Body mapping of cutaneous wetness perception across the human torso during thermo-neutral and warm environmental exposures

Davide Filingeri,1 Damien Fournet,2 Simon Hodder,1 and George Havenith1
1Environmental Ergonomics Research Centre, Loughborough Design School, Loughborough University, Loughborough, United Kingdom; 2Thermal Sciences Laboratory, Oxilane Research, Villeneuve d’Ascq, France

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Sensing skin wetness is linked to inputs arising from cutaneous cold-sensitive afferents. As thermosensitivity to cold varies significantly across the torso, we investigated whether similar regional differences in wetness perception exist. We also investigated the regional differences in thermal pleasantness and whether these sensory patterns are influenced by ambient temperature. Sixteen males (20 ± 2 yr) underwent a quantitative sensory test under thermo-neutral [air temperature (Tair) = 22°C; relative humidity (RH) = 50%] and warm conditions (Tair = 33°C; RH = 50%). Twelve regions of the torso were stimulated with a dry thermal probe (25 cm²) with a temperature of 15°C below local skin temperature (Tsk). Variations in Tsk, thermal, wetness, and pleasantness sensations were recorded. As a result of the same cold-dry stimulus, the skin-cooling response varied significantly by location (P = 0.003). The lateral chest showed the greatest cooling (−5 ± 0.4°C), whereas the lower back showed the smallest (−1.9 ± 0.4°C). Thermal sensations varied significantly by location and independently from regional variations in skin cooling with colder sensations reported on the lateral abdomen and lower back. Similarly, the frequency of perceived skin wetness was significantly greater on the lateral and lower back as opposed to the medial chest. Overall wetness perception was slightly higher under warm conditions. Significantly more unpleasant sensations were recorded when the lateral abdomen and lateral and lower back were stimulated. We conclude that humans present regional differences in skin wetness perception across the torso, with a pattern similar to the regional differences in thermosensitivity to cold. These findings indicate the presence of a heterogeneous distribution of cold-sensitive thermosensitive afferents (20).

As opposed to insects, in which humidity receptors subserving hygrosensation have been identified and widely described (57), humans seem not to be provided with specific receptors for the sensation of wetness (13). Thus we seem to “learn” to perceive the wetness experienced when the skin is in contact with a wet surface or when sweat is produced (6) through a complex multisensory integration (17) of thermal (i.e., heat transfer) and tactile (i.e., mechanical pressure and skin friction) inputs generated by the interaction between skin, moisture, and (if donned) clothing (22). This hypothesis has been supported by our previous findings. We have recently demonstrated 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 (19, 21), a temperature course that is similar to the one suggested to occur when the skin is physically wet (16). This could be due to the fact that we seem to interpret the coldness experienced during the evaporation of moisture from the skin as a signal of the presence of moisture (and thus wetness) on the skin’ surface. In line with this hypothesis, we have also observed that during the static contact with a warm-wet surface (with a temperature warmer than the skin), no local skin wetness was perceived, as no skin cooling and thus no cold sensations occurred (20). Finally, this concept has been further confirmed in our most
recent study, in which we observed that, when participants’ cold sensitivity was significantly reduced through a compression ischemia protocol, skin wetness perception in response to a wet stimulus was also significantly reduced both on hairy and glabrous skin sites (18). All in all, these recent findings have highlighted the critical role of thermosensitivity to cold in the ability to perceive skin wetness (18–21).

Appraising the importance of cold afferents in the ability to sense cutaneous wetness has led us to hypothesize that regional differences in wetness perception might exist across the body and might depend on the regional differences in thermosensitivity to cold. The distribution of cutaneous sensitivity to cold has been indeed repeatedly shown to vary significantly across different regions of the body (7, 31, 39), as well as within the same body region (44). For example, the torso is suggested to be among the most sensitive regions to cold (7, 31, 39). In this regard, the recent work of Ouzzahra et al. (44) has provided evidence for the presence of an uneven distribution of cold sensitivity across the front and back torso. If we accept the hypothesis that sensing skin wetness is primarily driven by the level of coldness experienced, it is reasonable to hypothesize that wetness perception varies significantly across the torso, with a pattern that could be similar to the one of thermosensitivity to cold. To our knowledge, only few studies have investigated whether humans present regional differences in cutaneous wetness perception (2, 22, 34).

In a study in which thermal comfort sensitivity was investigated in relation to locally manipulated skin wetness (as resulting from sweat production), Fukazawa and Havenith (22) found that the torso seems to have a lower sensitivity to wetness than the limbs, whereas, in a nonmanipulated condition (natural wetness distribution across the torso), Gerrrett et al. (25) showed that the torso seemed to dominate wetness perception. Similarly, Lee et al. (34) showed that, when asked, individuals reported the torso (i.e., chest and back) to be the region more often perceived as wet during rest and moderate exercise in 25°C and 32°C Tair and 50% RH. In line with Lee et al. (34), Ackerley et al. (2) have recently shown that, when wet stimuli with different moisture contents (range: 20–160 μl over a 0.0024-m² surface) were applied to different body regions, individuals were able to differentiate between moisture levels, with a tendency of the back as being among the most sensitive region to wetness. The outcomes of these studies have provided initial insights about the regions on which skin wetness might be perceived to a larger extent (e.g., the torso). However, by only measuring the physical wetness (whether due to sweat production or to contact with a wet surface), these studies have failed to provide a link between the thermal changes occurring locally at the skin’s surface when this is wet [variation in local Tsk (ΔTsk)] and how these are perceived in terms of thermal sensations and perception of skin wetness.

The aim of the present study was to investigate the regional distribution of skin wetness perception across the torso, in relation to the distribution of thermosensitivity to cold. Also, as local thermal sensations resulting from the same thermal stimulation have been shown to change according to the body’s thermal state (e.g., greater cold sensitivity can be observed during heat exposure) (4, 8, 21), we investigated whether the regional distribution of skin wetness perception is influenced by the environmental conditions (thermo-neutral vs. warm). Finally, as it has been previously suggested that the hedonic attribute (i.e., pleasure) of a thermal stimulus is dependent on the perception of the actual thermal state of the body (e.g., if the direction of the thermal stimulus is oriented toward a shift in the thermal state of the body from its natural homeostasis, then this will result in thermally unpleasant sensations) (4, 9), we investigated whether regional differences in thermal pleasantness in response to local skin cooling exist across the torso.

We tested the hypothesis that, during the short contact with the same cold-dry stimulus (i.e., 15°C lower than local Tsk), which we have previously shown to induce an illusion of skin wetness (21), local Tsk, thermal, and wetness sensations will vary significantly by location of stimulation. Regions with a high thermosensitivity to cold were expected to present a higher perception of skin wetness. Also, we hypothesized that, as local thermal sensations resulting from the same thermal stimulation have been shown to change according to the body’s thermal state (4, 8), thermal and wetness perceptions will be higher during a warm as opposed to a thermo-neutral environmental exposure. This was also hypothesized to impact the hedonic component of thermal stimulation (i.e., greater displeasure will be recorded during thermo-neutral as opposed to warm exposure), with regional differences in thermal pleasure/displeasure expected to follow a pattern similar to the one for thermosensitivity to cold.

MATERIALS AND METHODS

Participants. Sixteen healthy Caucasian male students (age 20 ± 2 yr; height 1.78 ± 0.10 m; body mass 77.4 ± 10 kg; body composition by skinfold analysis 8.0 ± 3% body fat) with no history of sensory-related disorders volunteered to participate in this study. To account for the interindividual variability in the hairiness of the torso, participants’ hair growth was visually graded using a modified Garn (25) scoring system (for an extensive review see Yildiz et al., Ref. 58). Photos of the front and back torso of each participant were taken. A score of 0–4 was assigned to chest, abdomen, and upper and lower back on the basis of the visual density of terminal hairs. A score of 0 represented the absence of terminal hairs; a score of 1 represented minimally evident hair growth; and a score of 4 represented extensive hair growth (58). Thirteen out of sixteen participants presented minimal hairs on the chest (score = 0.2 ± 0.1) and abdomen (score = 0.3 ± 0.1) and the absence of terminal hairs on the upper and lower back. Three out of sixteen participants presented a higher level of hairiness on the chest (score = 3 ± 0.6) and abdomen (score = 2.3 ± 0.3) and the absence of hairs on the upper and lower back.

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.

Experimental design. All participants underwent the same quantitative sensory test under thermo-neutral (Tair = 22°C; RH = 50%) and warm environmental conditions (Tair = 33°C; RH = 50%). The quantitative sensory test was based on the application of a cold-dry stimulus on 12 different skin sites distributed across the front and back torso of each participant. The exact anatomical locations of the areas targeted for stimulation are described in Fig. 1 and are in line with the work of Ouzzahra et al. (44). All tested sites were medial or on the left side of the body, assuming symmetry (14). During the contact with the stimulus, participants reported their local thermal, wetness, and pleasantness sensations on Likert scales. Local Tsk at the contact site was measured before and immediately after the contact with the stimulus using a single spot infrared thermometer (FLUKE 566, Fluke USA) with a temperature range of −40°C to 800°C and an accuracy of
±1°C. To maximize the accuracy of the temperature readings, during each test the infrared thermometer was calibrated against a matt black plate whose temperature was monitored with a thermistor (Grant Instruments). This method has been previously used by Filingeri et al. (21) and shown to be effective in allowing recording of poststimulation \( T_{sk} \) to be made consistently close to the when subjective sensations were rated. The cold-dry stimulus was delivered by a square thermal probe (Physitemp Instruments) with a contact surface of 0.0025 m². The relative temperature of the stimulus was 15°C lower than the local \( T_{sk} \), which was measured with the infrared thermometer. We chose a relative temperature of \(-15°C\), as we have previously shown this to evoke the highest levels of perceived wetness during a 10-s contact with the upper and lower back of resting and exercising individuals (21).

A single-blind psychophysical approach was used for this study. Participants were informed only about the body region objected to the stimulation, and no information was provided on the type and magnitude of the stimulation to limit any expectation effects. To assure that the participants could not see the stimulus applied on their torso, the following setup was designed. When the front torso was stimulated, participants were asked to lie on a bench above the participants’ neck. The screen was adjusted until each participant confirmed that they could not see either their front torso or the investigator. When the back torso was stimulated, participants were asked to lie on their back, with their arms alongside the body, and a rectangular-shaped textile screen (length: 0.8 m; height: 0.7 m) was placed above the participants’ neck. The screen was adjusted until each participant confirmed that they could not see either their front torso or the investigator. When the back torso was stimulated, participants were asked to lie on their back, with their arms alongside the body, and one participant was standing on the right hand side. Each participant confirmed that they could not see either their back torso or the investigator. The 12 skin sites were stimulated on a balanced order to prevent any order effect. The data collection took place in December (mean monthly temperature: 5.1°C; min-max temperature range: 2.0°C to 8.2°C).

**Experimental protocol.** Participants arrived at the laboratory 30 min before the time scheduled for the test to allow preparation procedures. First, semi-nude body mass, height, and skinfolds thickness (seven sites) were measured and recorded. For body composition calculations, American College of Sports Medicine guidelines for exercise testing and prescription were used (27). Body density was calculated using the following seven sites (chest, midaxillary, triceps, subscapular, abdomen, suprailiac, and thigh) and the following equation: body density = 1.112 − 0.00043499(sum of 7 skinfolds) + 0.00000055(sum of 7 skinfolds)² − 0.00028826(age). Participants then changed into shorts, socks, and running shoes. Five iButtons (Maxim) were taped to five skin sites on the right side of the body (i.e., cheek, abdomen, upper arm, lower back, and back lower thigh) to record local \( \Delta T \). 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 and Ring (29) to give an estimate of mean \( \Delta T \) for the entire body. The 12 skin sites targeted for stimulation were marked with a washable marker to assure consistency in the location of stimulation.

After preparation, participants entered a first environmental chamber set for the thermo-neutral exposure (22°C \( T_{air} \), 50% RH). Participants sat on a chair and waited 10 min to allow acclimation to the environmental conditions. During this period, participants were familiarized with the rating scales designed to record individual thermal, wetness, and pleasantness sensations: 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), and an 11-point pleasantness scale (–6 very unpleasant, –4 unpleasant, –2 slightly unpleasant, 0 neutral, +2 slightly pleasant, +4 pleasant) (21, 43). No descriptors were applied to intermediate scores (i.e., –5, –3, –1, 1, and +3). We defined the value –2 (labeled: “slightly wet”) of the wetness scale as our set threshold to identify a clearly perceived local skin wetness.

After the acclimation period and according to the order of stimulation, participants were asked to lie either on their front or back, and the quantitative sensory test was initiated. Participants were first asked to rate their thermal and wetness sensations only, just before the application of the stimulus (i.e., baseline whole body sensation), while the local \( \Delta T \) of the skin site targeted for stimulation was measured with the infrared thermometer. Then the thermal probe was set to the required relative temperature (i.e., \(-15°C\) below the recorded local \( \Delta T \)) and applied by hand to the skin site. To avoid an effect of surprise on the transient sensations, a verbal warning was given before 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 thermal, wetness, and also pleasantness sensations, using whatever number in the scales seemed appropriate (integers only). Immediately after this, the probe was removed and \( \Delta T \) of the stimulated area was recorded with the infrared thermometer. The same protocol was repeated for each of the 12 skin sites, allowing at least 1 min in between them. Each participant had only one presentation of each stimulus for each skin site. The quantitative sensory test lasted for 15 min.

After completion of the test, 10 min were allowed before participants moved from the first to the second environmental chamber set for the warm exposure (33°C \( T_{air} \), 50% RH). Once the participants
were in the second chamber, 10 min were allowed for acclimation before the same quantitative sensory test, as explained above, was performed.

**Statistical analysis.** In the present study, the independent variables were the skin site stimulated and the environmental condition. The dependent variables were mean, local $T_{sk}$, $\Delta T_{sk}$ (i.e., variation from pre- to poststimulation) and thermal, wetness, and pleasantness sensation. 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 for the thermo-neutral and warm exposure were compared using a paired $t$-test. Local $\Delta T_{sk}$ data were analyzed by a two-way repeated-measures ANOVA, with skin site stimulated (12 levels) and environmental condition (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 scores) data are reported as means $\pm$ SE. Furthermore, median and interquartile ranges [median; percentile] are reported for nonparametric data.

**RESULTS**

**Mean and local $T_{sk}$.** Mean $T_{sk}$ was calculated for each exposure and found to be normally distributed ($P > 0.05$). Mean $T_{sk}$ values for thermo-neutral and warm exposures were respectively $32.4 \pm 0.1^\circ C$ and $34.8 \pm 0.1^\circ C$. These values were found to be significantly different (mean difference $= 2.4^\circ C$; 95% CI: 2.2, 2.5°C; $t =$ 36.8; two-tailed $P < 0.001$). This result confirms the effectiveness of the environmental conditions we designed in inducing a significant change in the skin’s thermal state.

Baseline local $T_{sk}$ values (prestimulation) varied in a range between $31.8 \pm 0.1^\circ C$ (i.e., lateral chest) and $33.4 \pm 0.2^\circ C$ (i.e., medial upper back) for the thermo-neutral exposure and between $34.9 \pm 0.2^\circ C$ (i.e., lateral chest) and $36.1 \pm 0.1^\circ C$ (i.e., medial upper back) for the warm exposure. Local $\Delta T_{sk}$ (as a result of the relative cold-dry stimulus applied to each skin site during the thermo-neutral and warm exposures) was calculated and found to be normally distributed ($P > 0.05$). The data analysis indicated that only the skin site stimulated had a significant main effect on the local $\Delta T_{sk}$ [F = 4.4(4, 50.6), $P =$ 0.003]. No significant effect of the environmental condition [F = 2.2(1, 11), $P =$ 0.17] or significant interaction between the skin site stimulated and the environmental condition was found [F = 0.4(11, 121), $P =$ 0.4]. The regional distribution of $\Delta T_{sk}$ is shown in Fig. 2A. Post hoc analyses indicated that, depending on skin site, local $\Delta T_{sk}$ varied significantly in a range of $-1.9 \pm 0.4^\circ C$ (i.e., medial lower back) to $-5.0 \pm 0.4^\circ C$ (i.e., lateral chest), corresponding to a range of skin-cooling rates of $0.19 \pm 0.04$ to $0.5 \pm 0.04^\circ C/s$. These values were calculated as the ratio between the $\Delta T_{sk}$ from post- to prestimulation and the contact time (i.e., 10 s). The significance levels are presented separately for sites of the front and back torso (Table 1).

Overall, these outcomes indicated that, as a result of the same relative cold-dry stimulus, the skin-cooling response varied significantly by location across the torso, with a pattern that did not change between the thermo-neutral and warm environmental exposure.

**Thermal sensation.** Baseline thermal sensation scores (prestimulation) varied in a range of $0.1 \pm 0.1$ [median = 0; 0.0, 1.0] to $0.6 \pm 0.2$ [median = 1; 1.0, 1.0] for the thermo-neutral exposure and of $1.4 \pm 0.3$ [median = 1; 0.2, 2.7] to $1.7 \pm 0.2$ [median = 2; 1.0, 2.0] for the warm exposure. Expressed in terms of semantic labels, these were in the range of neutral for the thermo-neutral exposure and in a range going from neutral to slightly warm for the warm exposure.

In response to the stimuli, thermal sensation scores were overall less cold during the warm ($-3.5 \pm 0.1$ [median = -4; -4.0, -3.0]) than during the thermo-neutral exposure ($-3.7 \pm 0.1$ [median = -4; -5.0, -3.0]) ($Z = -3.5$, $P = 0.001$, $r = -0.25$). Expressed in terms of semantic labels, these were in a range going from slightly cool to cold for the warm exposure and in a range going from slightly cool to very cold for the thermo-neutral exposure. Thermal sensations differed significantly according to the skin site stimulated [$\chi^2(11, N = 32) = 143.2, P < 0.001$], with scores varying in a range of $-2.3 \pm 0.2$ [median = -2; -3.0, -1.2] (i.e., medial chest) to $-4.4 \pm 0.2$ [median = -4; -5.0, -4.0] (i.e., lateral lower back)
between sites. Expressed in terms of semantic labels, these were in a range going from slightly cool to very cold. Mean thermal sensations, averaged over both environmental conditions, are shown in Fig. 2B. The significance levels are presented separately for sites of the front and back torso (Table 1).

Overall, these outcomes indicated that the same relative cold-dry stimulus evoked thermal sensations, which were significantly colder when the stimulus was applied on specific regions (such as the lateral abdomen and the lateral and lower back) as opposed to other regions (such as the lateral and medial chest), in which the same stimulus evoked less cold thermal sensations. Also, the same relative cold-dry stimulus was overall perceived as slightly less cold during the warm than during the thermo-neutral exposure.

Wetness perception. Baseline wetness perception scores (prestimulation) varied in a range of 0.6 ± 0.3 [median = 0; 0.0, 2.0] to 1 ± 0.3 [median = 0; 0.0, 2.0] for the thermo-neutral exposure and 0.6 ± 0.4 [median = 0; 0.0, 1.7] to 0.8 ± 0.4 [median = 1; 1.0, 2.0] for the warm exposure. Expressed in terms of semantic labels, these were in a range going from neutral to slightly dry.

In response to the stimuli, local wetness perception scores were overall slightly wetter during the warm (−1.7 ± 0.1) [median = −2; −2.0, −1.0] than during the thermo-neutral
Table 1. Significance levels of the multiple comparisons for the 12 skin sites are reported for skin cooling, thermal sensation, wetness perception, and pleasantness sensation

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\(\Delta T_a\), change in skin temperature; TS, thermal sensation; WP, wetness perception; PS, pleasantness sensation. *P < 0.05; \(\dagger P < 0.01; \ddagger P < 0.001.\)
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The present study investigated the regional distribution of cutaneous wetness perception across the torso, in relation to the distribution of thermosensitivity to cold. Furthermore, we investigated whether these regional sensory patterns are influenced by different ambient temperatures as well as whether regional differences in thermal pleasantness in response to local skin cooling exist. During a thermo-neutral and warm environmental exposure, by exposing 12 skin sites of the torso to the static contact with the same relative cold-dry stimulus, we demonstrated the following: 1) cutaneous wetness perception varies significantly across the torso (see Fig. 2C), with regions showing high thermosensitivity to cold (e.g., the lower and lateral abdomen and back, see Fig. 2B) presenting wetness perception in larger magnitude and frequency (compare Fig. 2, B vs. C); 2) cutaneous wetness perception is slightly higher under warm than under thermo-neutral environmental conditions, despite that thermosensitivity to cold appears to be slightly lower; 3) regional variations in thermal pleasure/displeasure exist across the torso and show a pattern similar to the regional distribution in thermosensitivity to cold (i.e., greater coldness induced greater displeasure) (compare Fig. 2, B vs. D).

In summary, our results indicate that the existence of regional differences in cutaneous thermosensitivity to cold translates into significant regional differences in cutaneous wetness perception across the human torso. Interestingly, these regional sensory patterns were observed to be independent from the magnitude of local skin cooling. In other words, the regions in which the stimulus resulted in greater skin cooling (i.e., lateral chest) were not necessarily the ones in which the stimulus was perceived as colder, wetter, and more unpleasant (compare Fig. 2, A vs. B, C vs. D). To our knowledge, the present study is the first to take into account the regional variation in skin temperature occurring during contact cooling and to link this to the regional distribution of thermosensitivity to cold, skin wetness, and thermal pleasure/displeasure across the human torso. The
The outcomes of this study are in line with our previous findings, in which we have demonstrated that the contact with a cold-dry stimulus producing skin-cooling rates in a range of 0.14 to 0.41°C/s can evoke an illusion of skin wetness (19, 21). In the present study, the relative temperature stimulus we used resulted in skin-cooling rates ranging from 0.19 to 0.5°C/s. Although generated by a dry stimulus, these fluctuations in $T_{sk}$ evoked thermal sensations, which were associated to the perception of skin wetness, particularly on the back torso. Hence, this finding supports the hypothesis that the central integration of coldness, as primarily subserved by peripheral myelinated $\alpha$-nerve fibers, is critically involved in the neural processes underpinning humans’ ability to sense wetness (19, 21). This proposed theory finds support in a neurophysiological model of skin wetness that we have recently developed (18), which sees the activity of cold afferents being both behaviorally and physiologically necessary to give rise to the perception of wetness. As the skin seems not to be provided with hygroceptors (13), it is indeed hypothesized that the somatosensory cortex could be involved in generating a neural representation of a typical wet stimulus. This could be based on the multimodal transformation (i.e., information from one sensory modality can be transformed into a map or reference frame defined by another submodality) of the somatosensory inputs generated when the skin is physically wet (28). As the sensory inputs associated with the physical experience of cutaneous wetness are often generated by heat transfer in the form of evaporative cooling (2), the typical neural representation of a wet stimulus might therefore rely on experiencing a certain degree of coldness. This neural representation could be transformed into a firing rate code and then associated to the perception of wetness (46). Hence, when the memorized stimulus (i.e., coldness), as coded by the specific afferents (i.e., $\alpha$-nerve fibers) is presented, wetness will be sensed.

The role of thermosensitivity to cold in the ability to sense skin wetness. With regard to the role of thermosensitivity to cold in characterizing the ability to sense cutaneous wetness, the outcomes of this study are in line with our previous novelty of these findings is in providing the first detailed body maps of thermal, wetness, and pleasantness sensation across the human torso.

Physiological significance of regional differences in cutaneous skin wetness perception. Within the experimental conditions of this study, the lower back, lateral mid-back, and medial upper back, as well as the lateral abdomen, presented wetness perception in larger magnitude and frequency than the lateral and medial chest and medial upper abdomen (see Fig. 2C). These outcomes are in line with the work of Lee et al. (34), who have shown the upper and lower back to be most frequently perceived as wet during conditions of sweat-induced physical wetness. Although not statistically significant, a similar trend was observed by Ackerley et al. (2), who reported the back to present higher wetness perception than other body regions. However, in the mentioned works, no data are reported on any physiological change (e.g., regional differences in $\Delta T_{sk}$) that could have triggered the sensory inputs used by

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The outcomes of this study, in which a cold-dry stimulus evoked an illusion of skin wetness in blindfolded individuals, are in agreement with this sensory model for wetness. However, although the relative temperature stimulus used in this study resulted in skin-cooling rates that were within the range suggested to evoke wetness perceptions for all the regions investigated (i.e., 0.19 to 0.5°C/s) (16, 19, 21), significant regional variations in wetness perception were observed across the torso. Hence, this indicates that other factors than the degree of local skin cooling (e.g., regional differences in thermal sensitivity and habituation components) might play a significant role in characterizing the cutaneous distribution of wetness perception, at least across the human torso.
the participants to discriminate the level of wetness experienced regionally. In the present study, this issue was overcome by quantifying the local $\Delta T_{sk}$, recording thermal sensations, and eventually comparing these with the regional distribution of wetness perception. Thus, for the first time, we provide evidence in support of the physiological and behavioral significance of the regional differences in cutaneous wetness perception across the torso.

In the current study, the local thermal sensations in response to the cold stimulus were observed to be independent from the local $\Delta T_{sk}$. A comparison of the body maps of $\Delta T_{sk}$ (Fig. 2A) and thermal sensation (Fig. 2B) shows that the cold-dry stimulus was perceived as colder when applied to the lower back than to the lateral chest despite the fact that, when stimulated, the lower back presented a significantly smaller drop in $T_{sk}$ than the lateral chest. Interestingly, a similar trend was observed for the perception of wetness (see Fig. 2C). Hence, it could be proposed that, as well as for the thermosensitivity to cold, the regional differences in wetness perception could depend on an uneven weighting and integration of temperature-different information, which seems independent from the regional variations in $T_{sk}$ and, potentially, from the density of thermoreceptors (5, 7, 39). As shown in Fig. 2, $B$ and $C$, the regions with high wetness frequency presented a high sensitivity to cold, with the association between the level of experienced coldness and the frequency of perceived wetness being linear (i.e., greater coldness induces more frequent wetness) and statistically significant. Thus it could be suggested that the sensitivity to coldness (i.e., a neurophysiological variable) rather than local $\Delta T_{sk}$ (i.e., a physical variable) might be more critical in characterizing the regional distribution of cutaneous wetness perception. From a neurophysiological point of view, this is in line with what has previously been proposed on the critical role of thermosensitivity to cold in sensing cutaneous wetness (2, 21). The higher sensitivity to cold of some regions of the torso could indeed result in these regions being more sensitive to perceive skin wetness. The possibility that colder sensations are more likely to translate in wetter perceptions is also aligned to the work of Ackerley et al. (2). In their work, the authors have shown that individuals readily discriminated between very small amount of moisture on the skin (in the range of 40 $\mu l$ over a surface of 0.0024 m$^2$). Although in the mentioned study no recordings of local $\Delta T_{sk}$ and thermal sensations were performed, in line with the authors, we believe that participants distinguished the greater from the smaller levels of moisture due to the resulting greater evaporative cooling, which induced colder thermal sensations.

The fact that humans seem to associate feeling colder with feeling wetter is not entirely surprising and could be due to learning factors. For example, the contact with a wet surface or the exposure to a cold-humid environment often result in colder sensations than the ones resulting from the contact with a dry surface or the exposure to a cold-dry environment. In this regard, the skin’s contact with a wet fabric has been suggested to be perceived as wet, as the presence of moisture leads to higher heat losses from the skin (and thus colder sensations), due to a higher thermal conductivity of a wet as opposed to a dry fabric (41). As for the same physical process (i.e., higher rate of heat losses), a cold-humid environment is perceived to be colder than a cold-dry one (45). Habituation factors could also explain the observed regional pattern in wetness perception. As we are not provided with hygroseceptors (13), if we assume that, based on the concept of perceptual learning (46), we learn to perceive cutaneous wetness, it would be reasonable to hypothesize that the body regions more sensitive to skin wetness are the ones in which we are more used to experiencing high levels of physical wetness, e.g., attributable to sweating. The outcomes of this study could support this behavioral hypothesis. In the present study, the back torso, and particularly the lower back, a region that has been repeatedly shown to present some of the highest levels of sweat production (52, 53), was indeed observed to be the most sensitive region to wetness across the torso.

**Role of the thermal state of the body and the affective component of thermal stimulation.** The cutaneous wetness perception was observed to be slightly higher under warm than under thermo-neutral environmental conditions. As the thermosensitivity to cold was on the contrary found to be slightly lower during the warm environmental condition, the increase in overall wetness perception in the warm environment is more likely to be related to an expectation effect (i.e., participants might have expected to sweat under the warm exposure) than to a central sensory modulation of this perception. It could be argued that a higher level of whole body wetness, which might have influenced the way the cold-dry stimulus was perceived locally on the skin (22), occurred during the warm exposure. However, as the baseline wetness perceptions recorded pre-stimulation did not differ between the thermo-neutral and the warm environmental exposures, and because of the resting condition of the participants, it is unlikely that a higher level of whole body skin wetness occurred or was perceived by the participants. Nevertheless, the possibility to measure the skin’s local hydration status should be considered in future studies to investigate whether a swelling state of the skin (attributable to sweat production) can affect the regional perception of skin wetness (26).

With regards to the affective component of thermal stimulation, it deserves mention that the local cold-dry stimulation of the torso was overall perceived as being unpleasant and that the level of displeasure experienced varied significantly by location of stimulation. Interestingly, the topographical distribution of the displeasure resulting from local thermal stimulation corresponded to the regional distribution of cutaneous thermal and wetness perception (compare Fig. 2, $D$ vs. $B$ and $C$). In this respect, it was observed that regions with a higher thermosensitivity to cold and a higher frequency of wetness (e.g., the lower back, lateral mid-back, and medial upper back, as well as the lateral abdomen) were the ones in which the application of the stimulus resulted as the most unpleasant (see Fig. 3, $B$ and $C$). These outcomes confirm the physiological bases of pleasure (9, 10), particularly in the context of thermal sensation and comfort (8).

It has been previously suggested that the hedonic attribute of a thermal stimulus is dependent on the perception of the actual thermal state of the body; if the direction of the thermal stimulus is oriented toward a shift in the thermal state of the body from its natural homeostasis, then this will result in thermally unpleasant sensations; on the contrary, if the direction of thermal stimulus is toward a reestablishment of the thermal state to its set point, then this will result in thermally pleasant sensations (4). This concept, known as alliesthesia (9),
underpins the reason why a cold stimulus applied on normothermic individuals might be perceived as more unpleasant than if the same was applied on hyperthermic individuals. Because, during our experimental conditions, participants were not expected to become hyperthermic (attributable to resting conditions and short exposure duration), it is therefore clear why the application of the cold stimulus was overall perceived as unpleasant. However, the novelty of this study is to provide a detailed topographical distribution of the regions of the torso in which the exposure to cold stimuli might have a greater influence on the overall thermal displeasure and discomfort. The fact that the back as well as the lateral abdomen presented a higher sensitivity to thermal displeasure furthers our understanding of the role of the thermal comfort of the torso in the whole body thermal comfort. Nakamura et al. (39, 40) have repeatedly shown that humans prefer a warm trunk and that abdominal cooling is often perceived as more unpleasant than the cooling of other regions. This is in line with the findings of the present study, in which, e.g., we observed the lateral abdomen to be among the regions in which the application of the cold-dry stimulus was perceived as the most uncomfortable. As local cooling of the abdomen has been shown to induce vasoconstriction of the corresponding gastrointestinal tract, which in turn could affect the function of the organ (33), it is therefore reasonable to hypothesize that the higher sensitivity to thermal displeasure of this region might represent a form of thermal protection aiming to maintain homeostasis (40).

It has to be acknowledged that, with regard to linking the changes in the internal state of the body with the affective component of local thermal stimulation of the torso, the absence of a direct measurement of core temperature represents a limitation of the current study. It could be indeed speculated that, despite the fact that an increase in core temperature is unlikely to have occurred within the experimental conditions of this study, a potential (although slight) fall in this value could have occurred during the thermo-neutral exposure (attributable to the resting and semi-nude conditions of the participants). Therefore, the contribution of even small changes in core temperature to the overall hedonic component of thermal stimulation cannot be ruled out conclusively. Nevertheless, the outcomes of this study further our understanding of the role of cutaneous thermal afferents (as opposed to deep body) in influencing the hedonic attribute of tactile stimulations. Recent evidence on the neurophysiology of affective touch have indeed indicated that, apart from the role of core temperature, the presence of a particular class of cutaneous nerve fibers, i.e., C-Tactile afferents, which are specifically tuned to affective as opposed to discriminative touch, could also play a significant role in influencing the affective component of local thermal stimulation (1). In a recent study in which stroking-like stimuli at three different temperatures [i.e., warm, neutral (same as skin temperature) and cold] were applied on participants’ skin, Ackerley et al. (1) have shown that stimuli with temperatures that deviated from neutrality (i.e., warm and cold) were perceived as less pleasant than thermo-neutral stimuli. The authors concluded that the activity and role of C-Tactile fibers in contributing to the hedonic component of tactile stimuli seems therefore to be specifically tuned to the neutral temperature of a skin-stroking caress (1). These observations seem to be supporting the results of the present study, in which we have demonstrated that the further the stimuli deviated from thermo-neutrality (i.e., colder sensations), then the greater the displeasure experienced by the participants (see Fig. 3C). Therefore, our findings indicate that, despite the importance of monitoring core temperature, taking into account the potential contributions of cutaneous C-Tactile afferents should also be considered in future investigations, as these could play a role in the hedonic component of local thermal stimulation.

In conclusion, the present study found that cutaneous wetness perception varies significantly across the human torso. We found that the existence of regional differences in cutaneous thermosensitivity to cold translates into significant regional differences in cutaneous wetness perception; regions with a high thermosensitivity to cold (e.g., the lower and lateral abdomen and back) present skin wetness perceptions in greater magnitude and frequency. Also, it was found that the regional distribution of cutaneous thermal and wetness perception was matched by regional differences in the level of displeasure resulting from local thermal stimulation; regions with a higher thermal and wetness perception (e.g., the lower and lateral abdomen and back) present higher sensitivity to thermal displeasure. The outcomes of this study have a fundamental, clinical, and applied significance. From a fundamental point of view, these indicate that cutaneous thermal, wetness, and pleasantness sensations do not depend solely on regional variations in Tₘₐₜ but also on an uneven weighting and integration of peripheral thermoafferent information, which could be influenced by behavioral and habituation factors. From a clinical point of view, because of a recent interest in mapping bodily sensations such as pain (35), the body maps of torso thermal, wetness, and pleasantness sensation developed in this study could be used as a frame of reference for normal and altered somatosensory function in the context of multiple sclerosis or polyneuropathies, diseases that are usually accompanied by alteration of normal somatosensory function (30, 42, 47, 56). Finally, from an applied point of view, these body maps could be useful in improving the design of protective clothing to optimize thermal protection and maximize thermal comfort under extreme environmental conditions (e.g., cold air/water exposures).

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DISCLOSURES
Damien Fournet, a member of the sponsoring industry (Oxylane Research), contributed to the conception and design of the experiment and contributed to editing and revising the manuscript.

AUTHOR CONTRIBUTIONS
Author contributions: D. Filingeri, D. Fournet, S.H., and G.H. conception and design of research; D. Filingeri performed experiments; D. Filingeri analyzed data; D. Filingeri and G.H. interpreted results of experiments; D. Filingeri prepared figures; D. Filingeri drafted manuscript; D. Filingeri, D. Fournet, S.H., and G.H. edited and revised manuscript; D. Filingeri, D. Fournet, S.H., and G.H. approved final version of manuscript.

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