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Arm Cooling Selectively Impacts Sensorimotor Control

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Abstract

The benefits of cold have long been recognized in sport and medicine. However, it also brings costs, which have more rarely been investigated, notably in terms of sensorimotor control. We hypothesized that in addition to peripheral effects, cold slows down the processing of proprioceptive cues, which has an impact on both feedback and feedforward control. We therefore compared the performances of participants whose right arm had been immersed in either cold water (arm temperature: 14°C) or lukewarm water (arm temperature: 34°C). In Experiment 1, we administered a Fitts's pointing task and performed a kinematic analysis to determine whether sensorimotor control processes were affected by the cold. Results revealed i) modifications in late kinematic parameters, suggesting changes in the use of proprioceptive feedback, and ii) modifications in early kinematic parameters, suggesting changes in action representations and/or feedforward processes. To explore our hypothesis further, we ran a

second experiment in which no physical movement was involved, and thus no peripheral effects. Participants were administered a hand laterality task, known to involve implicit motor imagery and assess the internal representation of the hand. They were shown left- and right-hand images randomly displayed in different orientations in the picture plane and had to identify as quickly and as accurately as possible whether each image was of the left hand or the right hand. Results revealed slower responses and more errors when participants had to mentally rotate the cooled hand in the extreme orientation of 160°, further suggesting the impact of cold on action representations.

NEW & NOTEWORTHY

We investigated how arm cooling modulates sensorimotor representations and sensorimotor control. Arm cooling induced changes in early kinematic of pointing, suggesting an impact on feedforward process or hand representation. Arm cooling induced changes in late kinematic of pointing, suggesting an impact on feedback processes. Arm cooling also affected performance on a hand laterality task, suggesting that action representations were modified.

Keywords: sensorimotor control, Fitts's task, implicit motor imagery, cryotherapy

INTRODUCTION

The benefits of cold application have long been recognized. As early as 400 BCE, Hippocrates reported its analgesic effects (Adams 1929). Since then, a range of therapeutic effects have been demonstrated, and it is widely used today in sport and medicine. In sport, local cold or ice application is used to reduce pain, tissue swelling and inflammation in the treatment of traumatic injuries (Enwemeka et al. 2002; Knight 1995). Cold is also used to accelerate physiological recovery after exercise (Bouzigon et al. 2021; Dupuy et al. 2018; de Freitas et al. 2019; Moore et al. 2023). Immersion in cold water after exercise attenuates muscle soreness (Leeder et al. 2012) and accelerates the restoration of muscle function (Leeder et al. 2012; Poppendieck et al. 2013). Cold also brings benefits when used *before* exercise, notably in the case of endurance sports performed in hot weather (for a meta-analysis, see Ross et al. 2013). However, cold before exercise also comes with a cost, as it impacts neuromuscular performance (for a review, see Oksa 2002). More specifically, cold has an impact on musculotendinous and nerve function, thereby impairing the sensorimotor control of movements. Cooling is thought to slow down Nerve Conduction Velocity (NCV) and the response of sensory receptors (Chesterton et al. 2002), affecting the processing of tactile and proprioceptive cues. Cooling also leads to slower and weaker muscle contraction (Bigland-Ritchie et al. 1992; Denys 1991).

Sensorimotor control is based on *feedforward* and *feedback* processes. Pointing at a target requires the use of internal models, that is, representations of the action and its sensory consequences (i.e., future states of the arm during the pointing action; Wolpert et al. 1995). Based on these *feedforward* inputs of the limb, predictions of future states are compared with the current state, allowing for early corrections (Desmurget et al. 1995; Desmurget and Grafton 2000; Wolpert and Ghahramani 2000). This *feedforward* process is thought to be associated with early kinematic parameters (i.e., before peak velocity; Elliott et al. 2010; Meyer et al.

1982) The *feedback* process corresponds to the period during which sufficient time has elapsed to integrate online sensory cues and to compare them with the intended versus current states, and is associated with later kinematic parameters (i.e., after peak velocity; Elliott et al. 2010; Meyer et al. 1982). Therefore, *feedforward* control and *feedback* control are both based on the processing of sensory cues, notably visual and proprioceptive cues in the case of a pointing movement (for a review, see Sarlegna and Sainburg 2009). Interestingly, sensorimotor control appears to be modified when proprioceptive cues are impaired by short-term limb immobilization (Bassolino et al. 2012; Moisello et al. 2008; Scotto et al. 2020), deafferentation (Medina et al. 2009; Sarlegna et al. 2006), or aging (e.g., Haaland et al. 1993; Ketcham et al. 2002; Welford et al. 1969; York and Biederman 1990). Here, we tested the hypothesis that above and beyond peripheral effects, cold also has an impact on *feedforward* and *feedback* control due to the difficulty of using proprioceptive cues that are processed more slowly (i.e., reduction in NCV; Algafly et al. 2007). To this end, we administered a Fitts' pointing task and performed a kinematic analysis to determine whether *feedforward* and/or *feedback* motor control processes were affected (Experiment 1). The *feedforward* process is thought to be associated with early kinematic parameters (i.e., before peak velocity), while the *feedback* process is associated with later kinematic parameters (i.e., after peak velocity; Elliott et al. 2010; Meyer et al. 1982). As the pointing task required some movement, albeit limited in our task (i.e., 8 cm), we could not rule out peripheral effects of cold on musculotendinous function. We therefore tested our hypothesis further with a cognitive task that involved processing the mental representation of an action (i.e., internal model), but no actual movement. Following motor simulation theory (Jeannerod 2001), we used a motor imagery task (i.e., internal movement simulation) to investigate the cognitive level of action processing and avoid the confusion related to motor execution (Experiment 2). More specifically, participants were requested to identify the laterality of hands depicted in various orientations in the picture plane (40°, 80°,

120°, 160° in clockwise and counterclockwise directions (Parsons 1987, 1994). To solve the hand laterality task, participants had to mentally rotate their own hand from their current position to the orientation of the hand displayed on the computer screen. The hand laterality task implicitly triggers motor imagery processes, as evidenced in behavioral and neuroimaging studies (Kosslyn et al. 1998; de Lange et al. 2006; Parsons 1994; Parsons et al. 1998; Sekiyama 1982). It has already been used to show that restricting the input/output of signal processing by immobilizing a hand impairs internal upper-limb representations, in particular in the identification of the laterality of the images of the hand with the largest amplitude of rotation (Meugnot et al. 2014, 2016; Meugnot and Toussaint 2015; Toussaint et al. 2021; Toussaint and Meugnot 2013). Here, we tested whether these representations are modified when proprioceptive cue processing is manipulated through a cooling procedure.

METHODS

General Methods

The cooling procedure was based on the measurement of skin temperature. Although skin temperature is known to be poorly predictive of intramuscular temperature (Jutte et al. 2001), this noninvasive method is widely used (Herrera et al. 2010), as it correlates with NCV, a fundamental parameter for sensorimotor control. With cold, local analgesia associated with a reduction in NCV of approximately 10% and a decrease in sensory receptor response is achieved with a skin temperature of 12.5-13.6°C (Chesterton et al. 2002). In addition, the cellular hypometabolic effect appears below 15°C (Zachariassen 1991). In order to observe the effect of cold on Central Nervous System (CNS) processing, we set a target skin temperature of 14±1°C (Herrera et al. 2010).

Apparatus.

For the *Cooled* group, we filled a rectangular basin (L/W/D: 42 × 30 × 25 cm) with water and ice cubes to reach a temperature of ~9°C (Kennet et al. 2007; Myrer et al. 1998). More ice cubes were added during the cooling procedure to maintain this water temperature. By contrast, for the *Control* group, we filled the basin with lukewarm water to reach a thermoneutral temperature of ~33°C (Ntoumani et al. 2023). This temperature was then maintained by adding cold or warm water. For both groups, a thermometer with an electronic sensor (RS PRO; RS Components Ltd, Corby, United Kingdom; accuracy: ± 0.1°C; range: -70°C to +250°C) was fixed to the inside of the basin for temperature control. Skin temperature was measured with a thermal Infrared camera Fluke TiR32 (Flir Systems, Danderyd, Sweden; -20°C to +150°C). Emissivity was set at 0.97 (Douzi et al. 2021). Infrared images of participants' right wrist, hand and index finger were recorded and analyzed with SmartView® 4.3 software (Flir Systems, Danderyd, Sweden).

Procedure.

Figure 1 depicts the general procedure of each experiment. On Day 1 for both experiments, the right arm of each participant was immersed in either cold (*Cooled* group) or lukewarm (*Control* group) water. Before the cooling procedure, participants remained at rest for 10 min in the experimental room to stabilize their body temperature (mean room temperature: 19.1°C). After this temperature stabilization period, they had to immerse their right arm in the water up to their elbow and remain still. Participants in the *Cooled* group kept their arm in the water until they reached the target skin temperature of 14±1°C (temperature from 13 to 15°C were accepted). The duration of immersion was on average 22.8±0.5 min in Experiment 1 and 25.3±1.0 min in Experiment 2. The immersion duration for the *Control* group was matched to that of the *Cooled* group so that both groups exhibited the same duration of immobility. Indeed, position sense has been shown to decay as a function of time delay (e.g., Paillard and Brouchon 1968), and participants in the *Control* group were matched with a

participant in the *Cooled* group on age, size, and weight. After immersion, all participants had to remove their arm from the basin and place it on their right thigh, on top of a towel. They briefly dried their arm to avoid water contact with electronic devices. Skin temperature was measured at the forearm with the thermal imager (see Supplementa Material, <https://doi.org/10.17605/OSF.IO/63US9>). Participants then performed either the pointing task (Experiment 1) or the hand laterality task (Experiment 2). It should be noted that for Experiment 1, a second immersion was performed to run a second experimental condition (i.e., *Index of Difficulty* = 3 or 7; see below). The target temperature was reached in 7.1 ± 0.2 min. Twenty-four hours later, participants performed the same task (i.e., pointing or hand laterality), but without any immersion (*Nonimmersed* session). This procedure with a between-subject design (i.e., two independent groups *Cooled* and *Control*) was chosen instead of a within-subject design to minimize the potential learning over sessions as well as experiment duration. The second experimental session (*Nonimmersed*) was a control session that served as a double check to assess whether both groups performed equally without immersion. This control session was always performed the second day as implicit simulation processes (as implied in mental rotation tasks) are more developed the first time (Toussaint et al. 2023). As for the *Immersed* session, participants had to rest for 10 min in the experimental room to stabilize their temperature before beginning the task. It should be noted that no participant performed both tasks (Experiment 1 and Experiment 2). At the end of each experiment, a debriefing was conducted and participants did not report any side effect of cold immersion (e.g., pain).

Data processing.

We recorded thermal images of the right forearm: 1) on Day 1 before the immersion, 2) after immersion (i.e., when the target temperature had been reached or after the matched period for the *Control* group), 3) immediately after the task (either hand laterality or pointing), and iv) 24 h later (Day 2), before the task without immersion. It should be noted that postimmersion

images were recorded twice for Experiment 1, as participants experienced two immersions corresponding to the two ID conditions (see below). For both experiments, the forearm temperature of the *Control* group was considerably higher than that of the *Cooled* group during immersion (Experiment 1: *Control*= 34.1±0.1°C vs. *Cooled*= 14.8±0.1°C, Exp2. *Control*=34.3±0.2°C vs. *Cooled*=14.9±0.1°C). See Supplemental Material for data analysis of temperature (<https://doi.org/10.17605/OSF.IO/63US9>).

Experiment 1 – Fitts’s task

Participants.

A total of 48 self-reported right-handed participants (31 men and 17 women; mean age ± SE: 19.7±0.3 years) gave their written informed consent prior to the study, in accordance with the 1964 Declaration of Helsinki. The experimental protocol was approved by an institutional review board (no. 2017-25-01-14). All participants reported having normal or corrected-to-normal vision and no neurological or sensorimotor disorders. They were randomly assigned to either the *Control* group (24 participants; 16 men and 8 women; 20.8±0.7 years; Body Mass Index: 21.9±0.74) or the *Cooled* group (24 participants; 15 men and 9 women; 18.5±0.2 years; Body Mass Index: 22.1±0.35). They were asked to avoid consuming stimulants (e.g., alcohol, caffeine, chocolate) 2 h before the experiment (Chesterton et al. 2002; McMeeken et al. 1984).

Apparatus.

The pointing task was performed on a MacBook Pro Retina (OS X 10.11.6 El Capitan 2.5 GH Core i5) with a 8.6 × 10.5 cm trackpad (resolution of 400 CPI sampling at 125 Hz and a 13.3-inch screen (900 × 1,440 pixels refreshed at 60 Hz). A custom-built application written in C++ using Qt and libpointing (Casiez and Roussel 2011) was used to provide instructions, stimuli and acquire data from the trackpad and the screen. The gain between the trackpad and

the visual cursor was set at 1: movements made on the trackpad (horizontal plane) scaled directly to movements of the cursor on the screen (vertical plane).

Procedure.

The participants' task was to point to visual targets as fast and accurately as possible (Fitts's paradigm, Fitts, 1954). They were also asked to perform the pointing with a smooth and continuous movement on the trackpad and to avoid stopping outside the target (i.e., under or overshoots). The pointing task consisted of horizontal 2D pointing, either left to right or right to left; (for a similar procedure, see Scotto et al. 2020). The visual cursor for the pointing task corresponded to a vertical line 0.25 mm wide (1 px). The target was a rectangle with the same height as the screen, and with two possible widths (W): either 2 cm (101 px) or 0.125 cm (6 px), yielding two *Indexes of Difficulty* (IDs), ID3 or ID7, respectively. The ID is calculated according to W and the distance (D) from the starting point to the center of the target (here set to 8 cm, i.e., 403 px), as follows: $ID = \log_2(2D/W)$.

In a well-lit room, participants sat on a chair of adjustable height approximately 70 cm away from a laptop. The experimenter placed in a comfortable position the participant's right forearm on the table perpendicular to the laptop with the hand palm facing down. The joints were not restrained, and the pointing consisted mainly of a wrist movement (i.e., abduction when pointing from the left, and adduction when pointing from the right). A trial began when the participants reached the starting position: centered vertically on the trackpad and at -4 cm or +4 cm horizontally from the trackpad center (for rightward and leftward pointing, respectively). This position was reached without tactile feedback (i.e., no physical landmark on the trackpad) nor visual feedback (i.e., no visual cursor nor target position). When the participant's finger reached the starting position on the trackpad, the word "calibration" appeared on the screen. The position had to be maintained at least 0.5 s to launch the trial. The

cursor and the visual target appeared on the screen at the same time. Participants could then start pointing toward the target positioned at 8 cm distance as soon as they were ready. Participants were required to stop the cursor within the confines of the target for 0.5 s. The visual stimuli then disappeared, and the trial stopped. A new trial begun in the opposite direction (rightward or leftward). Vision of the arm was not obstructed.

As described in *General Methods* section, participants were divided into two groups: the *Cooled* group (i.e., immersion in cold water) or *Control* group (i.e., immersion in lukewarm water). The experiment was performed over two sessions on two consecutive days: *Immersed* and *Nonimmersed* session. The first session (*Immersed*) also included a practice phase featuring 10 trials to familiarize the participants with the task prior to data recording. This was performed before the immersion procedure. After immersion, participants performed 40 trials in either the *ID3* or the *ID7* condition. Their arm was then immersed a second time, in order to restore the target temperature using the same procedure (see *General Methods* section), before performing the same 40 trials in the other ID condition. The order of ID condition (*ID3* and *ID7*) was counterbalanced across the groups. This *Immersed* session lasted 45 min with a mean \pm SE duration to complete the *ID3* trials block of 2.5 \pm 0.07 min for the *Control* group and 3.1 \pm 0.09 min for the *Cooled* group. The *ID7* was completed in 3.2 \pm 0.07 min by the *Control* group and 4.0 \pm 0.10 min by the *Cooled* group. In the *Nonimmersed* session on Day 2, participants again performed 40 trials for each ID after resting for 10 min at ambient room temperature, but without any immersion. Participants performed the two sets of ID trials in the opposite order to the first session (Day 1). This *Nonimmersed* session lasted 15 min with a duration to complete the *ID3* trials block of 2.4 \pm 0.07 min for the *Control* group and 2.4 \pm 0.06 min for the *Cooled* group. The *ID7* was completed in 3.0 \pm 0.06 min by the *Control* group and 2.9 \pm 0.06 min by the *Cooled* group.

Data processing.

Positional data from the trackpad were low-pass filtered with a dual-pass, no-lag Butterworth filter (cutoff frequency: 10 Hz; order: 2). Velocity of the finger was computed to determine the Movement Time (MT) of the pointing. The MT corresponds to the period between movement onset and termination, which were defined when the velocity reached above and below 5% of Peak Velocity (PV), respectively. We further assessed the impact of the cold by analyzing pointing corrections. Although the participants were instructed to point to the target in a single movement (i.e., to point with a *smooth and continuous movement*), some movements stopped (velocity below 5% of PV) before or after reaching the target. We computed the percentage of these trials with under/overshoots of the primary submovement. We also analyzed early spatiotemporal kinematics parameters associated to the *impulse* phase of the movement (i.e., the phase from movement onset to peak velocity) with the Acceleration Time (AT; time from movement onset to PV) and the impulse direction variability (within-subject SD of the direction from movement onset to PV). In addition, later kinematic parameters were also analyzed with the deceleration Time (DT; time between PV and movement termination) known to be associated with the *homing* phase (Elliott et al. 2010; Meyer et al. 1982). It covered the deceleration period of the first submovement (from PV) and any additional submovements until the movement stopped (velocity below 5% of PV and cursor position in the target). We first tested whether the impact of cold might vanish over the trial repetitions with a repeated-measures analysis of variance (ANOVA) on MT, using a mixed design with *Group* (*Control* vs. *Cooled*) as a between-participants factor, and *Session* (*Immersed* vs. *Nonimmersed*), *ID* (*ID3* vs. *ID7*) and *Trial* (*mean of the 10 first trials* vs. *mean of the 10 last trials*) as within-participants factors. As the results revealed that the cold impact was still present at the end of the trials block (i.e., in the *Immersed* session *Control* and *Cooled* groups still differed for the last ten trials, $p < 0.001$) we considered the mean of all 40 repetitions for subsequent analyses. We then ran repeated-measures analyses of variance (ANOVAs) on the

dependent variables, using a mixed design with *Group* (*Control* vs. *Cooled*) as a between-participants factor, and *Session* (*Immersed* vs. *Nonimmersed*) and *ID* (*ID3* vs. *ID7*) as within-participants factors. Post hoc tests (Newman-Keuls) were performed when necessary, and the level of significance was set at 0.05 for all statistical analyses. The effect size was reported with partial eta square (η^2_p). Data is available at <https://doi.org/10.17605/OSF.IO/63US9>.

Experiment 2 – Hand laterality task

Participants.

A total of 42 self-reported right-handed participants (27 men and 15 women; mean age \pm SE: 19.8 \pm 0.4 years) gave their written informed consent prior to the study, in accordance with the 1964 Declaration of Helsinki. The experimental protocol was approved by an institutional review board (no. 2017-25-01-14). All participants reported having normal or corrected-to-normal vision and no neurological or sensorimotor disorders. Participants were randomly assigned to either the *Control* group (21 participants; 13 men and 8 women; 19.3 \pm 0.4 years, Body Mass Index: 22.4 \pm 0.57) or the *Cooled* group (21 participants; 14 men and 7 women; 20.3 \pm 0.5 years; Body Mass Index: 21.7 \pm 0.36).

Apparatus.

The hand laterality task was performed on a PC computer (spatial resolution 1280 \times 800 pixels; temporal resolution 60 Hz). Instructions and stimuli (hand images) were provided using E-Prime 2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA), and participants' response times were recorded via a microphone connected to the computer. For each trial, the experimenter wrote the participant's response on a sheet. Hand images were created with Poser 6.0 software (H/W: 15.7 \times 13.5 cm, palm down).

Procedure.

Participants were seated approximately 70 cm away from a computer screen. Their hands were placed palm down on their thighs. The hand laterality task consisted of 16 left- or right-hand images presented randomly in different orientations in the picture plane (medial and lateral rotations of 40°, 80°, 120° and 160°; **Fig. 2**). Each participant performed 80 trials (5 blocks of 16 trials).

Participants were asked to identify the laterality of hand images as quickly and as accurately as possible. Each trial began with a fixation cross that was displayed in the center of the computer screen for 0.5 s. A hand image then appeared, and remained visible until the participant had provided a verbal response. Participants responded “left” or “right”.

As described in *General Methods* section, participants were divided into two groups (*Cooled* group and *Control* group) and participated in two sessions (*Immersed* and *Nonimmersed*) on two consecutive days. As in Experiment 1, for the *Immersed* session the *Cooled* group had their right arm immersed until they reached the target skin temperature of $14\pm 1^\circ\text{C}$ and the *Control* group in lukewarm water of $\sim 33^\circ\text{C}$ which lasted 12.7 ± 0.04 min for the *Control* group and 13.6 ± 0.62 min for the *Cooled* group. The *Nonimmersed* session lasted 11.5 ± 0.36 min for the *Control* group and 11.7 ± 0.41 min for the *Cooled* group.

Data processing.

We ran repeated-measures ANOVAs on accuracy (i.e., number of correct responses, expressed as a percentage) and response times (i.e., interval between appearance of a hand image and participant’s response, expressed in ms) using a mixed design with one between-participants factor *Group* (*Control* vs. *Cooled*) and three within-participants factors: *Session* (*Immersed*: immediately after the arm was removed from the water vs. *Nonimmersed*: 24h later without immersion), *Hand* (*Left* vs. *Right*) and *Orientation* (40°, 80°, 120° and 160°). We only analyzed response times for correct responses. Response time outliers (± 2.5 SDs from mean for each orientation) were excluded from the analyses (fewer than 2% in each group and not

concentrated on a specific orientation). Post hoc comparisons were carried out by means of a Newman-Keuls test. Alpha was set at 0.05 for all analyses. Data is available at <https://doi.org/10.17605/OSF.IO/63US9>.

RESULTS

Experiment 1 -Fitts's task

Overall movement time and errors.

The mixed *Group* \times *ID* \times *Session* ANOVA on MT revealed main effects of *Group* [$F_{(1,46)}=22.9$; $p<0.001$, $\eta^2p=0.33$], *ID* [$F_{(1,46)}=1063.6$; $p<0.001$, $\eta^2p=0.96$] and *Session* [$F_{(1,46)}=65.0$; $p<0.001$, $\eta^2p=0.59$] as well as an interaction *Group* \times *Session* [$F_{(1,46)}=158.8$; $p<0.001$, $\eta^2p=0.76$], *ID* \times *Session* [$F_{(1,46)}=13.7$; $p<0.001$, $\eta^2p=0.23$] and *Group* \times *Session* \times *ID* [$F_{(1,46)}=29.4$; $p<0.001$, $\eta^2p=0.39$].

Figure 3 depicts the *Group* \times *Session* \times *ID* interaction. For the *Cooled* group, MT was higher in the *Immersed* session than in the *Nonimmersed* session for *ID3* (571.1 ± 25.4 ms vs. 444.8 ± 23.6 ms, respectively; $p<0.001$) and this difference was even greater for *ID7* (1289.4 ± 41.2 ms vs. 978.4 ± 31.8 ms, respectively; $p<0.001$). For the *Control* group, no significant decreases were observed between the *Immersed* and *Nonimmersed* sessions for either *ID3* (*Immersed* = 375.0 ± 14.1 ms vs. *Nonimmersed* = 405.6 ± 17.2 ms; $p=0.14$) or *ID7*, which actually exhibited a significant increase in MT (*Immersed* = 897.2 ± 25.4 ms vs. *Nonimmersed* = 962.6 ± 39.9 ms; $p=0.002$). In addition, MT differed between the two groups in the *Immersed* session ($p=0.001$ for *ID3* and $p<0.001$ for *ID7*), whereas no significant difference appeared in the *Nonimmersed* session ($p=0.43$ for *ID3* and $p=0.75$ for *ID7*).

Analysis of under/overshoots of the primary submovement (%) revealed effects of *ID* [$F_{(1,46)}=119.7$; $p<0.001$, $\eta^2p=0.72$] and *Session* [$F_{(1,46)}=5.5$; $p=0.02$, $\eta^2p=0.11$] but no main

effect of *Group* [$F_{(1,46)}=0.5$; $p=0.47$] and no *ID* \times *Session* interaction effect [$F_{(1,46)}=3.5$; $p=0.07$]. The ANOVA did, however, reveal *Group* \times *Session* [$F_{(1,46)}=4.2$; $p=0.04$, $\eta^2p=0.08$], and *Group* \times *Session* \times *ID* [$F_{(1,46)}=7.0$; $p=0.01$, $\eta^2p=0.13$] interactions. As observed in **Figure 4**, the cooling procedure induced an increase in under/overshoots for *ID7*: the correction rate was higher for the *Cooled* group ($14.5\pm 1.9\%$) than the *Control* group in the *Immersed* session ($9.7\pm 1.4\%$, $p=0.02$, difference that disappeared in the *Nonimmersed* session ($p=0.65$). For the *Cooled* group, under/overshoot rate was higher in the *Immersed* session than in the *Nonimmersed* session for *ID7* ($14.5\pm 1.9\%$ vs. $8.4\pm 1.7\%$, respectively; $p<0.001$). There was no effect of cooling for the easier task (i.e., *ID3*).

Kinematics of impulse and homing phases.

AT corresponded to the interval between movement onset and peak velocity. AT constitutes a temporal parameter for early kinematics that would be associated with the impulse phase of motor control. The *Group* \times *ID* \times *Session* mixed ANOVA on AT revealed main effects of *ID*, [$F_{(1,46)}=113.3$; $p<0.001$, $\eta^2p=0.71$] and *Session* [$F_{(1,46)}=37.6$; $p<0.001$, $\eta^2p=0.45$] but no main effect of *Group* [$F_{(1,46)}=3.1$; $p=0.08$]. The ANOVA also revealed *Group* \times *Session* [$F_{(1,46)}=106.7$; $p<0.001$, $\eta^2p=0.70$], *ID* \times *Session* [$F_{(1,46)}=21.3$; $p<0.001$, $\eta^2p=0.32$] and *Group* \times *Session* \times *ID* [$F_{(1,46)}=6.3$; $p=0.02$, $\eta^2p=0.12$] interactions.

Figure 5 depicts the *Group* \times *Session* \times *ID* interaction for AT. For the *Cooled* group, AT was higher for the *Immersed* session than for the *Nonimmersed* session for *ID3* (161.6 ± 4.6 ms vs. 127.7 ± 6.2 ms, respectively; $p<0.001$), and the difference was even greater for *ID7* (213.9 ± 10.0 ms vs. 143.4 ± 5.9 ms, respectively; $p<0.001$). For the *Control* group, there was no significant decrease between the *Immersed* and *Nonimmersed* sessions either for *ID7* (158.2 ± 6.2 ms vs. 166.2 ± 6.6 ms, respectively; $p=0.28$) or for *ID3*, which even exhibited an

increase in AT between sessions (124.6 ± 4.2 ms vs. 143.3 ± 6.4 ms, respectively; $p=0.002$). In addition, AT differed between groups in the *Immersed* session ($p=0.02$ for *ID3* and $p<0.001$ for *ID7*), whereas no significant differences appeared in the *Nonimmersed* session ($p=0.18$ for *ID3* and $p=0.20$ for *ID7*).

In addition, with AT, we computed a spatial parameter of early kinematics that corresponded to the within-subject variability (SD) over the 40 trials of the direction between the movement onset to the PV. The *Group* \times *ID* \times *Session* mixed ANOVA on SD impulse direction revealed main effects of *Group* [$F_{(1,46)}=4.2$; $p=0.04$, $\eta^2p=0.08$], *ID* [$F_{(1,46)}=103.2$; $p<0.001$, $\eta^2p=0.69$] and *Session* [$F_{(1,46)}=100.2$; $p<0.001$, $\eta^2p=0.68$]. Results did not revealed a significant interaction for *ID* \times *Session* [$F_{(1,46)}=0.4$; $p=0.53$] contrary to the interactions *Group* \times *Session* [$F_{(1,46)}=29.8$; $p<0.001$, $\eta^2p=0.39$], and *Group* \times *Session* \times *ID* [$F_{(1,46)}=67.3$; $p<0.001$, $\eta^2p=0.59$].

Figure 6 depicts the *Group* \times *Session* \times *ID* interaction for SD impulse direction. For *ID3*, no statistical difference appeared between groups whatever the session. However, when the spatiotemporal constraints increased (*ID7*), the *Cooled* group exhibited a higher SD impulse direction for the *Immersed* session (*Cooled* = 5.5 ± 0.3 deg vs. *Control* = 3.7 ± 0.2 deg, $p<0.001$) while no difference appeared for the *Nonimmersed* session for *ID3* (*Cooled* = 3.6 ± 0.2 deg vs. *Control* = 3.7 ± 0.2 deg, $p=0.99$).

DT corresponded to the interval between peak velocity and the end of the movement. This parameter would be associated with the homing phase of motor control, reflecting the online movement corrections of the *feedback* process (e.g., Meyer et al. 1982; Woodworth 1899). The *Group* \times *ID* \times *Session* mixed ANOVA on DT revealed main effects of *Group* [$F_{(1,46)}=30.7$; $p<0.001$, $\eta^2p=0.40$], *ID* [$F_{(1,46)}=1243.3$; $p<0.001$, $\eta^2p=0.96$] and *Session* [$F_{(1,46)}=57.9$; $p<0.001$, $\eta^2p=0.56$] as well *Group* \times *Session* [$F_{(1,46)}=128.3$; $p<0.001$, $\eta^2p=0.74$],

$ID \times Session$ [$F_{(1,46)}=5.1$; $p=0.03$, $\eta^2p=0.10$] and $Group \times Session \times ID$ [$F_{(1,46)}=22.1$; $p<0.001$, $\eta^2p=0.33$] interactions. The pattern of results was similar to that of MT and AT.

Figure 7 depicts the $Group \times Session \times ID$ interaction. For the *Cooled* group, DT was higher for the *Immersed* session than for the *Nonimmersed* session for *ID3* ($403.9.1 \pm 22.4$ ms vs. 312.7 ± 18.0 ms, respectively; $p<0.001$), and the difference was even greater for *ID7* (1049.7 ± 41.2 ms vs. $825.2.4 \pm 26.7$ ms, respectively; $p<0.001$). As the *Nonimmersed* session was performed on Day2, one could have expected a decrease of DT compared to the *Immersed* session, due to the decrease of over/undershoots with repetitions. For the *Control* group, there was no significant decrease between the *Immersed* and *Nonimmersed* session for *ID3* ($242.9.1 \pm 10.2$ ms vs. 250.5 ± 10.4 ms, respectively; $p=0.69$) and for *ID7*, which even exhibited a significant increase in DT (729.7 ± 20.6 ms vs. 784.0 ± 35.3 ms, respectively; $p=0.007$). In addition, DT differed between groups in the *Immersed* session ($p<0.001$ for *ID3* and $p<0.001$ for *ID7*), whereas no significant differences emerged in the *Nonimmersed* session ($p=0.12$ for *ID3* and $p=0.30$ for *ID7*).

The aim of Experiment 1 was to test whether the *impulse* phase and/or the *homing* phase of pointing movements were affected by a cooling procedure. Using Fitts's task, we found that cold induced several kinematic modifications, including a general slowdown, as well as a decrease in accuracy. Modifications in late kinematic parameters (i.e., cold-induced increases in DT and under/overshoots rate) pointed to a change in the use of proprioceptive *feedback* (Elliott et al. 2010; Meyer et al. 1982). Modifications in early kinematic parameters with cold also appeared with an increase of temporal parameter (i.e., AT) and spatial parameter (i.e., variability of the impulse direction) pointed to a change at the representational level. Early kinematic modifications have been shown to reflect the use of internal models, that is, representations of the action and its sensory consequences (e.g., future states of the arm at the end of pointing; Wolpert et al. 1995) which would have been modified by cold. To further test

our hypothesis of a central influence of cold on action representations, we performed a second experiment where no physical movement was involved, and thus no peripheral effects.

Experiment 2 – Hand laterality task

The analysis of accuracy revealed main effects of *Session* [$F_{(1,40)}=7.82$; $p<0.01$, $\eta^2p=0.16$], and *Orientation* [$F_{(3,120)}=18.90$, $p<0.001$, $\eta^2p=0.32$] as well as a *Group* \times *Hand* \times *Orientation* interaction [$F_{(3,120)}=2.95$; $p<0.05$, $\eta^2p=0.07$]. No significant effects were found for *Group*, [$F_{(1,40)}=0.21$; $p=0.65$], *Hand* [$F_{(1,40)}=2.31$; $p=0.14$], *Group* \times *Session* [$F_{(1,40)}=0.04$; $p=0.84$], *Group* \times *Hand* [$F_{(1,40)}=1.75$; $p=0.19$], *Group* \times *Orientation* [$F_{(3,120)}=0.59$; $p=0.62$], *Session* \times *Hand* [$F_{(1,40)}=0.05$ $p=0.95$], *Session* \times *Orientation* [$F_{(3,120)}=1.24$; $p=0.30$], *Hand* \times *Orientation* [$F_{(3,120)}=1.64$; $p=0.18$], *Group* \times *Session* \times *Hand* [$F_{(1,40)}=2.07$; $p=0.16$], *Group* \times *Session* \times *Orientation* [$F_{(3,120)}=2.02$; $p=0.11$], *Session* \times *Hand* \times *Orientation* [$F_{(3,120)}=0.46$; $p=0.71$], *Group* \times *Session* \times *Hand* \times *Orientation* [$F_{(3,120)}=0.58$; $p=0.63$].

The main effect of *Session* and *Orientation*, showed respectively that accuracy was higher in the *Nonimmersed* session ($97.9\pm 5.6\%$) than in the *Immersed* session ($96.7\pm 7.7\%$) and decreased between 40° and 160° (40° : $100 \pm 2\%$; 80° : $98 \pm 4\%$; 120° : $97 \pm 5\%$; 160° : $94 \pm 11\%$). **Figure 8** depicts the *Group* \times *Hand* \times *Orientation* interaction. Only for hand images at 160° , accuracy was poorer for the right hand than for the left hand in the *Cooled* group ($p=0.012$) whereas there was no difference between hands in the *Control* group ($p=0.96$).

Analysis of response times (ms) revealed main effects of *Session* [$F_{(1,40)}=58.93$; $p<0.001$, $\eta^2p=0.60$], *Hand* [$F_{(1,40)}=18.72$; $p<0.001$, $\eta^2p=0.32$], *Orientation* [$F_{(3,120)}=139.49$; $p<0.001$, $\eta^2p=0.78$], as well as significant *Session* \times *Orientation* [$F_{(3,120)}=13.19$; $p<0.001$, $\eta^2p=0.25$], *Hand* \times *Orientation* [$F_{(3,120)}=3.83$; $p<0.012$, $\eta^2p=0.09$] and *Group* \times *Session* \times *Hand* \times *Orientation* [$F_{(3,120)}=5.01$; $p<0.001$, $\eta^2p=0.11$] interactions. There was no significant main effect of *Group* [$F_{(1,40)}=0.70$; $p=0.41$] and no significant *Group* \times *Session* [$F_{(1,40)}=0.91$; $p=0.17$],

Group × *Hand* [$F_{(1,40)}=1.41$; $p=0.24$], *Group* × *Orientation* [$F_{(3,120)}=1.72$; $p=0.16$], *Session* × *Hand* [$F_{(1,40)}=0.90$; $p=0.35$], *Group* × *Session* × *Hand* [$F_{(1,40)}=0.07$; $p=0.79$], *Group* × *Session* × *Orientation* [$F_{(3,120)}=1.15$; $p=0.33$], *Group* × *Hand* × *Orientation* [$F_{(3,120)}=1.64$; $p=0.18$], *Session* × *Hand* × *Orientation* [$F_{(3,120)}=1.61$; $p=0.19$] interactions.

The main effect of *Session* showed that response time was shorter in the *Nonimmersed* session (871 ± 198 ms) than in the *Immersed* session (984 ± 257 ms), possibly due to test/retest effect (*Nonimmersed* session being performed 24 h after *Immersed* session). The main effect of *Hand* and *Orientation* showed respectively, that response time was shorter for the right hand (902 ± 236 ms) than for the left hand (953 ± 234 ms) and increased between 40° and 160° (40° : 808 ± 144 ms; 80° : 831 ± 143 ms; 120° : 946 ± 213 ms; 160° : 1125 ± 273 ms). **Figure 9** depicts the *Group* × *Session* × *Hand* × *Orientation* interaction. Immediately after immersion (**Fig. 9A**), the laterality effect (i.e., shorter response time for the dominant right hand than for the nondominant left hand) observed in the *Control* group for the greatest hand orientation (160° ; $p=0.02$) was no longer statistically significant in the *Cooled* group ($p=0.06$), where response times tended to be shorter for the nondominant left hand (**Fig. 9A**). Moreover, for the right hand, response times were higher for the *Cooled* group than for the *Control* group for 160° hand images immediately after immersion ($p=0.03$). In the *Nonimmersed* session, no difference emerged between groups ($p=0.35$; **Fig. 9B**).

The aim of Experiment 2 was to examine whether the cognitive level of action processing was affected by a cooling procedure. Using a hand laterality task, we observed that cold resulted in poorer performances in terms of accuracy and response times for 160° right-hand images (i.e., images corresponding to the cooled arm). It should be noted that performances did not differ across groups for the left-hand pictures. These results were similar to those reported following a short-term upper limb immobilization procedure, which selectively impaired hand representations for the immobilized limb (Meugnot et al. 2014, 2016;

Toussaint and Meugnot 2013). Here we showed for the first time that the immersion of an effector in cold water affects the sensorimotor representation of that specific effector. This cooling procedure, which is known to disrupt the response of sensory receptors and/or slow down NCV (Algaflly et al. 2007), leads to more complex proprioceptive information processing. This would result in slower sensorimotor information processing abilities, reflecting the impact of altered sensory *feedback* on the cognitive level of action.

DISCUSSION

General Discussion

The aim of these experiments was to assess how cooling affected sensorimotor control, from CNS representations to end-movement modifications. In Experiment 1, we examined whether the *impulse* and/or *homing* phase of pointing movements was affected by a cooling procedure with water immersion. Using Fitts's task, we showed that cold induced modifications in performance, with increases in MT and movement modifications, depending on task difficulty (i.e., *ID*). When the requirement for accuracy increased (*ID7*), cold induced more submovements to hit the target due to more under- and overshoots of the primary submovement. More importantly, we showed that cold induced modifications in both early (i.e., AT and SD impulse direction) and late (i.e., DT) kinematic parameters of pointing movements. Albeit these results suggested modifications at the representation level (i.e., early kinematic parameters) in this experiment, we could not exclude the possibility that these results partially stemmed from the impact of cold on musculotendinous and nerve function, as it is known to reduce nerve and muscle conduction velocities, leading to slower and weaker muscle contraction (Bigland-Ritchie et al. 1992; Denys 1991). To eliminate this possibility, we performed a second experiment without any motion (Experiment 2). In this experiment, participants in the *Cooled* and *Control* groups performed a hand laterality task that required them to mentally rotate their

right or left hand. Results showed that cold impacted the implicit motor imagery processes specifically linked to the effector that was cooled (i.e., right arm): participants in the *Cooled* group were slower and produced more errors when they had to mentally rotate their cooled hand at the extreme orientation of 160°, compared with the control hand or control group. Taken together, the results of these two experiments support the hypothesis that cold modifies CNS processing by modifying the sensorimotor representation involved in the action as well as the online process of proprioceptive feedback.

Several studies have already demonstrated the impact of cooling on sensorimotor control, with effects on dexterity (Giesbrecht and Bristow 1992; Phetteplace 2000), tracking performance (Goonetilleke and Hoffmann 2009), and motor coordination (de Jong et al. 1966). Here, we observed that cooling an arm to $14\pm 1^\circ\text{C}$ (skin temperature) also impacts pointing movements, which require a tradeoff between accuracy and velocity. Our results suggested an additional effect of temperature on sensorimotor control, for although the repetition of trials in the second, *Nonimmersed*, session generally led to improved performances, we observed a contrasting effect for the *Control* group, as AT increased for *ID3* and MT and DT increased for *ID7*. Accordingly, whereas cooling would slow movements down, lukewarm water immersion would accelerate them. Further studies are required to confirm this observation, but water immersion per se has already been shown to decrease perceived fatigue and increase recovery, owing to the impact of hydrostatic pressure on cardiovascular function (for a review, see Wilcock et al. 2006). We found that cooling lengthened MT, in line with previous observations for Fitts's tasks requiring fine finger movement, such as smartphone (Goncalves et al. 2016) or trackball (Blomkvist and Gard 2000) use. It could be argued that MT lengthening reflects the impact of the cold on musculotendinous and nerve functions, leading to slower and weaker muscle contraction (Bigland-Ritchie et al. 1992; Denys 1991). We suggest, however, that above and beyond peripheral causes, cold also has an impact on CNS processing, owing to the

difficulty of using proprioceptive *feedback*. We could surmise that proprioceptive cues are integrated less accurately and/or more slowly by the CNS (i.e., NCV reduction; Algafly et al. 2007), thereby impairing/delaying both *feedback* and *feedforward* motor control. Interestingly, this MT lengthening for pointing has also been observed in other cases of proprioceptive cue modification, such as short-term limb immobilization (Bassolino et al. 2012; Moisello et al. 2008; Scotto et al. 2020) and deafferentation (Medina et al. 2009; Sarlegna et al. 2006).

First, we observed a deleterious effect of cold on early temporal and spatial kinematic parameters. As cold reduces NCV (Algafly et al. 2007) and slows down the response of sensory receptors (Chesterton et al. 2002), the somatosensory signals would be altered to the extent that the perception of the initial state of the limb would be impaired. Indeed, even if vision would be the main sensory source to generate a spatial plan for pointing toward visual targets, proprioception is essential to transform this plan into the motor commands to produce the desired kinematics (see Sarlegna & Sainburg 2009). Here, the altered sensory signals by cold would lead to an impaired perception of the initial limb position, which might result in selecting the incorrect set of muscle commands to perform the movement. In the present study, while movement direction was not constrained, cold induced more SD impulse variability. As cold also impacted later kinematic parameters, it might be that the initial impaired perception of the limb position last longer for *feedback* control. Further studies would be required to assess the effect of cold on movement parametrization of direction versus amplitude. Studies already showed arm position sense alteration with cold possibly due to modification of muscle spindles activity and muscle thixotropy (Seiki-hara et al. 2007). Conversely, stimulating massage, performed by a physiotherapist, activates the proprioceptive mechanoreceptors and improves the sense of position (Henriksen et al. 2009) as well as the internal representation of the body part (Rulleau and Toussaint 2018) that was massaged. In addition, studies on limb vibration have underlined the essential initial role of proprioception: final errors occurred when the limb

was vibrated with no visual feedback available prior to the movement, suggesting that perception of limb position is biased by the altered proprioceptive feedback with vibration (DiZio et al. 1993; Lackner and Taublieb 1984; Larish et al. 1984). An alternative hypothesis would be that the *feedforward* control of movement would be impacted by the cold, probably because the internal model of the cooled limb was updated either incorrectly or not at all. Indeed, early kinematic modifications have been shown to reflect the use of internal models, that is, representations of the action and its sensory consequences (e.g., future states of the arm at the end of pointing; Wolpert et al. 1995). Based on this *feedforward* input from the limb, predictions of future states are compared with the current state, allowing for early corrections (Desmurget and Grafton 2000; Wolpert et al. 1995; Wolpert and Ghahramani 2000). As the CNS does not integrate the profound effects of cold on the functional properties of skeletal muscles (for a review, see Oksa 2002), cold increases the time to maximum force level (Ranatunga et al. 1987) or the co-contraction of antagonist muscles, leading to a *braking effect* (Oksa et al. 1995). In addition, stiffness of tendons and joints has been reported to increase with cold (Hunter et al. 1952; Rice 1967). According to this hypothesis, these profound effects of cold on musculotendinous and nerve functions would be partially/erroneously integrated for the *feedforward* control of the movement. Overall, our results suggested that more than peripheral causes, cold would have an impact on central processing (i.e., *feedforward* control and/or erroneous perception of initial limb position): both temporal and spatial early kinematic parameters (i.e., AT and SD impulse variability) were impaired by cold and this impairment was found to depend on the task complexity (i.e., *ID*). Our results of Experiment 2 gave more weight to this assumption as we found an impact of cold on sensorimotor representations (see below).

This hypothesis of *feedforward* control being modified by the cold was supported by an interaction between *Group* (*Cooled* vs. *Control*) and *ID* (*ID3* vs. *ID7*) on the kinematic

parameters (i.e., AT, DT, MT) that was independent of peripheral musculotendinous function. A pointing movement that requires greater accuracy (e.g., *ID7*) needs a more detailed representation of the action and its sensory consequences in the environment, to reach the target. The cold therefore acts upon what is an already complex *feedforward* process. A second argument in favor of the cold modifying *feedforward* control concerns the results of Experiment 2. In this experiment, participants were slower when they had to mentally rotate the cooled hand to the extreme orientation of 160°, i.e., the effect of cold became significant only for the orientation that required the largest amplitude, or that reached the limits of what is biomechanically possible. As suggested by Wilson et al. (2004), “the added (cognitive) computation required to calibrate rotation of hands is functionally equivalent to the time required to generate an efference copy of an intended (but uninitiated) movement”. This result is similar to those reported in studies on short-term hand immobilization, where difficulties of mental rotation were more pronounced or were only seen at extreme hand orientation corresponding to harder movement to be simulated;(Meugnot et al. 2014; Toussaint and Meugnot 2013). It is possible that the lack of integration of proprioceptive cues with cold, due mainly to reduced NCV (Algaflly et al. 2007) and slower sensory receptors response (Chesterton et al. 2002), may have weakened the construction of the arm representation needed to mentally rotate the cooled arm. In the second experiment, in addition to the slowing of response times with cold, an increase of incorrect responses was observed, arguing for a less accurate sensorimotor representation. This is consistent with several studies reporting decreased knee position sense (Oliveira et al. 2010) and ankle position sense (Hopper et al. 1997). Here, however, this interpretation must be viewed with caution, as inaccuracy of proprioceptive receptor functioning after cooling has not been confirmed by all authors (e.g., Costello and Donnelly 2010). Nevertheless, even if further studies are needed to clarify the origin of the central disturbances induced by a cooling procedure, our study suggests that arm cooling

impairs prediction of the sensory consequences of the mental rotation, and thence *feedforward* processing of the imagined action.

Our results suggest that cold also modifies *feedback* control of movement, above and beyond the peripheral consequences of cold on musculotendinous function (Oksa 2002). We found an effect of the interaction between task complexity (*ID3* vs. *ID7*) and *Group* (*Cooled* vs. *Control*) on DT, as well as under/overshoots of the primary submovement. With cold, DT increased, as well as final submovements to reach the visual target, suggesting disruption of the processing of proprioceptive cues to correct the movement online. This is in line with the NCV reduction observed with cold (Algafly et al. 2007). Several studies have already suggested a failure of joint position sense in cold temperatures (Hopper et al. 1997; Oliveira et al. 2010; Sekihara et al. 2007; Surenkok et al. 2008; Uchio et al. 2003). In the present study, the decrease in proprioceptive *feedback* presumably led to delayed processing of the actual position of the arm, and thus to delayed corrections and more pointing under/overshoots. Visual cues are mainly used to compensate for this type of decrease, notably with online visual comparisons between the cursor and the target position. This *feedback* control of the pointing movement through vision has been shown to start later than proprioceptive one (Sarlegna et al. 2004; Saunders and Knill 2004), which could explain why the *homing* phase lasted longer (i.e., longer DT).

The present study aimed to assess the impact of cold-water immersion of the dominant arm in right-handers, from CNS representations to sensorimotor control. Our results suggest that above and beyond peripheral causes, cold also has an impact at a representational level (*feedforward* control and/or hand representation) and on *feedback* control. This finding might be taken into account for performance purposes when applying cold (e.g., for pain reduction or in prevision of high exertional heat stress), notably when the individual has to do arm goal-directed movements immediately afterwards. Further experiments would be required to

generalize these findings over global physical skills such as athletics performance. Our findings would also have implications for the medical field, as well as for people working in cold environments (e.g., cold storage warehouses).

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Disclosures

The authors declare no conflicts of interest, financial or otherwise.

Author Contributions

L.T., C.R.S., O.D., B.D. and G.C. conceived and designed the research; F.P. performed the experiments; C.R.S., L.T. and F.P. analyzed the data; C.R.S, L.T. and F.P. interpreted the results of the experiments; C.R.S. and L.T. prepared the figures; C.R.S. and L.T. drafted the manuscript; and C.R.S., L.T., O.D., B.D. and G.C. edited and revised the manuscript.

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Figure Captions

Figure 1: General procedure. **A:** For the Fitts's task, on Day 1 participants were first immersed either on cold water (*Cooled* group) or lukewarm water (*Control* group). All participants then performed the pointing task with a first ID (*ID3* or *ID7*). A second immersion was performed to run the second ID (*ID3* or *ID7*). On Day 2, participants were not immersed and directly performed the Fitts's task with each of the ID, in the reverse order as Day 1. **B:** For the Hand laterality task, on Day 1 participants were immersed either on cold water (*Cooled* group) or lukewarm water (*Control* group) and then run the task. On Day 2, participants were not immersed and directly performed the Hand laterality task.

Figure 2: Images used for the hand laterality task. Left- and right-hand images with different orientations (40°, 80°, 120° and 160°) following medial or lateral rotations

Figure 3: Movement Time (MT) for *ID3* (**A**) and *ID7* (**B**) according to *Session* (*Immersed* vs. *Nonimmersed*) for the *Control* and *Cooled* groups. **: $p < 0.01$; ***: $p < 0.001$. Error bars denote standard error

Figure 4: Under/overshoots of the primary submovement (%) for *ID3* (**A**) and *ID7* (**B**) according to *Session* (*Immersed* vs. *Nonimmersed*) for the *Control* and *Cooled* groups. *: $p < 0.05$; ***: $p < 0.001$. Error bars denote standard error

Figure 5: Acceleration Time (AT) for *ID3* (**A**) and *ID7* (**B**) according to *Session* (*Immersed* vs. *Nonimmersed*) and group. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Error bars denote standard error

Figure 6: Variability of the impulse direction. Standard Deviation of impulse direction (deg) according to *Session* (*Immersed* vs. *Nonimmersed*) and *Group* (*Control* and *Cooled*). ***: $p < 0.001$. Error bars denote standard error

Figure 7. Deceleration Time (DT) for **(A) ID3** and **(B) ID7** according to *Session (Immersed vs. Nonimmersed)* and *Group (Control and Cooled)*. **: $p < 0.01$; ***: $p < 0.001$. Error bars denote standard error







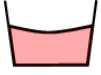
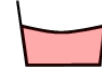
Figure 8: Accuracy (%) according to *Orientation (40°, 80°, 120°, and 160°)* and *Hand (left vs. right)* for the *Control* and *Cooled* groups. Error bars denote standard error. *: $p < 0.05$

Figure 9. Response times (ms) according to *Orientation (40°, 80°, 120°, and 160°)* and *Hand (Left vs. Right)* for the *Control* and *Cooled* groups in **A**) the *Immersed* session (i.e., immediately after immersion, and **B**) the *Nonimmersed* session, 24 h later. Error bars denote standard error. *: $p < 0.05$

Figure 1

A

Exp 1: Fitts's task

	Day 1: Immersed Session				Day 2: NonImmersed Session	
	Immersion	Task ID n°1	Immersion	Task ID n°2	Task ID n°2	Task ID n°1
Cooled group						
Control Group		ID3 or ID7		ID7 or ID3	ID7 or ID3	ID3 or ID7

B

Exp 2: Hand laterality task




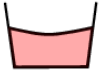


	Day 1: Immersed Session		Day 2: NonImmersed Session
	Immersion	Task	Task
Cooled group			
Control Group			

Figure 2

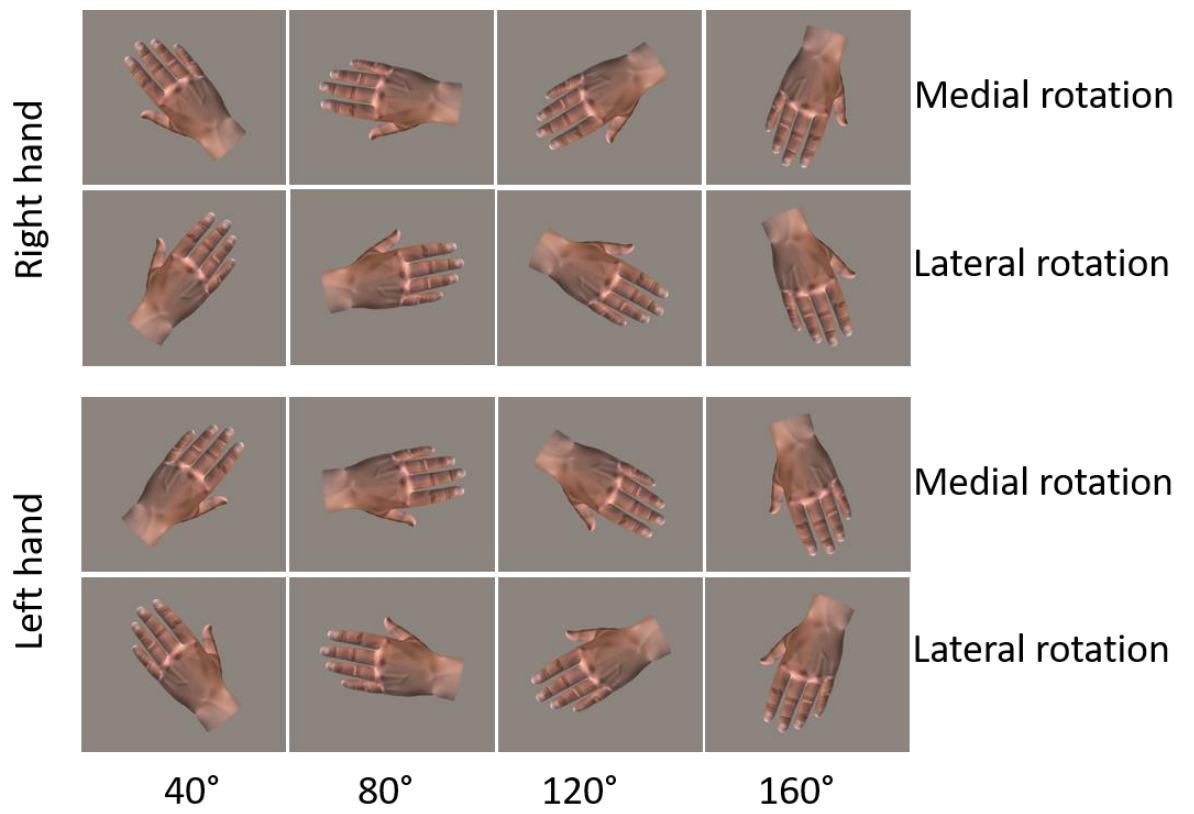


Figure 3

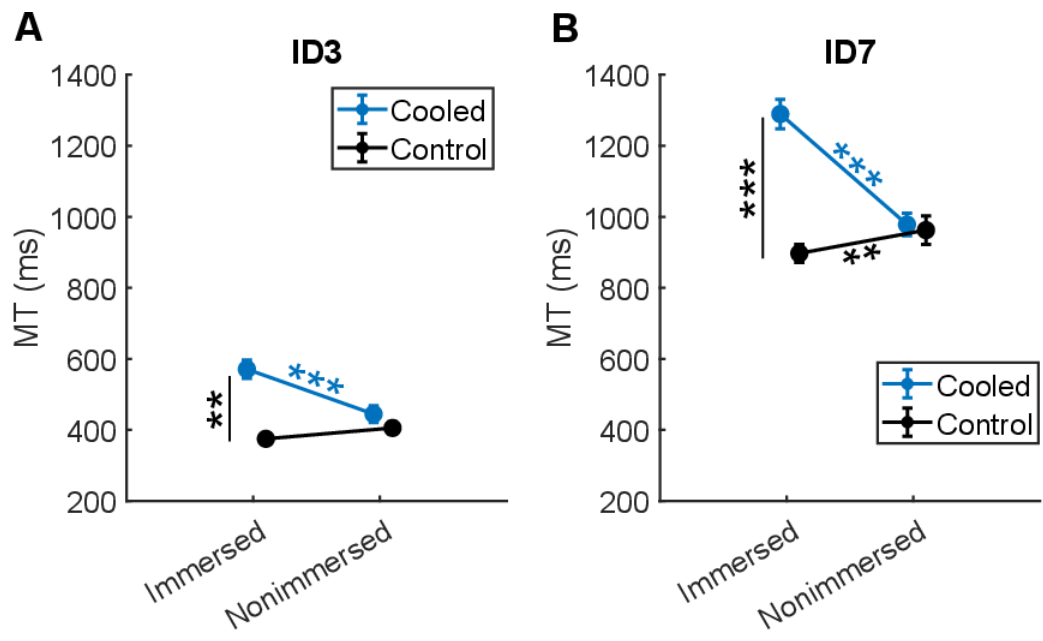


Figure 4

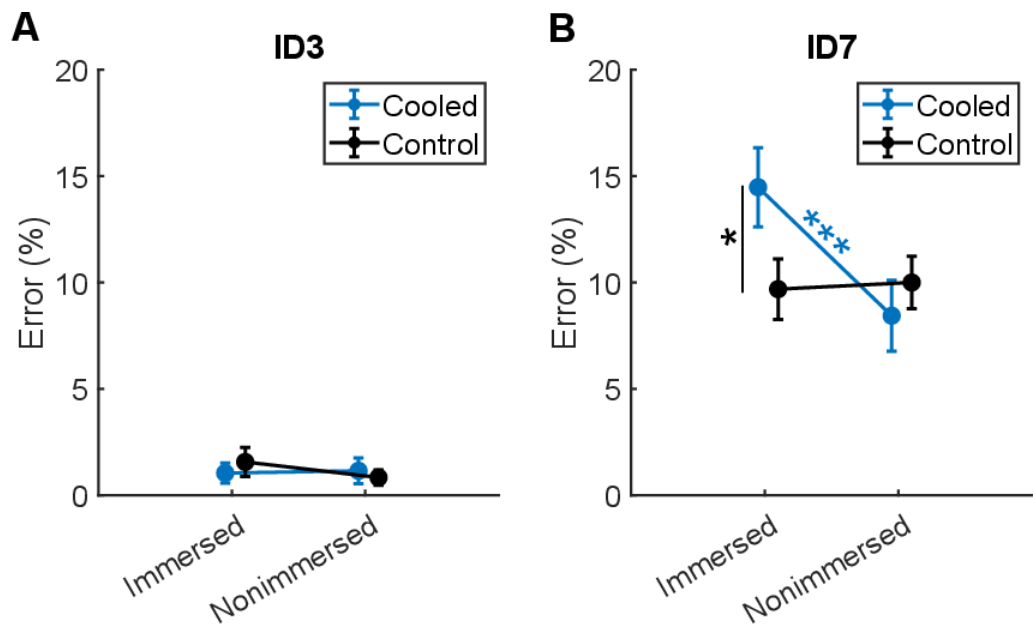


Figure 5

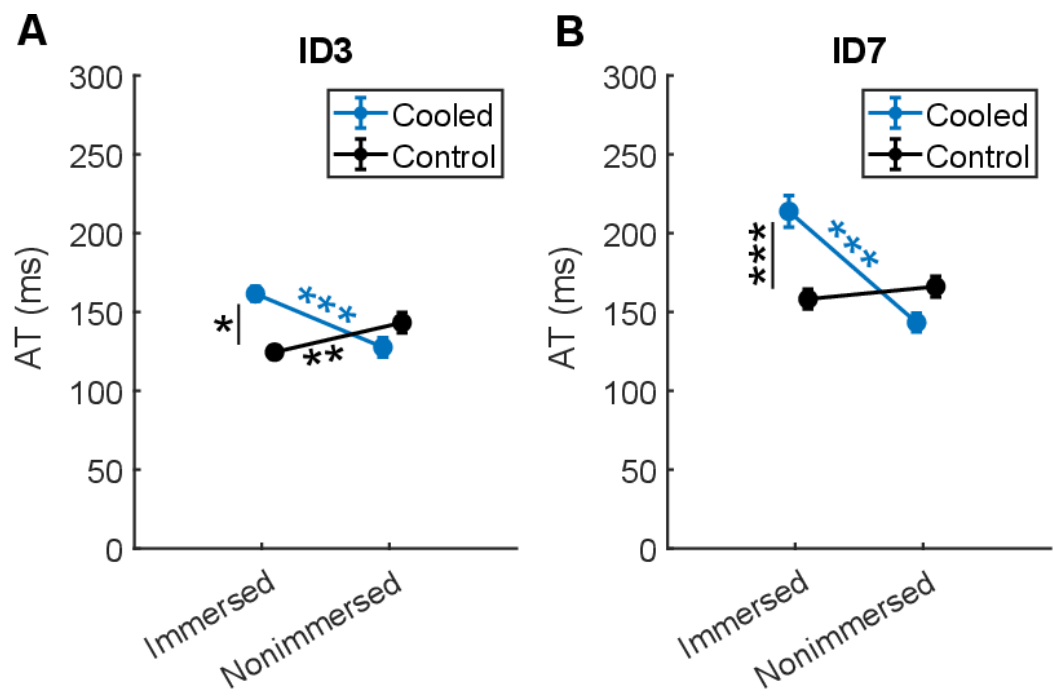


Figure 6

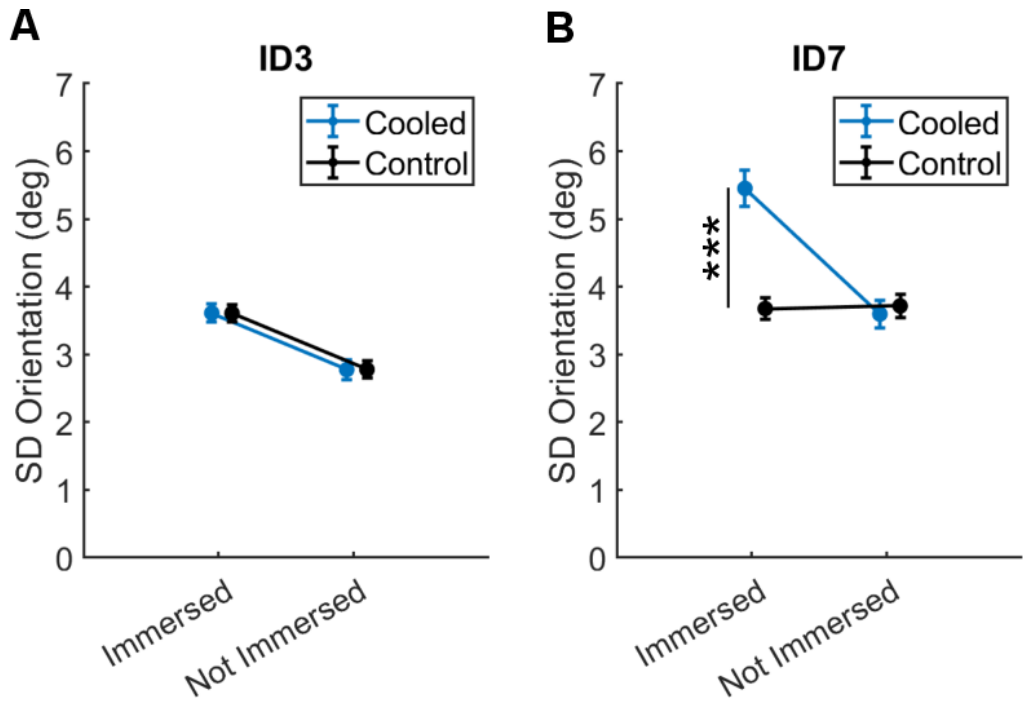


Figure 7

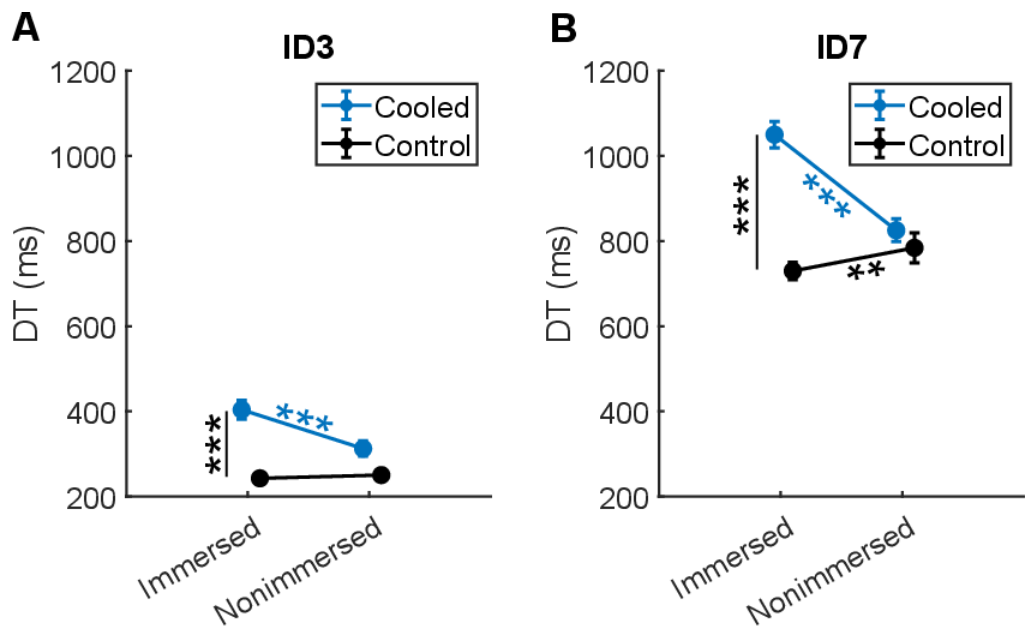


Figure 8

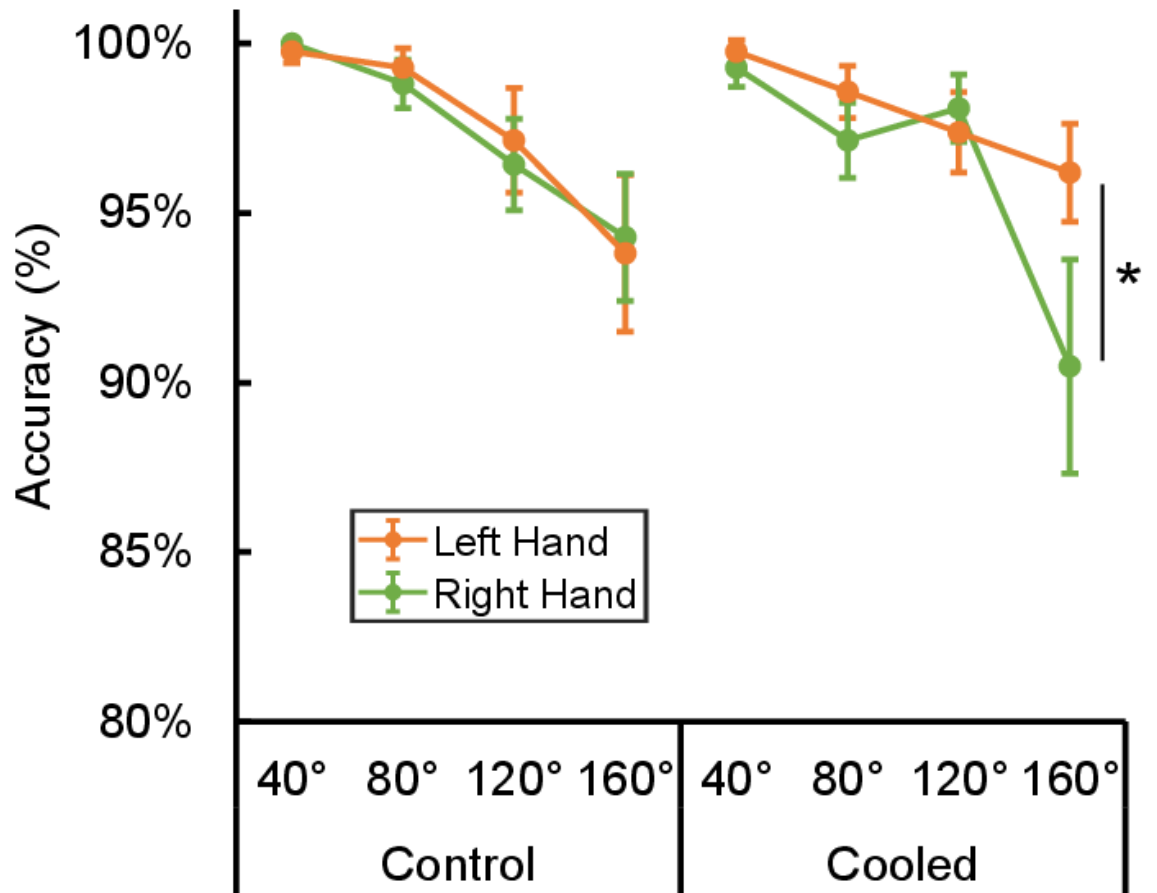


Figure 9

