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Thermal and tactile interactions in the perception of local skin wetness at rest and during exercise in thermo-neutral and warm environments

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Abbreviations

T_{sk} , Skin temperature

LP, Low pressure

HP, High pressure

ΔT_{sk} , Variation in local skin temperature

Abstract

The central integration of thermal (i.e. cold) and mechanical (i.e. pressure) sensory afferents is suggested as to underpin the perception of skin wetness. However, the role of temperature and mechanical inputs, and their interaction, is still unclear. Also, it is unknown whether this intra-sensory interaction changes according to the activity performed or the environmental conditions. Hence, we investigated the role of peripheral cold afferents, and their interaction with tactile afferents, in the perception of local skin wetness during rest and exercise in thermo-neutral and warm environments. Six cold-dry stimuli, characterised by decreasing temperatures [i.e. -4, -8 and -15°C below the local skin temperature (T_{sk})] and by different mechanical pressures [i.e. low pressure (LP): 7 kPa; high pressure (HP): 10 kPa], were applied on the back of 8 female participants (age 21 ± 1 years), while they were resting or cycling in 22 or 33°C ambient temperature. Mean and local T_{sk} , thermal and wetness perceptions were recorded during the tests. Cold-dry stimuli produced drops in T_{sk} with cooling rates in a range of 0.06 to 0.4°C/s. Colder stimuli resulted in increasing

coldness and in stimuli being significantly more often perceived as wet, particularly when producing skin cooling rates of 0.18°C/s and 0.35°C/s . However, when stimuli were applied with HP, local wetness perceptions were significantly attenuated. Wetter perceptions were recorded during exercise in the warm environment. We conclude that thermal inputs from peripheral cutaneous afferents are critical in characterizing the perception of local skin wetness. However, the role of these inputs might be modulated by an intra-sensory interaction with the tactile afferents. These findings indicate that human sensory integration is remarkably multimodal.

Keywords: skin wetness; thermo-receptors; mechano-receptors; sensory integration; perception

The perception of skin wetness is a complex somatosensory experience which seems to result from the intra-sensory integration of temperature and mechanical inputs (Ackerley et al. 2012; Bergmann Tiest et al. 2012; Bentley, 1900). Although humidity-receptors have been previously described in some insects (Yokohari and Tateda, 1976), these receptors have not been identified in human skin (Clark and Edholm, 1985). It is currently suggested that as human beings, we “learn” to perceive the wetness experienced when our skin is in contact with a wet surface, when a liquid is touched, or when sweat is produced (Bergmann Tiest et al. 2012) through a complex multisensory integration (Driver and Spence, 2000; Gescheider and Wright, 2012). The physical processes which occur when the skin is in contact with moisture (i.e. heat transfer and mechanical interactions between the skin and the environment) generate thermal and mechanical inputs which could be integrated and combined at different anatomical levels through specific multisensory pathways (Cappe et al. 2009). Hence, it is not the contact of the skin with moisture *per se*, but rather the integration of particular sensory inputs which seems driving the perception

of local skin wetness during the contact with a wet surface (Bentley, 1900). It could therefore be suggested that the perception of local skin wetness is a “perceptual illusion” shaped by sensory experience.

The thermal sense, and specifically the cold sensations (as resulting from the afferent activity of the cold sensitive skin’s thermo-receptors, i.e. small myelinated A δ and unmyelinated C-fibers) (Campero and Bostock, 2010), could play a critical role in the ability to perceive local skin wetness. For example, we seem to interpret the coldness experienced during the evaporation of water from the skin as a signal of the presence of water (and thus wetness) on the skin’ surface (Bergmann Tiest et al. 2012; Daanen, 2009). The importance of sensing coldness in order to experience local skin wetness has been highlighted by our previous findings. We have demonstrated that an illusion of local skin wetness can be evoked during the skin’s contact with a cold-dry surface producing a range of skin cooling rates of 0.14 to 0.41°C/s (Filingeri et al. 2013a). Also, we have observed that no local wetness was perceived during the contact with a warm-wet surface (with a temperature warmer than the skin), when no skin cooling, and thus no cold sensations, occurred (Filingeri,

et al. 2013b). Nevertheless, the mechanical sense could play a role as determinant as the one played by the thermal sense in characterising this perception. Everyday experience indicates that we perceive skin wetness even in the absence of coldness, e.g. when in contact with warm liquids. Bergmann Tiest et al. (2012) have shown that, when thermal cues (e.g. thermal conductance of a wet material) provide insufficient sensory inputs, individuals seem to use mechanical cues (e.g. stickiness resulting from the adhesion of a wet material to the skin) to aid them in the perception of wetness. Thus, in particular conditions, the mechanical and pressure related sensations, as resulting from the afferent activity of the cutaneous mechano-receptors (for review, see Abraira and Ginty, 2013), might contribute significantly to the perception of wetness (Ackerley et al. 2012; Wang et al. 2002). However, although thermal and mechanical inputs seem to be acknowledged as the principal inducers of the perception of local skin wetness (Bentley, 1900; Ackerley et al. 2012; Bergmann Tiest et al. 2012), to date it is unclear how and to what extent these sensory inputs interact in characterising this complex perception. Furthermore, to our knowledge, whether and how this intra-sensory interaction is influenced by factors

such as the activity performed (i.e. rest vs. exercise) and the ambient temperature (i.e. thermo-neutral vs. warm) has never been investigated.

Thermal sensitivity to cold has been previously shown to be reduced during exercise, possibly due to hormonal and neurological factors (Ouzzahra et al. 2012). Also, local thermal sensations resulting from the same thermal stimulation have been shown to change according to the whole-body thermal state (e.g. greater cold sensitivity can be observed during heat exposure) (Arens et al. 2006; Attia and Engel, 1982; Cabanac et al. 1972). Thus, as we believe that sensing coldness is the primary inducer of the “perceptual illusion” of skin wetness (Filingeri et al. 2013a), it would be reasonable to hypothesise that the perception of local skin wetness is reduced during exercise (due to a reduced sensitivity to cold), as well as increased during warm environmental conditions (e.g. due to an increased sensitivity to cold).

The aim of this study was therefore to investigate the role of thermal and mechanical inputs, as well as their interaction, in the perception of local skin wetness, using a single-blinded psychophysical approach. Also, we investigated whether and how this

intra-sensory interaction is influenced by factors such as the activity performed (i.e. rest vs. exercise) and the ambient temperature (i.e. thermo-neutral vs. warm).

We hypothesised that, due to its synthetic nature, an illusion of skin wetness can be evoked through the application of particular cold-dry stimuli, resulting in specific rates of skin cooling (i.e. range of 0.14 to 0.41°C/s) (Filingeri et al. 2013a). Also, we hypothesised that, as the mechanical inputs generated by experiencing skin wetness (e.g. when sweating or immersing a body part into a liquid) usually refers to modest levels of pressure, and due to the complex interconnecting, intermodal and cross modal networks our sensory systems operate within (McGlone and Reilly, 2010), the interaction of different mechanical inputs (in the form of higher pressures) might attenuate the way this illusion is evoked.

1. Experimental Procedures

1.1 Participants

Eight healthy university female students (age 21 ± 1 years; height 166 ± 6 cm; body mass 60.5 ± 8 Kg; body composition by skinfold analysis $16.8 \pm 3.4\%$ body fat) with

no history of sensory-related disorders volunteered to participate in this study.

Female participants were preferred to male as they are less hairy. All participants gave their informed consent for participation. The test procedure and the conditions were explained to each participant. The study design had been approved by the Loughborough University Ethics Committee and testing procedures were in accordance with the tenets of the Declaration of Helsinki.

1.2 Design

The experimental design was based on the application (in a balanced order) of six cold-dry stimuli with different temperatures and mechanical pressures, on the bare upper and lower back of each participant. During the application of the stimuli participants were resting or cycling in an environmental chamber set at 22°C (thermo-neutral exposure) or at 33°C (warm exposure) and 50% relative humidity.

Each participant took part in four experimental tests: i) thermo-neutral rest; ii) warm rest; iii) thermo-neutral exercise; iv) warm exercise. These were performed in a balanced order, on separate days with at least 48 hours in between of them. The data collection took place during May and June. A single-blind psychophysical

approach was used for this study. Participants were informed only about the body region objected to the stimulation. No information was provided on the type and magnitude of the stimulation to limit any expectation effects.

1.3 Stimuli

Six cold-dry stimuli, resulting from combining three relative temperatures [-4, -8 and -15°C below the local skin temperature (T_{sk})] and two mechanical pressure [low pressure (LP): 7 kPa; high pressure (HP): 10 kPa] were used in this study: -4°C LP; -4°C HP; -8°C LP; -8°C HP; -15°C LP; -15°C HP. The stimuli were delivered by a square thermal probe (Physitemp Instruments Inc., USA) with a contact surface of 25 cm². The exact temperatures of the stimuli were calculated on an individual basis, by measuring the local T_{sk} with an infrared thermometer (Fluke Corporation, USA).

To manipulate and control the mechanical pressures applied by the thermal probe, we designed and developed a pressure control system (fig. 1). The system consisted of an air bladder, inserted into a frame attached to the thermal probe, which was connected to a manometer (containing water) throughout a silicon tube. The frame consisted of two wooden discs laid one upon the other and coupled by three springs

which allowed the top disc to scroll down freely. A handle was attached to the top disc so that the probe could be applied to the skin. When this happened, the air bladder deformed, producing a pressure change in the system which resulted in displacing the water in the manometer from its set “null” point (no pressure applied). The point reached by the water in the tube as a result of the pressure change was used as an indicator to control the mechanical pressure. To calibrate and standardize this last one, a digital scale (Mettler Toledo Inc., USA) was used to measure the force resulting from the application of the probe. The range between the lowest and the highest pressure applicable and measurable by the system resulted in 7 to 55 kPa. For the purposes of this study, two levels of mechanical pressure were chosen. The LP represented the pressure applied by the probe when this was just in contact with the skin surface (i.e. light touch). This pressure (i.e. 7 kPa) was considered as a reference pressure, as it was the lowest applicable and measurable by the pressure control system. The HP (i.e. 10 kPa) was then chosen to be just slightly greater than the reference pressure. We wanted our participants to perceive a difference between the two stimuli, without however applying an excessive

mechanical stimulation. Preliminary data indicated that individuals were able to perceive differences between the two levels of pressure chosen for this study. Tests were performed prior to the main experiment to check the accuracy and repeatability of the nominal pressures applied with the pressure control system. 100 trials (i.e. 50 for the LP and 50 for HP) were conducted. These consisted of measuring the force resulting from the application of the probe on a digital scale (Mettler Toledo Inc., USA) while controlling that the water displacement on the manometer was the one required for the pressures selected. 95% confidence interval values were calculated for the two nominal pressures and resulted as follow:

LP (i.e. 7 kPa) = 7.1 kPa (lower bound) – 7.2 kPa (upper bound); HP (i.e. 10 kPa) = 10.4 kPa (lower bound) – 10.6 kPa (upper bound). To ensure precision in the application of the stimuli and repeatability of the data, the same investigator conducted all trials.

1.4. Experimental Protocol

Participants arrived to the laboratory 30 min before the time scheduled for the test to allow preparation procedures. During the first visit, semi-nude body mass, height and

skinfolds thickness (seven sites) were recorded. For body composition calculations

ACSM's guidelines for exercise testing and prescription were used (Thompson et al. 2010).

Participants then changed into sport bra, shorts, socks and trainers. Five iButtons (Maxim, USA) were taped to five left skin sites (cheek, abdomen, upper arm, lower back and back lower thigh) to record T_{sk} (1 min intervals). The five temperature measurements were recorded at 1 min intervals throughout the tests, averaged every 5 min, and then weighted according to the work of Houdas, to give an estimate of mean T_{sk} for the entire body (Choi et al. 1997; Houdas and Ring, 1982). The skin sites targeted for stimulation were marked with a washable marker to assure consistency in the location of stimulation. These corresponded to: 5 cm upwards the inferior angle of the right scapula (i.e. upper back skin site); 5 cm upwards the right posterior superior iliac spine (i.e. lower back skin site). The back was chosen as targeted area for stimulation in order to eliminate any visual feedback which could have affected the way participants perceived the stimuli.

After preparation, participants entered the environmental chamber and 10 min were allowed for acclimation. During this period, participants familiarised with the rating scales designed to record individual thermal sensations and wetness perceptions: an 11 point thermal scale (-6 very cold; -4 cold; -2 slightly cool; 0 neutral; +2 slightly warm; +4 warm); an 11 point wetness scale (-6 dripping wet; -4 wet; -2 slightly wet; 0 neutral; +2 slightly dry; +4 dry) (Olesen and Brager, 2004). No descriptors were applied to intermediate scores (i.e. -5; -3; -1; +1; +3). We defined the value -2 (labelled: “slightly wet”) of the wetness scale as our set threshold to identify a clearly perceived local wetness. After the acclimation period, participants were asked to maintain a seated position, or to move to an electromagnetically braked cycle ergometer (Lode Excalibur, The Netherlands) and start cycling at 40 rpm, with a workload of 60 W. During the experimental test, participants were first asked to rate their thermal sensations and wetness perceptions just before the application of the stimulus (i.e. baseline whole-body sensation), while the local T_{sk} of the skin site targeted for stimulation was measured with the infrared thermometer. Then the thermal probe was set to the required relative temperature and applied by hand to the skin site with the set pressure. To avoid an effect of surprise on the transient

sensations, a verbal warning was given prior to stimulation. The application of the probe consisted of a short contact lasting 10 s. During the stimulation, the probe was not moved and participants could not see the stimulated area. At the end of the 10 s stimulation, participants were instructed and encouraged to verbally report their local sensation and perception, using whatever number in the scales seemed appropriate (integers only). Immediately after this the probe was removed and T_{sk} of the stimulated area was recorded with the infra-red thermometer. This method allowed rating to be made consistently close to the time when post-stimulation T_{sk} was recorded. This sequence was repeated for each stimulus allowing at least one minute in between them. This time interval, as well as the short duration of the stimulation and the balanced order of application (e.g. upper vs. lower back) allowed the local T_{sk} to return to baseline values before a new stimulus was applied. Each participant had only one presentation of each stimulus for each body region. All participants completed all conditions.

1.5 Statistical Analysis

In the present study, the independent variables were the probe temperature (the relative cold stimulus based on the individual baseline T_{sk}) and pressure, the body region stimulated, the activity performed and the environmental condition. The dependent variables were mean, local T_{sk} , average variations in local T_{sk} (ΔT_{sk}) (from pre- to post-stimulation), thermal sensation and wetness perception.

All data were first tested for normality of distribution and homogeneity of variance using Shapiro-Wilk and Levene's tests respectively. Mean T_{sk} data were analysed by a 2-way repeated measure analysis of variance, with activity performed (2 levels: rest and exercise) and ambient temperature (2 levels: thermo-neutral and warm) as repeated measures variables. Local ΔT_{sk} data were analysed by a 5-way repeated measure analysis of variance, with temperature of the stimuli (3 levels: -4, -8 and -15°C), pressure (2 levels: 7 and 10 kPa), body region (2 levels: upper and lower back), activity (2 levels: rest and exercise) and ambient temperature (2 levels: thermo-neutral and warm) as repeated measures variables. Data were tested for sphericity and if the assumption of sphericity was violated, Huynh-Feldt or Greenhouse-Geisser corrections were undertaken to adjust the degrees of freedom for the averaged tests of significance. Estimated marginal means and 95%

confidence intervals were used to investigate the main effects and interactions of the variables. When a significant main effect was found, Tukey's post-hoc analyses were performed. Observed power was computed using $\alpha=0.05$ and reported when a significant effect was observed.

Thermal sensation and wetness perception scores were analysed by Friedman's analysis of variance (X^2) and Wilcoxon signed rank tests (Z). First, the main effect of each independent variable was tested by collapsing the data over probe temperature (3 levels of comparison), pressure, body regions, activity and ambient temperature (2 levels of comparison) respectively. A Friedman's analysis of variance was performed for the 3 levels comparisons whereas a series of Wilcoxon Signed-ranks tests were performed for each of the 2 levels comparisons. Then, interactions between variables were investigated, using Friedman's analysis of variance (main effect) and Wilcoxon Signed-ranks test (post-hoc comparisons). It was decided to focus on specific interactions (i.e. probe temperature with pressure, 6 levels of comparison; activity with ambient temperature, 4 levels of comparison) in order to restrict the number of comparisons and thus reducing the risk of Type II errors. Effect size was calculated and reported as r . This analysis was considered advantageous

for its “planned comparison-approach” to interactions, drawing on clear conceptualization (Acock, 2010). Although the authors acknowledge that non-parametric statistics tend to have less power for well distributed dependent variables, they can be more sensitive to effects when variables are not normally distributed, as in the case of this study (Acock, 2010). Statistical analysis was performed using IBM SPSS Statistics 19 (IBM, USA). In all analyses, $p < 0.05$ was used to establish significant differences. Data are reported as mean $\pm$ standard error of the mean.

1.5.1 Frequency distribution analysis of wetness scores

To further investigate the effect of temperature and pressure of the stimuli on wetness perception scores, a frequency distribution analysis was performed. Wetness perception scores were averaged by temperature and pressure of the stimuli and collapsed over condition (i.e. activity and ambient temperature) and body region. Then, as the value -2 of the wetness scale (labelled: “slightly wet”) was defined as our set threshold to identify a clearly perceived local wetness, wetness scores from -2 (i.e. “slightly wet”) to -6 (i.e. “dripping wet”) were grouped and considered as referring to a clear perception of wetness (“wet”), whereas any score

in between -1 and +4 (i.e. “dry”) was considered as representing no perception of wetness (“dry”). At this point, the frequency of times the same cold-dry stimulus was perceived as “dry” or as “wet” was calculated and analysed by a Chi-square test. A similar frequency distribution analysis of thermal ratings has been previously reported in the literature (see Gan et al. 2012). In line with Gan et al. 2012, we believe that because of the variable nature of subjective responses, reorganizing the collected data in this format would make the potential thermal-tactile interaction in the perception of wetness easier to identify.

2. Results

2.1 Parametric data

2.1.1 Mean T_{sk}

Mean T_{sk} values were calculated for each condition and found to be normally distributed ($p > 0.05$). A significant main effect of activity performed ($F = 18.89_{(1, 7)}$, $p < 0.01$, observed power = 0.96), ambient temperature ($F = 300.23_{(1, 7)}$, $p < 0.01$, observed power = 1) and a significant interaction between these two ($F = 6.54_{(1, 7)}$, $p < 0.05$, observed power = 0.6) was found on the mean T_{sk} , whose values (as recorded

and averaged for each test) were respectively: $31 \pm 0.2^{\circ}\text{C}$ (thermo-neutral rest); $33.5 \pm 0.2^{\circ}\text{C}$ (warm rest); $31.2 \pm 0.3^{\circ}\text{C}$ (thermo-neutral exercise); $34.5 \pm 0.2^{\circ}\text{C}$ (warm exercise). Post-hoc analysis indicated that conditions of exercise and warm ambient temperature resulted in a significantly higher mean T_{sk} than conditions of rest and thermo-neutral ambient temperatures ($p < 0.01$).

2.1.2 Local T_{sk}

Baseline local T_{sk} values (pre-stimulation) varied in a range between $29.6 \pm 0.2^{\circ}\text{C}$ (thermo-neutral exercise) and $33.6 \pm 0.2^{\circ}\text{C}$ (Warm rest) for the upper back, and between $27 \pm 0.2^{\circ}\text{C}$ (thermo-neutral exercise) and $32.1 \pm 0.2^{\circ}\text{C}$ (Warm rest) for the lower back. Average ΔT_{sk} from pre- to post-stimulation (as a result of each of the six stimuli, applied to each skin site, during each of the four experimental conditions), were calculated and found to be normally distributed ($p > 0.05$). These varied in a range of $-0.6 \pm 0.08^{\circ}\text{C}$ to $-4 \pm 0.2^{\circ}\text{C}$ (depending on probe condition), corresponding to a range of skin cooling rates of $0.06 \pm 0.01^{\circ}\text{C/s}$ to $0.4 \pm 0.02^{\circ}\text{C/s}$. These values were calculated as the ratio between the ΔT_{sk} from pre- to post-stimulation and the contact time (i.e. 10 s). The data analysis indicated that only the temperature of the

stimuli had a significant main effect on the local ΔT_{sk} ($F = 123.36_{(1.17, 8.2)}$, $p < 0.01$, observed power = 1). No significant effect of the pressure applied ($F = 3.66_{(1, 7)}$, $p > 0.05$), the body region stimulated ($F = 0.2_{(1, 7)}$, $p > 0.05$), the activity performed ($F = 0.3_{(1, 7)}$, $p > 0.05$) and the ambient temperature ($F = 2.13_{(1, 7)}$, $p > 0.05$) was found.

Figure 2 shows ΔT_{sk} and corresponding cooling rates, as a result of each cold-dry stimulus applied with LP and HP. Data were collapsed over the conditions performed (i.e. resting or exercising in thermo-neutral and warm environment) and the skin sites where the stimuli were applied. Post-hoc analysis indicated that colder stimuli resulted in significantly greater decreases in local T_{sk} ($p < 0.01$). No significant interactions between the temperature of the stimuli and any other repeated-measures variables were found ($p > 0.05$).

2.2 Non-parametric data

2.2.1 Thermal sensation

Baseline thermal sensation scores (pre-stimulation) were respectively: -1.1 ± 0.1 (thermo-neutral rest); $+0.9 \pm 0.1$ (Warm rest); $+0.7 \pm 0.1$ (thermo-neutral exercise);

+2.8 $\pm$ 0.1 (Warm exercise). Expressed in terms of semantic labels, these were in a range going from “slightly cold” to “warm”.

A first analysis was performed to investigate the main effects of temperature and pressure of the probe. A significant effect of temperature [X^2 (2, N = 128) = 187.69, p < 0.01] and a significant effect of pressure of the stimuli (Z = 4.26, p < 0.01, r = 0.3) on local thermal sensations was found. At this point, the interaction between temperature and pressure of the probe was investigated. Figure 3 shows the local thermal sensation scores as a result of each cold-dry stimulus applied with LP and HP, with data collapsed over the conditions performed and the skin sites where the stimuli were applied. A significant interaction between the temperature and pressure of the stimuli was found [X^2 (5, N = 64) = 204.51, p < 0.01] caused by the presence of a pressure effect at -8°C (Z = -3.26, p < 0.01, r = -0.4) and -15°C (Z = -2.52, p < 0.01, r = -0.32), but absence of this at -4°C (p > 0.05). The results confirmed that colder stimuli resulted in significantly colder sensations, and indicated that stimuli of same relative temperature (i.e. -8 °C and -15°C) were perceived as significantly less cold when were applied with HP than when they were applied with LP.

A subsequent analysis was performed to investigate the main effect of ambient temperature and activity on thermal sensations.

A significant main effect of ambient temperature ($Z = 2.91$, $p < 0.01$, $r = 0.21$) and activity ($Z = 3.1$, $p < 0.01$, $r = 0.22$) was found on thermal sensations. At this point, the interaction between activity and ambient temperature was investigated and found to be statistically significant [$\chi^2 (3, N = 96) = 20.18$, $p < 0.01$]. Significant differences were found only between conditions of rest in the thermo-neutral and warm environment ($Z = -2.56$, $p < 0.01$, $r = -0.26$). These results indicated that stimuli were perceived as being less cold when participants were resting in a warm environment than when they were resting in a thermo-neutral one. No significant main effect of body region was found ($p > 0.05$).

2.2.2 Wetness perception

Baseline wetness perception scores (pre-stimulation) were respectively: 0 ± 0.1 (thermo-neutral rest); 0 ± 0.1 (Warm rest); -0.5 ± 0.1 (thermo-neutral exercise); -2.2 ± 0.1 (Warm exercise). Expressed in terms of semantic labels, these were in a range going from “neutral” to “slightly wet”.

A first analysis was performed to investigate the main effect of temperature and pressure of the probe. A significant effect of temperature [$X^2(2, N = 128) = 75.36, p < 0.01$], and a significant effect of pressure of the stimuli ($Z = -3.27, p < 0.01, r = -0.23$) on local wetness perceptions was found. At this point, the interaction between temperature and pressure of the probe was investigated. Figure 4 shows the local wetness perception scores as a result of each cold-dry stimulus applied with LP and HP, with data collapsed over the conditions performed and the skin sites where the stimuli were applied. A significant interaction between temperature and pressure of the stimuli was found [$X^2(5, N = 64) = 87.31, p < 0.01$], caused by the presence of a pressure effect at -8°C ($Z = -2.98, p < 0.01, r = -0.4$) and -15°C ($Z = -2.3, p < 0.05, r = -0.3$), but absence of this at -4°C ($p > 0.05$).

These results indicated that colder stimuli resulted in significantly wetter sensations, and that stimuli of same relative temperature (i.e. -8°C and -15°C) were perceived as significantly less wet when were applied with HP than when they were applied with LP.

A subsequent analysis was performed to investigate the main effect of ambient temperature and activity on wetness perceptions.

A significant effect of ambient temperature ($Z = -3.65$, $p < 0.01$, $r = -0.26$), and a significant effect of activity ($Z = -4.25$, $p < 0.01$, $r = -0.32$) on local wetness perceptions was found. At this point, the interaction between the activity and ambient temperature was investigated and found to be statistically significant [$\chi^2(3, N = 96) = 20.97$, $p < 0.01$]. Significant differences were found only between conditions of exercise in the thermo-neutral and warm environment, as well as between rest and exercise performed in the warm environment. These results indicated that stimuli were perceived as being wetter when participants were exercising in a warm environment than when they were resting in the same environment ($Z = -3.75$, $p < 0.01$, $r = -0.4$), as well as when they were exercising in the thermo-neutral one ($Z = -3.75$, $p < 0.01$, $r = -0.38$). No significant main effect of body region was found ($p > 0.05$).

2.2.2.1 Frequency distribution analysis of wetness scores

A frequency distribution analysis of wetness scores was performed and data for each of the six cold-dry stimuli are shown in figure 5. The results indicated a main effect, as well as a significant interaction, between temperature and pressure of the stimuli

on the frequency of “wet” scores (Pearson Chi-square $p < 0.01$). Colder stimuli were significantly more often perceived as wet (i.e. -4°C LP= 21.9%; -8°C LP= 46.9%; -15°C LP= 60.9%). However, when stimuli with the same relative temperature were applied with HP, local wetness perceptions were significantly attenuated (i.e. -4°C HP= 20.3%; -8°C HP= 32.8%; -15°C HP= 45.3%).

3. Discussion

The aim of this study was to investigate the sensory integration responsible for the perception of local skin wetness, with regards to thermal (i.e. cold) and mechanical (i.e. pressure) afferents. The experimental protocol was designed to assure that two bare and dry skin sites would be exposed to the contact with a range of cold-dry stimuli, applied with two different mechanical pressures, during experimental trials consisting of resting or exercising in a thermo-neutral or warm environment.

The results of this study indicated that cold-dry stimulations can evoke artificial wetness perception, with colder stimuli resulting in a higher frequency and magnitude of wet perceptions. Also, we observed that the application of stimuli with a higher mechanical pressure on the skin reduced the frequency of times artificial

wetness perceptions were evoked. Finally, we found that cold-dry stimuli were perceived as being wetter during exercise performed in the warm environment than during rest in the same environment, as well as than during exercise in the thermo-neutral one.

3.1 The role of thermal inputs in the perception of local skin wetness

The first main outcome of this study is that the perception of local skin wetness did relate to the activation of the thermal afferents responding to skin cooling. When cold-dry stimuli, resulting in skin cooling rates in a range of 0.06 to 0.4°C/s, were applied on participants' skin, these were frequently perceived as being not only cold, but as also wet. Cold-dry stimuli were more frequently perceived as cold-wet (i.e. 46.9% and 60.9% of times they were applied) when these resulted in skin cooling rates of 0.18°C/s (i.e. -8°C LP stimulus) and 0.35°C/s (i.e. -15°C LP stimulus). This is aligned to our previous findings. We have recently shown that an illusion of local skin wetness can be evoked during the skin's contact with a cold-dry surface producing skin cooling rates in a range of 0.14 to 0.41°C/s (Filingeri, et al. 2013a). This range of skin cooling rates is also aligned to the one which occurs during the evaporation of

water from the skin' surface as suggested by Daanen (2009), who measured the temperature course of the skin (i.e. temperature's drop of 1 to 5°C with a 0.05 to 0.2°C/s cooling rate) when this was wetted with drops of water with volumes in a range of 0.01 to 0.1ml. However, in the present study, and in line with our previous findings (Filingeri, et al. 2013a), we observed that the cooling rates which more often evoked perceptions of wetness (i.e. 0.18 and 0.35°C/s) were slightly faster than the ones proposed by Daanen (2009). A possible explanation to this difference might be related to the different types of cooling used in the two experiments, as in Daanen's work, skin cooling resulted from evaporation whereas in our study cooling resulted from conduction (i.e. contact with a surface colder than the skin). Recent evidence has indicated that the perception of skin wetness comprises a number of different cues, amongst which evaporation and thermal conductance, and that evaporation might require slower cooling rates than thermal conductance to evoke the perception of wetness (Bergmann Tiest et al. 2012). This seems to be due to the fact that evaporation is only sensed with a thin layer of moisture on the skin, whereas increased thermal conductance is only a factor with a larger volume of liquid (Bergmann Tiest et al. 2012). This could result in greater heat extraction from the skin

and thus greater coldness experienced. In the light of this, the outcomes of this study provide evidence in support of the hypothesis that different thermal cues (i.e. evaporation or conductance) might require different rates of skin cooling to evoke the perception of local skin wetness.

The fact that an illusion of local skin wetness was experienced when the skin was in contact with a cold-dry surface resulting in particular rates of skin cooling (and thus cold sensations), unmasked the synthetic nature of this complex perception (Bentley, 1900). Furthermore, it highlighted the remarkable ability of the central nervous system to learn through sensory experiences (Gescheider and Wright, 2012).

Perceptual learning, and specifically somatosensory-decision making, seems to be a critical neuronal process which underlines our ability to link sensation, memory and decision making (Pleger and Villringer, 2013). Studies in primates have shown how somatosensory stimuli might be represented in the brain, and how such representation relates to sensation, memory and decision making (Romo and Salinas, 1999). The somatosensory cortex seems to be involved in generating a neural representation of the sensory stimulus, which is used for further processing in

downstream areas. These areas transform the neural representation into a simple firing rate code representing the stimulus frequency during presentation, working memory and decision components (Lemus et al. 2007). Thus, we hypothesise that a similar process might occur during the experience of skin wetness. As we are apparently not provided with specific hygro-receptors (Clark and Edholm, 1985), the somatosensory inputs which our brain encodes when the skin is wet (e.g. thermal cues due to skin cooling), might be coded into particular neural representations and then associated to the perception of skin wetness. This hypothesis could explain why in our study the exposure to thermal inputs similar to the ones occurring when the skin is physically wet, evoked a perceptual illusion of wetness, even if no contact with moisture occurred. However, this speculation needs further experimental evidence, as somatosensory decision making is still an almost unexplored area in humans (Pleger and Villringer, 2013).

3.2 The interaction between thermal and mechanical inputs

The second main outcome of this study is that the illusion of local skin wetness was significantly attenuated by an increase in the mechanical pressure applied to the skin.

Although thermal stimuli applied with HP and LP resulted in similar skin cooling rates, HP were perceived as significantly less cold and less wet. This finding is of high interest, as to our knowledge this is the first study to report an interaction between thermal and mechanical inputs, which attenuated the perceptual illusion of local skin wetness.

Interactions between thermal and mechanical inputs during dynamic contact cooling (i.e. skin cooling occurs when the thermal probe first contacts the skin) have been previously reported (see Green, 2004 for an extensive review). Based on the outcomes of these studies, cold sensations have been suggested to involve interactions between the pathways for cold, nociception and touch. These interactions seem to occur particularly at mild temperatures (Green and Pope, 2003; Green and Schoen, 2005; Green and Schoen, 2007), such as the ones resulting from the stimuli used in this study (i.e. skin temperature's drop between 0.6 and 4°C). Green et al. (2003, 2005, 2007) have reported an attenuation (i.e. -13%) in cold sensation by dynamic contact cooling (as opposed to static contact, i.e. skin cooling occurs when the thermal probe is already in contact with the skin), during the application of stimuli with a mild temperature (i.e. 31°C) to the volar surface of the

forearm (when this had a baseline T_{sk} of 33°C). In these studies, thermal sensations were unaffected by dynamic touch at lower temperatures (i.e. 27, 24 and 20°C).

The outcomes of our study seems aligned to the ones reported by Green et al. (2003, 2005, 2007) as we observed attenuations in thermal sensation (and wetness perception) due to an increased mechanical stimulation to the skin. This attenuation was significantly accentuated by those stimuli which reduced T_{sk} by 1.8 to 4°C (i.e. -8 and -15°C stimuli respectively), from an average baseline value of 30.5°C. Although Green et al. concluded that their results are a demonstration that tactile stimulation has only a relatively weak inhibitory effect on the cold pathway (which quickly becomes insignificant at colder levels of stimulations) (Green and Schoen, 2007), we believe that this “weak” inhibitory effect could have been sufficient enough to alter the cold sensations, and thus the evoked skin wetness, experienced by our participants. As we have previously shown that local skin wetness is strongly related to the level of coldness experienced (Filingeri, et al. 2013a), we believe that even small changes in the cold sensations occurring during contact cooling might affect the way skin wetness is evoked. Furthermore, as stimulation of the rapidly-adapting skin mechanoreceptors during dynamic touch has been shown to be critical for other

previously described intra- and inter-sensory interactions (e.g. touch-pain and thermal-pain, in which touch and thermal stimuli reduce the perception of pain) (Bolanowski et al., 2001; Green, 2009; Green and Pope, 2003; Green and Schoen, 2005), it is reasonable to hypothesise that changes in mechanical afferents might influence the way a complex perception such as skin wetness is experienced. It could be suggested that the LP stimuli used in this study (i.e. light touch) generated mechanical sensations which could have been closer to the mechanical inputs experienced when individuals are “physically wet” (e.g. when sweating or immersing a body part into a liquid). As these inputs usually refers to modest levels of pressure (Bergmann Tiest et al. 2012), it would be then reasonable to expect that LP stimuli, as opposed to HP ones, would increase the occurrence of wetness perceptions, as observed in this study. High static pressures during contact cooling of the skin, despite providing more cooling, might have generated “unfamiliar” sensations which are not commonly associated to the way we *learn* to perceive skin wetness.

Perception is well known to be a cognitive process which relies on the multisensory integration of information from different sensory systems, which are combined at different levels of the neuraxis (Cappe et al. 2009; Driver and Spence, 2000; Stein et

al. 2009). The impact of multisensory integration on cognition and behaviour has been amply demonstrated by sensory phenomena such as the “skin parchment illusion”, in which audio-tactile interactions change the perception of roughness (Jousmäki and Hari 1998). The outcomes of this study might therefore provide evidence in support of the hypothesis of a tactile-mediated attenuation of the perception of local skin wetness. Also, these findings indicate that cold sensation and wetness perception might not depend solely on the parameters of the thermal stimulus. However, one should note that any generalization of these findings should be carefully considered in the light of the regional differences (e.g. glabrous vs. hairy skin) in the thermal and spatial sensitivity (i.e. thermo- and mechano-receptors innervation) across the body (Abraira and Ginty, 2013; Ackerley et al. 2012; Nakamura et al. 2008; Ouzzahra et al. 2012).

3.3. Effects of activity performed and ambient temperature on thermal and wetness perceptions

The third main outcome of this study is that cold-dry stimuli were perceived as wetter during exercise performed in the warm environment than during rest in the same

environment, as well as than during exercise in the thermo-neutral one. This outcome might indicate that environmental factors, such as exercise and ambient temperature, could have a central effect on modulating the sensory pathway of complex perceptions such as skin wetness. However, we hypothesised that the changes observed in the local wetness perception during the condition of exercise in the warm environment are more likely to be related to an effect of the whole body level of wetness, than to a central sensory modulation. Indeed, by the end of this trial, participants' skin was wet due to sweat production. It is therefore reasonable to hypothesise that experiencing a whole body perception of wetness during the trial might have influenced the way cold-dry stimuli were perceived locally on the skin (Fukazawa & Havenith 2009). Our previous findings (Filingeri, et al. 2013a), as well as the results of this study, indicate that local wetness is strongly driven by local coldness. Hence, if local changes in the sensory pathway for this perception occurred due to a central effect of exercise or ambient temperature, we would have expected similar changes in local thermal sensations. However, local thermal sensations were significantly different only between the conditions of rest in thermo-neutral and warm ambient, with cold-dry stimuli being perceived as less cold during

exposure to the warm than to the thermo-neutral ones. The different trends observed between thermal sensation and wetness perceptions amongst conditions might therefore highlight the possibility that other factors than ambient temperature and exercise (e.g. the level of moisture on the skin regions not targeted for stimulation, as well as the whole body perception of wetness) might have influenced the perception of local wetness. Nevertheless, the lack of studies investigating the central effects of factors such as exercise or ambient temperature on complex percepts makes any conclusion on this topic difficult to draw. Most of the studies looking into sensory perception have focused on exercise and/or ambient temperature-induced changes in thermal sensation (Burke and Mekjavic, 1991; Nakamura et al. 2008; Norrsell et al. 1999, Ouzzahra et al. 2012). More studies are therefore needed in order to appraise how e.g. different levels of whole body wetness could affect the perception of local skin wetness.

3.4. Limitations

The absolute values for skin cooling reported in this study should be carefully considered. Indeed, the cooling rates presented should not be indented as the exact

representation of the skin cooling profiles which occurred during the stimulations, but rather, as a close approximation. These values were calculated as the ratio between the ΔT_{sk} from pre- to post-stimulation and the contact time (10 s). Thus, the resulting skin cooling profile was in principle assumed to be linear. However, based on the skin's biological characteristics, it is more likely that the skin cooling had an exponential profile, with a greater drop in temperature during the first seconds of contact, followed by a smaller one towards the end (Jay and Havenith, 2004a; Jay and Havenith, 2004b). Therefore, it is reasonable to hypothesise that the values we calculated represent an underestimation of the skin cooling rates which occurred during the first seconds of stimulation, though a high correlation of these rates with the presented ones can be assumed based on the nature of the cooling curve (Jay and Havenith, 2004a; Jay and Havenith, 2004b).

4. Conclusion

We conclude that thermal inputs from peripheral cutaneous afferents are critical in characterizing the perception of skin wetness. However, the role of these inputs might be modulated by an intra-sensory interaction with the tactile afferents. Taken

together, these findings indicate that human sensory perception is remarkably multimodal. The outcomes of this study have a fundamental as well as an applied significance. On the fundamental side, these could contribute to a better understanding of how the peripheral and central nervous system interact to generate complex somatic perceptions. On the applied side, taking into account the neurophysiology of the perception of skin wetness might help to improve the design of protective clothing and thus thermal comfort in strenuous work conditions (e.g. fire-fighting).

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Author contributions

D. F., B. R., S. H. and G. H. conception and design of research;

D. F. performed experiments and analysed data; D. F., B. R., and G. H. interpreted results of experiments; D.F. prepared figures and drafted manuscript; D. F. and G. H. edited and revised manuscript; D. F., B. R., S. H. and G. H. approved final version of manuscript.

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Figure 1: The thermal probe and pressure control system used in this study. The system consists of an air bladder, inserted into a frame attached to the thermal probe. The air bladder is connected to a manometer (containing water) throughout a silicon tube (A). When no pressure is applied to the system, the water in the manometer sets to its “null” point (B). When pressure is applied, the air bladder deforms, producing a pressure change in the system which displaces the water in the manometer from its set “null” point (C). The point reached by the water in the tube, as a result of the pressure change, was used as an indicator to control the mechanical pressure applied to the skin.

Figure 2: Relative variations in skin temperature drop from baseline (ΔT_{sk}), and corresponding cooling rates, as a result of each cold-dry stimulus applied with low (i.e. grey bars) and high pressure (i.e. black bars). Data were collapsed over the conditions performed (i.e. resting or exercising in thermo-neutral and warm environment) and the skin sites where the stimuli were applied. Differences are reported as statistically ($*p<0.05$) or as not statistically significant (i.e. ns).

Figure 3: Local thermal sensation scores as a result of each cold-dry stimulus applied with low (i.e. grey dots) and high pressure (i.e. black dots). Data were collapsed over the conditions performed (i.e. resting or exercising in thermo-neutral and war environment) and the skin sites where the stimuli were applied. Differences are reported as statistically ($*p<0.05$) or as not statistically significant (i.e. ns).

Figure 4: Local wetness perception scores as a result of each cold-dry stimulus applied with low (i.e. grey dots) and high pressure (i.e. black dots). Data were collapsed over the conditions performed (i.e. resting or exercising in thermo-neutral and war environment) and the skin sites where the stimuli were applied. Differences are reported as statistically ($*p<0.05$) or as not statistically significant (i.e. ns).

Figure 5: Frequency distribution of local wetness perception scores as a result of each cold-dry stimulus applied with low and high pressure. The frequency of times the same cold-dry stimulus was perceived as “dry” (i.e. wetness scores in between -1 and +4, labelled “dry”), or as “wet” (i.e. wetness score between -2, labelled “slightly wet”, and -6, labelled “dripping wet”), is indicated as a fraction (%) of the total responses recorded for each stimulus. Data were collapsed over the conditions performed (i.e. resting or exercising in thermo-neutral and war environment) and the skin sites where the stimuli were applied. Differences are indicated as statistically (* $p < 0.05$) or as not statistically significant (i.e. ns).

Figure 1

Figure 2

Figure 3

ACCEPTED MANUSCRIPT

Figure 4

Figure 5

Highlights

- Thermal afferents are critical in characterizing the perception of skin wetness
- Tactile afferents can modulate the perception of skin wetness
- Exercise seems not to have a central effect on the sensory pathway for skin wetness