation rate in heated muscle. In this regard, the reduction in VA may be caused by the muscle $Q_{10}$ effect on tetanic fusion and the consequent reduction in the efficiency of the sustained contractions in warm muscle (10, 40, 70, 76). Such an effect can explain why the corresponding effect was not observed in a remote muscle group i.e. the contralateral leg, where no thermal influence on metabolite production rate was present. If so, a proportional change in VA due to changes in peripheral fatigue rate may still have important implications for whole-body dynamic exercise, where metabo-receptive feedback in active muscle is accelerated by cardiovascular (heat) and biomechanical (cold) strain (41, 42).
Local improvements in muscle recruitment

The reduction in VA in the temperature-manipulated but not in the contralateral leg may also result from a decrease in sarcolemmal action potential propagation amplitude and/or the reduction in efficiency of peripheral transmission of neural drive, as $T_m$ increases (18, 54, 65). In this regard, an increase in VA at lower $T_m$ could be attributed to longer depolarization time in the peripheral nerve and sarcolemma (54, 65), thereby more effective recruitment of inactive muscle fibers. However, this does not explain why discomfort is increased in some participants, nor why the effect is not exhibited during a brief MVC (40) or at the start of the sustained MVC (Figure 3). Importantly, a combination of factors – direct and indirect influences on afferent feedback as well as sarcolemmal transmission - should not be excluded from the present conclusions.

No influence of whole-body heat content, cerebral or core temperature

Since during both brief and sustained contractions the contralateral leg was unaffected by condition, the change in temperature-manipulated leg VA can only be attributed to local $T_m$ and $T_{sk}$. This opposes changes in $T_{core}$, cerebral temperature, true mean body temperature and/or mean $T_{sk}$, which would have resulted in similar observations in both legs. This finding helps to further elucidate the observations by Lloyd et al. (40), where the impact of $T_{core}$ and $T_{sk}$ could not be fully excluded. From the present study, it can be unequivocally concluded that the changes in motor drive here, and in Lloyd et al. (40) are independent of $T_{core}$, mean $T_{sk}$ or true mean body temperature (body mass normalized whole-body heat content) and the measurement modality of these variables e.g. rectal vs esophageal temperature assessment.

Local skin temperature

Feedback from localized $T_{sk}$ cannot be ruled out as a potential explanation for the present findings. Recent research indicates a strong link between human behavior, voluntary movement and the activation of cutaneous-thermal group III [Aδ] and IV [C] fibers (66, 67). Given the skin is more densely innervated with thermoreceptors than muscle (31, 49), a reasonable conclusion may be that local $T_{sk}$ is responsible for the alterations in central drive to the active muscle in this study. However, if so, it remains unclear why
this did not influence both legs proportionally, given that the cutaneous thermoreceptive feedback remains active during the sustained contractions in both legs.

Conscious awareness and post-exercise muscle ischemia

The differential roles of autonomic and conscious pathways to reduction in VA under thermal strain are not well understood. As such, it is not possible to exclude a supracortical influence of $T_m$ on VA in the present study (15–17, 62). Indeed, the conscious assimilation of metabo- and thermo-receptive afferents may be influenced by whether a fatigued muscle group is under voluntary control. In the present study, participants would have been consciously aware that reducing VA would not alleviate the increased sensory discomfort of fatigue. In contrast, this is not the case during PEMI and contralateral leg exercise; in which any attenuation of contralateral leg drive will not relieve discomfort experienced in a temperature-manipulated leg.

Final considerations

The absence of a thermoneutral trial may be considered a potential limitation of the present study. However, a linearity between local VA and $T_m$ for the range investigated presently has already been shown (40). Moreover, the present study aimed at understanding whether a local thermal stimulus had any capacity to impose changes in limb discomfort and systemic VA, for which a thermoneutral trial was not required. Had an influence on VA been observed in the contralateral leg, further research may have been warranted to compare dynamic exercise in a neutral (e.g. 33-36°C $T_m$) or hot environment (e.g. 40-42 °C $T_m$); although it is important to note, that substantial methodological difficulties are associated with investigating very high $T_m$ in large muscle masses, independently of large changes in $T_{core}$ (31).

Another consideration is that during the later stages of the sustained MVC in the temperature-manipulated leg, muscle force output was lower in the warm muscle (21%MVC) compared to the cool muscle (29%MVC). Consequently, this may have resulted in a different intramuscular pressure and metabolite flushing in the seconds prior to the inflation of the occlusion cuff (10-second before relaxation). On the contrary, research studies have widely reported that muscle is kept fully ischemic at isometric contractions
forces above 10% MVC (25, 72). It should also be recognized that the insertion of a solid needle thermocouple may have impacted the participants’ ability to perform a maximal voluntary contraction.

**Conclusions**

The present study examined the interaction between thermal and metaboreceptive feedback from muscle, to the distribution of central motor drive to a remote and thermoneutral body part. It was shown that increased cutaneous and quadriceps muscle temperature combined with metaboreceptive feedback in a single leg has little or no effect on voluntary activation of a remote muscle group during a 120-s isometric contraction. The foremost implications of these findings are: a) the effects of local skin and muscle temperature change on central motor drive and limb discomfort are localized to actively driven warm muscle groups only; b) if metaboreceptive feedback is enhanced due to afferent nerve warm-sensitization, it is unlikely to systemically or autonomically inhibit motor drive of other (thermoneutral) muscles; and c) the previously observed changes in central motor drive at different local skin and muscle temperatures (40) appear to be unrelated to the change in either core, whole-body mean skin temperature, or true mean body temperature. Further research is necessary to understand the individual and combined impacts of local mechano-, baro-, thermo- and metabo-receptive feedback on exercise performance during thermal strain (38).
REFERENCES


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Périard JD, Racinais S. Self-paced exercise in hot and cool conditions is associated with the maintenance of %Vo2peak within a narrow range. J Appl Physiol 118: 1258–1265, 2015.


74. **Stolwijk JA.** A mathematical model of physiological temperature regulation in man. National Aeronautics and Space Administration.


Table 1: Temperature recordings before (PRE-WI) and after water-immersion (POST-WI) and immediately post-exercise (POST-EX). TEMP-LEG indicates the muscle temperature-manipulated leg; CL-LEG indicates the contralateral-thermoreutral leg. The two experimental conditions are COOL: 25 minutes single-leg immersion in 8°C water, and WARM: 15 minutes single-leg immersion in 44°C water. Core temperature is measured rectally. Mean $T_{sk}$ was calculated using equal weighting from each of the six measurement sites. Muscle temperature is displayed at each measured depth (1, 2 and 3-cm). All data are presented as mean ± SD (n = 8). *significant difference between WARM and COOL, p < 0.05. †trend for difference between WARM and COOL, p < 0.1.

Table 2: Neuromuscular function during a brief (3-s) maximal voluntary contraction (MVC). Data is displayed for the assessments before water-immersion (PRE-WI), in both the temperature-manipulated (TEMP-LEG) and the contralateral, thermoneutral leg (CL-LEG), as well as after water-immersion (POST-WI), in the CL-LEG only (see Figure 1). The two experimental conditions are COOL: 25 minutes single-leg immersion in 8°C water, and WARM: 15 minutes single-leg immersion in 44°C water. VA1, voluntary activation calculated using equation 1; VA2, voluntary activation calculated using equation 2; $Q_{tw,super}$, superimposed twitch force; $Q_{tw,pot}$, resting potentiated twitch force; mean RFD, resting twitch mean rate of force development; mean RFR, resting twitch mean rate of relaxation. All PRE-WI and POST-WI values are in relation to the MVC with highest peak force. Each set of $Q_{tw,super}$ and each set of $Q_{tw,pot}$ were averaged for each MVC. All data are presented as mean ± SD (n = 8). *significant difference between WARM and COOL, p < 0.05.

Table 3: Subjective ratings of mental effort and limb discomfort immediately post-exercise. TEMP-LEG indicates the muscle temperature-manipulated leg; CL-LEG indicates the contralateral-thermoreutral leg. The two experimental conditions are COOL: 25 minutes single-leg immersion in 8°C water, and WARM: a 15 minutes single-leg immersion in 44°C water. All perceptions were assessed using modified Borg’s
CR-10 scale. All data are presented as mean ± SD (n = 8). *significant difference between WARM and COOL, p < 0.05.

Figure 1: The general methods. Panel A illustrates schematic of the general procedure. White boxes indicate the schematic overview of the experimental protocol. Grey boxes indicate the outcome measures. Dark grey provides a visual reference for muscle contraction and supramaximal twitches. Panel B shows an example force trace during a brief (3-s) maximal voluntary contraction in one participant. Vertical lines indicate the doublet simulation of the femoral nerve. The two corresponding superimposed twitches evoked during each contraction are indicated using the abbreviation Qtw,sup. The two resting potentiated twitches are indicated by the abbreviation Qtw,pot. Tre, rectal temperature; Tm, muscle temperature; Tsk, skin temperature; MVC, maximal isometric voluntary contraction force of knee extensors; HR, heart rate; TEMP-LEG, the muscle temperature-manipulated leg; CL-LEG, the contralateral-thernoneutral leg.

Figure 2: The effect of temperature condition on mean contraction force and mean voluntary activation percentage (equation 1) during a 120-s sustained maximal isometric voluntary knee extension. Panel A shows the contraction force in the both the TEMP-LEG and the contralateral, thermoneutral leg (CL-LEG). Panel B shows the voluntary muscle activation in the TEMP-LEG and the CL-LEG. For the 120-s MVCs, mean VA1 was calculated using the mean Qtw,sup (thirteen twitches total) and mean pre- and post- Qtw,pot (four twitches total). All data are presented as mean ± SD (n = 8). The p-value for each repeated measured one-way ANOVA (t-test) is displayed above the corresponding set of bars. *significant difference between WARM and COOL, p < 0.05.

Figure 3: The effect of muscle temperature (Tm) on contraction force (as a percentage of pre-water-immersion values) and voluntary activation percentage (equation 2 as a percentage of pre-water-immersion values) during a 120-s sustained maximal isometric voluntary contraction. Panel A shows the contraction force in the temperature-manipulated leg (TEMP-LEG). Panel B shows the contraction force in the contralateral, thermoneutral leg (CL-LEG). Panel C shows the voluntary muscle activation in the TEMP-LEG. Panel D shows the voluntary muscle activation in the CL-LEG. Grey lines represent the COOL
condition, while black lines represent WARM. All data are presented as mean ± SD (n = 8). In all panels, the p-value for each repeated measured one-way ANOVA is displayed for each 30-s mean of the contraction. In addition, panels C and D are analyzed for each superimposed twitch (13 total). *significant difference between WARM and COOL, p < 0.05. #trend for difference between WARM and COOL, p < 0.1.
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<td>POST-EX</td>
<td>33.2 ± 0.4</td>
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Table 2:

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<td>Peak MVC Force (N)</td>
<td>PRE-WI CL-LEG</td>
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<td>1086 ± 226</td>
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<td>1-s Mean MVC Force (N)</td>
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<td>791 ± 272</td>
<td>791 ± 264</td>
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<td>Peak VA₁ (%)</td>
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<td>115 ± 53</td>
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<td>114 ± 62</td>
<td>108 ± 66</td>
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<td>415 ± 118</td>
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<td>431 ± 118</td>
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<td>5.66 ± 2.02</td>
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<td>Mean RFR (N.ms⁻¹)</td>
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<td>1.72 ± 0.52</td>
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<td>Mental Effort (CR-10)</td>
<td>TEMP-LEG</td>
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<td>CL-LEG</td>
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<td>Sense of Limb Discomfort (CR-10)</td>
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<td>CL-LEG</td>
<td>7.9 ± 2.8</td>
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Figure 1:
Figure 2:

(A) Mean contractile force (N)

- TEMP-LEG: P < 0.001
- CL-LEG: P = 0.304

(B) Voluntary activation 1 (VA, %)

- TEMP-LEG: P = 0.039
- CL-LEG: P = 0.880
Figure 3:

**Panel A**
- TEMPLE-LEG
- COOL: CONTRACTILE FORCE (% of PRE)
- WARM: CONTRACTILE FORCE (% of PRE)
- PEAK FORCE: P = 0.480
- FIRST 30-s: P = 0.341
- SECOND 30-s: P = 0.001
- THIRD 30-s: P = 0.015
- LAST 30-s: P = 0.011

**Panel B**
- CL-LEG
- COOL: CONTRACTILE FORCE (% of PRE)
- WARM: CONTRACTILE FORCE (% of PRE)
- PEAK FORCE: P = 0.695
- FIRST 30-s: P = 0.893
- SECOND 30-s: P = 0.745
- THIRD 30-s: P = 0.847
- LAST 30-s: P = 0.088

**Panel C**
- TEMP-LEG
- COOL: VOLUNTARY ACTIVATION 2 (%VA)
- WARM: VOLUNTARY ACTIVATION 2 (%VA)
- PEAK FORCE: P = 0.666
- FIRST 30-s: P = 0.062
- SECOND 30-s: P = 0.035
- THIRD 30-s: P = 0.039
- LAST 30-s: P = 0.007

**Panel D**
- CL-LEG
- COOL: VOLUNTARY ACTIVATION 2 (%VA)
- WARM: VOLUNTARY ACTIVATION 2 (%VA)
- PEAK FORCE: P = 0.627
- FIRST 30-s: P = 0.894
- SECOND 30-s: P = 0.976
- THIRD 30-s: P = 0.518
- LAST 30-s: P = 0.250
A

**TEMP-LEG**

- Peak Force: P = 0.480
- First 30-s: P = 0.341
- Second 30-s: P = 0.001
- Third 30-s: P = 0.015
- Last 30-s: P = 0.011

COOL: 

WARM: 

B

**CL-LEG**

- Peak Force: P = 0.695
- First 30-s: P = 0.893
- Second 30-s: P = 0.745
- Third 30-s: P = 0.847
- Last 30-s: P = 0.088

COOL: 

WARM: 

C

**TEMP-LEG**

COOL: 

WARM: 

D

**CL-LEG**

COOL: 

WARM: 

**Peak Force**

- First 30-s: P = 0.966
- Second 30-s: *P = 0.062*
- Third 30-s: *P = 0.035*
- Last 30-s: *P = 0.039*
- **Last 30-s:** *P = 0.007*

**Voluntary Activation 2: VA:**

- Peak: P = 0.627
- 30-s: P = 0.894
- 60-s: P = 0.975
- 90-s: P = 0.518
- 120-s: P = 0.250

**TIME (S):**

- Peak
- 30
- 60
- 90
- 120

**Voluntary Activation 2: VA:**

- CL-LEG
- Cool
- Warm
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<td>CL-LEG 1 - cm muscle temperature (°C)</td>
<td>PRE-WI</td>
<td>33.7 ± 2.2</td>
<td>33.8 ± 2.3</td>
</tr>
<tr>
<td></td>
<td>POST-WI</td>
<td>33.5 ± 2.2</td>
<td>33.7 ± 1.4</td>
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<td>POST-EX</td>
<td>34.9 ± 2.0</td>
<td>34.7 ± 2.1</td>
</tr>
<tr>
<td>TEMP-LEG 2 - cm muscle temperature (°C)</td>
<td>PRE-WI</td>
<td>35.1 ± 1.2</td>
<td>35.0 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>POST-WI</td>
<td>29.4 ± 4.0</td>
<td>37.6 ± 0.4*</td>
</tr>
<tr>
<td></td>
<td>POST-EX</td>
<td>32.9 ± 2.2</td>
<td>37.5 ± 0.5*</td>
</tr>
<tr>
<td>CL-LEG 2 - cm muscle temperature (°C)</td>
<td>PRE-WI</td>
<td>35.1 ± 1.1</td>
<td>35.3 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>POST-WI</td>
<td>35.3 ± 0.7</td>
<td>35.2 ± 1.0</td>
</tr>
<tr>
<td></td>
<td>POST-EX</td>
<td>36.6 ± 0.7</td>
<td>36.7 ± 0.8</td>
</tr>
<tr>
<td>TEMP-LEG 3 - cm muscle temperature (°C)</td>
<td>PRE-WI</td>
<td>35.8 ± 1.0</td>
<td>35.5 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>POST-WI</td>
<td>31.4 ± 2.9</td>
<td>37.7 ± 0.4*</td>
</tr>
<tr>
<td></td>
<td>POST-EX</td>
<td>34.0 ± 1.5</td>
<td>37.8 ± 0.4*</td>
</tr>
<tr>
<td>CL-LEG 3 - cm muscle temperature (°C)</td>
<td>PRE-WI</td>
<td>35.8 ± 0.7</td>
<td>35.9 ± 0.6</td>
</tr>
<tr>
<td></td>
<td>POST-WI</td>
<td>35.7 ± 0.5</td>
<td>35.7 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>POST-EX</td>
<td>36.8 ± 0.4</td>
<td>37.2 ± 0.5#</td>
</tr>
<tr>
<td>Mean skin temperature (°C)</td>
<td>PRE-WI</td>
<td>33.2 ± 0.8</td>
<td>32.5 ± 1.7</td>
</tr>
<tr>
<td></td>
<td>POST-WI</td>
<td>33.0 ± 0.8</td>
<td>32.2 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>POST-EX</td>
<td>33.2 ± 0.4</td>
<td>30.5 ± 2.5*</td>
</tr>
<tr>
<td>Variable</td>
<td>Time Point</td>
<td>COOL</td>
<td>WARM</td>
</tr>
<tr>
<td>---------------------------</td>
<td>--------------</td>
<td>--------------</td>
<td>--------------</td>
</tr>
<tr>
<td>Peak MVC Force (N)</td>
<td>PRE-WI CL-LEG</td>
<td>983 ± 268</td>
<td>977 ± 268</td>
</tr>
<tr>
<td></td>
<td>PRE-WI TEMP-LEG</td>
<td>1086 ± 226</td>
<td>1029 ± 232</td>
</tr>
<tr>
<td></td>
<td>POST-WI CL-LEG</td>
<td>1039 ± 287</td>
<td>1052 ± 238</td>
</tr>
<tr>
<td>1-s Mean MVC Force (N)</td>
<td>PRE-WI CL-LEG</td>
<td>791 ± 272</td>
<td>791 ± 264</td>
</tr>
<tr>
<td></td>
<td>PRE-WI TEMP-LEG</td>
<td>917 ± 206</td>
<td>892 ± 258</td>
</tr>
<tr>
<td></td>
<td>POST-WI CL-LEG</td>
<td>890 ± 279</td>
<td>908 ± 202</td>
</tr>
<tr>
<td>Peak VA₁ (%)</td>
<td>PRE-WI CL-LEG</td>
<td>68.7 ± 16.1</td>
<td>63.8 ± 22.0</td>
</tr>
<tr>
<td></td>
<td>PRE-WI TEMP-LEG</td>
<td>73.0 ± 12.5</td>
<td>73.1 ± 13.3</td>
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<tr>
<td></td>
<td>POST-WI CL-LEG</td>
<td>73.9 ± 11.9</td>
<td>74.5 ± 10.4</td>
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<tr>
<td>Peak VA₂ (%)</td>
<td>PRE-WI CL-LEG</td>
<td>85.4 ± 9.7</td>
<td>83.8 ± 10.6</td>
</tr>
<tr>
<td></td>
<td>PRE-WI TEMP-LEG</td>
<td>89.1 ± 5.4</td>
<td>88.8 ± 6.5</td>
</tr>
<tr>
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<td>POST-WI CL-LEG</td>
<td>88.0 ± 8.4</td>
<td>89.8 ± 5.5</td>
</tr>
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<td>Mean Q₁w,sup (N)</td>
<td>PRE-WI CL-LEG</td>
<td>134 ± 89</td>
<td>144 ± 99</td>
</tr>
<tr>
<td></td>
<td>PRE-WI TEMP-LEG</td>
<td>115 ± 53</td>
<td>108 ± 57</td>
</tr>
<tr>
<td></td>
<td>POST-WI CL-LEG</td>
<td>114 ± 62</td>
<td>108 ± 66</td>
</tr>
<tr>
<td>Mean Q₁w,prot (N)</td>
<td>PRE-WI CL-LEG</td>
<td>415 ± 118</td>
<td>400 ± 93</td>
</tr>
<tr>
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<td>PRE-WI TEMP-LEG</td>
<td>424 ± 88</td>
<td>399 ± 71</td>
</tr>
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<td></td>
<td>POST-WI CL-LEG</td>
<td>431 ± 118</td>
<td>403 ± 94</td>
</tr>
<tr>
<td>Mean RFD (N.ms⁻¹)</td>
<td>PRE-WI CL-LEG</td>
<td>5.66 ± 2.07</td>
<td>5.12 ± 1.59</td>
</tr>
<tr>
<td></td>
<td>PRE-WI TEMP-LEG</td>
<td>5.91 ± 1.57</td>
<td>5.73 ± 1.29</td>
</tr>
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<td>POST-WI CL-LEG</td>
<td>5.66 ± 2.02</td>
<td>6.02 ± 2.65</td>
</tr>
<tr>
<td>Mean RFR (N.ms⁻¹)</td>
<td>PRE-WI CL-LEG</td>
<td>1.68 ± 0.75</td>
<td>1.76 ± 0.60</td>
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<tr>
<td></td>
<td>PRE-WI TEMP-LEG</td>
<td>1.72 ± 0.52</td>
<td>1.42 ± 0.52*</td>
</tr>
<tr>
<td></td>
<td>POST-WI CL-LEG</td>
<td>1.66 ± 0.75</td>
<td>1.53 ± 0.53</td>
</tr>
<tr>
<td>Variable</td>
<td>Time Point</td>
<td>COOL</td>
<td>WARM</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>------------</td>
<td>----------</td>
<td>----------</td>
</tr>
<tr>
<td>Mental Effort (CR-10)</td>
<td>TEMP-LEG</td>
<td>10.0 ± 0.0</td>
<td>9.9 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>CL-LEG</td>
<td>9.9 ± 0.4</td>
<td>10.0 ± 0.0</td>
</tr>
<tr>
<td>Sense of Limb Discomfort (CR-10)</td>
<td>TEMP-LEG</td>
<td>7.4 ± 3.0</td>
<td>8.6 ± 2.3*</td>
</tr>
<tr>
<td></td>
<td>CL-LEG</td>
<td>7.9 ± 2.8</td>
<td>7.9 ± 3.1</td>
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