

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

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26 **ABSTRACT**

27 Sensing skin wetness is linked to inputs arising from cutaneous cold-sensitive afferents. As
28 thermosensitivity to cold varies significantly across the torso, we investigated whether similar
29 regional differences in wetness perception exist. Also, we investigated the regional
30 differences in thermal pleasantness and whether these sensory patterns are influenced by
31 ambient temperature. Sixteen males (20 ± 2 yr) underwent a quantitative sensory test under
32 thermo-neutral ($T_{\text{air}}=22^{\circ}\text{C}$; RH=50p.100) and warm conditions ($T_{\text{air}}=33^{\circ}\text{C}$; RH=50p.100).
33 Twelve regions of the torso were stimulated with a dry thermal probe (25cm^2) with a
34 temperature of 15°C below local skin temperature (T_{sk}). Variations in T_{sk} , thermal, wetness
35 and pleasantness sensations were recorded. As a result of the same cold-dry stimulus, the skin
36 cooling response varied significantly by location ($p=0.003$). The lateral chest showed the
37 greatest cooling ($-5 \pm 0.4^{\circ}\text{C}$) while the lower back the smallest ($-1.9 \pm 0.4^{\circ}\text{C}$). Thermal
38 sensations varied significantly by location and independently from regional variations in skin
39 cooling with colder sensations reported on the lateral abdomen and lower back. Similarly, the
40 frequency of perceived skin wetness was significantly greater on the lateral and lower back as
41 opposed to the medial chest. Overall wetness perception was slightly higher under warm
42 conditions. Significantly more unpleasant sensations were recorded when the lateral abdomen
43 and lateral and lower back were stimulated. We conclude that humans present regional
44 differences in skin wetness perception across the torso, with a pattern similar to the regional
45 differences in thermosensitivity to cold. These findings indicate the presence of a
46 heterogeneous distribution of cold-sensitive thermo-afferent information.

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48 **KEYWORDS:** skin wetness, temperature, body mapping, thermoreceptors, pleasure

49 INTRODUCTION

50 Thermosensitivity (*i.e.* the ability to perceive thermal changes in the surrounding
51 environment) represents an important drive of thermoregulatory responses in humans and in
52 other mammalian and non-mammalian species (23, 54). In humans, cutaneous
53 thermosensitivity is peripherally sub-served by cold-sensitive, myelinated A δ -nerve fibers
54 (conduction velocities ranging from 5-30 m s⁻¹) and by cold- and warm-sensitive,
55 unmyelinated C-nerve fibers (conduction velocities ranging from 0.2-2 m s⁻¹) (11, 48) and
56 centrally integrated by the primary and secondary somatosensory cortices as well as the
57 insular cortex (a cortical region involved in cold and warm temperatures sensation, as well as
58 pain and touch) (15) through the spino-thalamic tract and the the dorsal-column medial
59 lemniscal pathway (36). Fluctuations in skin temperature (T_{sk}) due to environmental stimuli
60 [e.g. changes in ambient temperature (T_{air}) and humidity (RH)] and the related thermal
61 sensations have been shown to trigger autonomic (e.g. vasomotor tone and
62 sweating/shivering response) (32, 51) and behavioral responses (e.g. adding or removing
63 clothing) (50). These responses aim to maintain thermal homeostasis and comfort (8, 49).
64 Despite the critical role of thermosensitivity, sensing temperature is not the only factor
65 amongst the cutaneous sensory afferent to contribute to thermoregulatory responses in
66 humans. Sensing cutaneous wetness is also critical both for behavioral and autonomic
67 responses. Perceiving changes in both ambient humidity and skin wetness have been shown
68 to impact thermal comfort (22) and thus the thermoregulatory behavior (49), both in healthy
69 and clinical populations (e.g. individuals suffering from rheumatic pain) (55). From an
70 autonomic perspective, the degree of skin wetness influences sweat gland function through a
71 progressive suppression of the sweat output (*i.e.* hidromeiosis) in the presence of wetted skin
72 (38). This results in a reduced ability to lose heat to the environment via evaporative cooling,
73 potentially affecting the thermal balance of the body (12). However, although the ability to

74 sense skin wetness plays an important role in several behavioral and thermophysiological
75 functions, little it is known on how skin wetness is sensed in humans (37).

76 As opposed to insects, in which humidity receptors sub-serving hygrosensation have been
77 identified and widely described (57), humans seem not to be provided with specific receptors
78 for the sensation of wetness (13). Thus, we seem to “learn” to perceive the wetness
79 experienced when the skin is in contact with a wet surface or when sweat is produced (6)
80 through a complex multisensory integration (17) of thermal (*i.e.* heat transfer) and tactile (*i.e.*
81 mechanical pressure and skin friction) inputs generated by the interaction between skin,
82 moisture and (if donned) clothing (22). This hypothesis has been supported by our previous
83 findings. We have recently demonstrated that an illusion of local skin wetness can be evoked
84 during the skin’s contact with a cold-dry surface producing skin cooling rates in a range of
85 0.14 to $0.41\text{ }^{\circ}\text{C}\cdot\text{s}^{-1}$ (19, 21), a temperature course which is similar to the one suggested to
86 occur when the skin is physically wet (16). This could be due to the fact that we seem to
87 interpret the coldness experienced during the evaporation of moisture from the skin as a
88 signal of the presence of moisture (and thus wetness) on the skin’ surface. In line with this
89 hypothesis, we have also observed that during the static contact with a warm-wet surface
90 (with a temperature warmer than the skin) no local skin wetness was perceived, as no skin
91 cooling, and thus no cold sensations occurred (20). Finally, this concept has been further
92 confirmed in our most recent study, in which we observed that, when participants’ cold
93 sensitivity was significantly reduced through a compression ischemia protocol, skin wetness
94 perception in response to a wet stimulus was also significantly reduced both on hairy and
95 glabrous skin sites (18). All in all, these recent findings have highlighted the critical role of
96 thermosensitivity to cold in the ability to perceive skin wetness (18–21).

97 Appraising the importance of cold afferents in the ability to sense cutaneous wetness has led
98 us to hypothesize that regional differences in wetness perception might exist across the body

and might depend upon 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 as amongst the most sensitive regions to cold (7, 31, 39). In this regard, the recent work of Ouzzahra *et al.* (2012) (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 which 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 (2009) (22) found that the torso seems to have a lower sensitivity to wetness than the limbs, while in a non-manipulated condition (natural wetness distribution across the torso) Gerrett *et al.* (2013) (25) showed that the torso seemed to dominate wetness perception. Similarly, Lee *et al.* (2011) (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 and 32 °C T_{air} and 50 p.100 RH. In line with Lee *et al.* (2011) (34), Ackerley *et al.* (2012) (2) have recently shown that when wet stimuli with different moisture contents (range: 20-160 μL over a 0.0024 m^2 surface) were applied to different body regions, individuals were able to differentiate between moisture levels, with a tendency of the back as being amongst 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 T_{sk} (ΔT_{sk})], 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 towards 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 T_{sk}) which we have previously shown to induce an illusion of skin wetness (21), local T_{sk} , 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 p.100 body fat) with no history of sensory-related disorders volunteered to participate in this study.

To account for the inter-individual variability in the hairiness of the torso, participants' hair growth was visually graded using a modified Garn (1951) (25) scoring system (for an extensive review see Yildiz *et al.* 2010) (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, based on the visual density of terminal hairs. A score of 0 represented the absence of terminal hairs, a score of 1 minimally evident hair growth, and a score of 4 extensive hair growth (58). Thirteen out of 16 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 16 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 ($T_{\text{air}} = 22\text{ }^{\circ}\text{C}$; RH= 50 p.100) and warm environmental conditions ($T_{\text{air}} = 33\text{ }^{\circ}\text{C}$; RH= 50 p.100). 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 figure 1 and are in line with the work of Ouzzahra *et al.* (2012) (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 T_{sk} at the contact site was measured before and immediately after the contact with the stimulus using a single spot infrared thermometer (FLUKE 566, Fluke Corporation, USA) with a temperature range of -40 to 800 $^{\circ}\text{C}$ and an accuracy of $\pm 1\text{ }^{\circ}\text{C}$. In order to maximize the accuracy of the temperature readings, during each test the infrared thermometer was calibrated against a black plate whose temperature was monitored with a thermistor (Grant Instruments, Cambridge, UK). This method has been previously used (see Filingeri *et al.* 2014) (21) and shown to be effective in allowing recording of post-stimulation 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 Inc., USA) with a contact surface of 0.0025 m². The relative temperature of the stimulus was 15 $^{\circ}\text{C}$ lower than the local T_{sk} which was measured with the infrared thermometer. We chose a relative temperature of -15 $^{\circ}\text{C}$ 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 set up was designed. When the front torso was stimulated, participants were asked to lie on a bench 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 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 front, with their arms alongside the body, and to face towards the left, while the investigator was standing on their 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 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 ACSM's 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) equation:

$$\begin{aligned} \text{Body density} = & 1.112 - 0.00043499(\text{sum of seven skinfolds}) \\ & + 0.00000055(\text{sum of seven skinfolds})^2 - 0.00028826(\text{age}) \end{aligned}$$

Participants then changed into shorts, socks and running shoes. Five iButtons (Maxim, USA) 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 T_{sk} . 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 (1982) (29) to give an estimate of mean T_{sk} 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 p.100 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); 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; +3). We defined the value -2 (labelled: “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 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 (*i.e.* 15 °C below the recorded local T_{sk}) and applied by hand to the skin site. 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 10s. 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 T_{sk} of the stimulated area was recorded with the infra-red thermometer. The same protocol was repeated for each of the 12 skin sites allowing at least one minute in between them. Each participant had only one presentation of each stimulus for each skin site. The quantitative sensory test lasted for 15min. After completion of the test, 10min were allowed before participants moved from the first to the second environmental chamber set for the warm exposure (33 °C T_{air} , 50 p.100 RH). Once in the second chamber, 10min 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} , ΔT_{sk} (*i.e.* variation from pre- to post-stimulation) 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 ΔT_{sk} data were analysed by a 2-way repeated measures analysis of variance, 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 means and 95 p.100 confidence intervals were used to investigate the main effects and

interactions of the variables. Observed power was computed using $\alpha = 0.05$. When a significant main effect was found, Tukey's post-hoc analyses were performed.

As absolute thermal, wetness and pleasantness sensations were obtained in the form of ordinal ratings, these were analysed by means of non-parametric statistics. The main effect of the environmental condition (2 levels of comparison) was tested by a Wilcoxon signed rank test (Z) whereas the main effect of the skin site stimulated (12 levels of comparison) was tested by a Friedman's analysis of variance (X^2). Post-hoc analyses for the effect of skin site stimulated were performed by a Wilcoxon signed rank test (Z) and adjusted for multiple comparisons. Effect size was calculated and reported as r . 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 (3).

To further investigate the regional distribution of cutaneous wetness perception, a frequency distribution analysis of skin wetness was performed. Wetness perception scores as recorded during both environmental conditions were collapsed over the skin site stimulated. 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 (p.100) the cold-dry stimulus was perceived as "dry" or as "wet" was calculated and analysed by a Chi-square test. This analysis was performed for each of the 12 skin sites. Also, frequency data were grouped and compared between the front and back torso. The same frequency distribution analysis of wetness ratings has been performed in one of our recent studies (see Filingeri *et al.*, 2014) (21). Also, a similar frequency distribution analysis of thermal ratings

has been previously reported in the literature (see Gan *et al.*, 2012) (24). In line with Gan *et al.* (2012) (24) and with our previous findings (18), we believe that, because of the variable nature of subjective responses, reorganizing the collected data in this format would make the potential differences in the regional distribution of wetness perception across the torso easier to identify.

Finally, a Spearman's rank correlation coefficient was calculated to investigate the degree of association between: 1. thermal sensation and frequency of wetness perception; 2. pleasantness sensation and frequency of wetness perception; 3. thermal sensation and pleasantness sensation. Statistical analysis was performed using IBM SPSS Statistics 19 (IBM, USA). In all analyses, $p < 0.05$ was used to establish significant differences. Parametric and non-parametric (perceptual scores) data are reported as mean \pm standard error of the mean. Furthermore, median and inter-quartile ranges [median; percentile] are reported for non-parametric 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 ± 0.1 °C and 34.8 ± 0.1 °C. These values were found to be significantly different (mean difference = 2.4 °C; 95 p.100 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 (pre-stimulation) varied in a range between 31.8 ± 0.1 °C (*i.e.* lateral chest) and 33.4 ± 0.2 °C (*i.e.* medial upper back) for the thermo-neutral exposure, and

between 34.9 ± 0.2 °C (*i.e.* lateral chest) and 36.1 ± 0.1 °C (*i.e.* medial upper back) for the warm exposure. Local ΔT_{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 ΔT_{sk} ($F= 4.4_{(4.6, 50.6)}$, $p=0.003$). No significant effect of the environmental condition ($F= 2.2_{(1, 11)}$, $p=0.17$) nor 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 ΔT_{sk} is shown in figure 2A. Post-hoc analyses indicated that, depending on skin site, local ΔT_{sk} varied significantly in a range of -1.9 ± 0.4 °C (*i.e.* medial lower back) to -5.0 ± 0.4 °C (*i.e.* lateral chest), corresponding to a range of skin cooling rates of 0.19 ± 0.04 to 0.5 ± 0.04 °C·s⁻¹. These values were calculated as the ratio between the ΔT_{sk} from post- to pre-stimulation and the contact time (*i.e.* 10s). The significance levels are presented separately for sites of the front and back torso (Tab.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 which did not change between the thermo-neutral and warm environmental exposure.

Thermal sensation

Baseline thermal sensation scores (pre-stimulation) varied in a range of 0.1 ± 0.1 [median= 0; 0.0, 1.0] to 0.6 ± 0.2 [median= 1; 1.0, 1.0] for the thermo-neutral exposure and of 1.4 ± 0.3 [median= 1; 0.2, 2.7] to 1.7 ± 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 ± 0.1) [median= -4; -4.0, -3.0] than during the thermo-neutral exposure (-3.7 ± 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 [$X^2(11, N = 32) = 143.2$, $p < 0.001$], with scores varying in a range of -2.3 ± 0.2 [median= 2; -3.0, -1.2] (i.e. medial chest) to -4.4 ± 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 figure 2B. The significance levels are presented separately for sites of the front and back torso (Tab.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 (pre-stimulation) 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 exposure (-1.4 ± 0.1) [median= -1; -2.0, -1.0] ($Z = -2.9$, $p = 0.004$, $r = -0.2$). Expressed in terms of

semantic labels, these were in a range going from “neutral” to “slightly wet” for both warm and thermo-neutral exposure. Wetness perceptions differed significantly according to the skin site stimulated [$X^2(11, N = 32) = 58.4, p < 0.001$], with scores varying in a range of -1.1 ± 0.1 [median = -1; -1.0, -1.0] (i.e. medial chest) to -2.1 ± 0.2 [median = -2; -3.0, -1.0] (i.e. medial lower back) between sites. Expressed in terms of semantic labels, these were in a range going from “neutral” to “slightly wet”. The significance levels are presented separately for sites of the front and back torso (tab.1). To further investigate the regional distribution of wetness perception, a frequency distribution analysis of wetness scores was performed. The data analysis indicated a main effect of skin site stimulated on the frequency of “wet” scores (Pearson Chi-square $p < 0.001$). Data for each of the 12 skin sites stimulated are shown in figure 2C. The results indicated that the relative cold-dry stimulus was significantly more often perceived as wet when applied to the lower back (lateral = 56 p.100; medial = 59 p.100) and the medial upper back (53 p.100). The same stimulus was significantly less often perceived as wet when applied to the medial chest (22 p.100) and medial upper abdomen (28 p.100). Overall, the back presented a significantly greater frequency of wetness perception (53 p.100) than the front torso (39 p.100) (Pearson Chi-square $p = 0.047$). Overall, these outcomes indicated that, the same relative cold-dry stimulus evoked wetness perceptions which were significantly “wetter”, and more often perceived as wet, when the stimulus was applied on specific regions (such as the medial and lateral lower back) as opposed to other regions (such as the medial and lateral chest), in which the same stimulus evoked “less wet” and less frequent wetness perceptions.

Pleasantness sensation

Pleasantness sensations were recorded only during the stimulation as we were primarily interested in the affective and discriminative sensations aroused by the application of the thermal stimulus with regards to the whole body's thermal state.

Pleasantness sensation scores were overall "less unpleasant" during the warm (-1.8 ± 0.1) [median= -2; -3.0, -1.0] than during the thermo-neutral exposure (-2.2 ± 0.1) [median= -2; -3.0, -1.0] ($Z = -3.8$, $p < 0.001$, $r = -0.3$). Expressed in terms of semantic labels, these were in a range going from "neutral" to "unpleasant" for both the thermo-neutral and warm exposure. Pleasantness sensation scores differed significantly according to the skin site stimulated [$X^2(11, N = 32) = 108.1$, $p < 0.001$], with scores varying in a range of -1.1 ± 0.2 [median= -1; -1.0, -0.2] (i.e. medial chest) to -2.7 ± 0.2 [median= -2; -4.0, -2.0] (i.e. lateral lower back). Expressed in terms of semantic labels, these were in a range going from "neutral" to "unpleasant". Mean pleasantness sensations averaged over conditions, as reported during the application of the relative cold-dry stimulus to each skin site, are shown in figure 2D.

Overall, these outcomes indicated that, the same relative cold-dry evoked sensations which were significantly "more unpleasant" when the stimulus was applied on specific regions (such as the lateral abdomen and lateral lower back) as opposed to other regions (such as the medial chest and medial upper abdomen), in which the same stimulus evoked "less unpleasant" sensations. Interestingly, the regional variation in displeasure showed a pattern similar to the regional distribution in thermosensitivity to cold. Finally, the same relative cold-dry stimulus was overall perceived as slightly less unpleasant during the warm than during the thermo-neutral exposure.

Correlation analysis between thermal sensation, frequency of perceived wetness and pleasantness sensation

The degree of association between the level of coldness experienced and the frequency of perceived wetness (assessed by a Spearman's rank correlation test) was found to be statistically significant ($p < 0.01$; Spearman's $\rho = 0.79$), indicating a significant correlation between increasing coldness and increasing frequency of perceived wetness (fig. 3A). Similarly, the degree of association between the level of pleasantness experienced and the frequency of perceived wetness was found to be statistically significant ($p < 0.01$; Spearman's $\rho = 0.76$), indicating a significant correlation between decreasing pleasantness and increasing frequency of perceived wetness (fig. 3B). Finally, the degree of association between the level of coldness and the level of pleasantness experienced was also found to be statistically significant ($p < 0.01$; Spearman's $\rho = 0.97$), indicating a significant correlation between increasing coldness and decreasing pleasantness (fig. 3C).

DISCUSSION

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 that: 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. 2B vs. 2C); 2. cutaneous wetness perception is slightly higher under warm than under thermo-neutral environmental conditions, despite 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. 2B vs. 2D).

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. 2A with 2B, 2C and 2D). 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 novelty of these findings is in providing the first detailed body maps of thermal, wetness and pleasantness sensation across the human torso.

The role of thermosensitivity to cold in the ability to sense skin wetness

With regards 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 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⁻¹ 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⁻¹. 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 sub-served by peripheral myelinated A δ -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 hygroreceptors (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 sub-modality can be transformed into a map or reference frame defined by another sub-modality) of the somatosensory inputs generated when the skin is physically wet (28). As the sensory inputs associated to 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.* A δ -nerve fibers) is presented, wetness will be sensed.

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 which were within the range suggested to evoke wetness perceptions for all the regions investigated (*i.e.* 0.19 to 0.5 °C·s⁻¹) (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.

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.* (2011) (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.* (2012)(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 ΔT_{sk}) which could have triggered the sensory inputs used by the participants to discriminate the level of wetness experienced regionally. In the present study, this issue was overcome by quantifying the local ΔT_{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 ΔT_{sk} . A comparison of the body maps of ΔT_{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 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 upon an uneven weighting and integration of thermoafferent information, which seems independent from the regional variations in T_{sk} and, potentially,

from the density of thermoreceptors (5, 7, 39). As shown in figures 2B and 2C, 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 ΔT_{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.* (2012) (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 μL over a surface of 0.0024 m^2). Although in the mentioned study no recordings of local ΔT_{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 hygroreceptors (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 experience high levels of physical wetness, e.g. due 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 which 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 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 due to the resting condition of the participants, it is unlikely that a higher level of whole-body 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, in order to investigate whether a swelling state of the skin (due 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. 2D with 2B and 2C). 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. 3B and 3C). 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 towards 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 towards a re-establishment 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. As during our experimental conditions participants were not expected to become hyperthermic (due 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 further our understanding of the role of the torso's thermal comfort in the whole-body thermal comfort. Nakamura *et al.* (2008, 2013) (39, 40) have repeatedly shown that humans prefer a warm trunk and that abdominal cooling is often perceived as more unpleasant than other regions' cooling. This is in line with the findings of the present study, in which e.g. we observed the lateral abdomen to be amongst 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 organ's function (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 regards 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 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 (due 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 3 different temperatures [i.e. warm, neutral (same as skin temperature) and cold)] were applied on participants' skin, Ackerley *et al.* (2014) (1) have shown that stimuli with temperatures which 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 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), 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 as well as an 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 T_{sk} 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, due to 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 which 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 in order to optimize thermal protection and maximize thermal comfort under extreme environmental conditions (e.g. cold air/water exposures).

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Figure 1: Name and exact anatomical locations of the 12 skin sites targeted for stimulation.

Figure 2: Body maps showing the regional distribution of (A) skin cooling ($^{\circ}\text{C}$), (B) absolute mean votes for thermal sensation, (C) frequency of wetness perception and (D) absolute mean votes for pleasantness sensation, as a result of the 10 s application of the relative cold-dry stimulus (15°C lower than local T_{sk}) to each skin site, collapsed over all conditions. Data were collected on the left side of the body and the body maps presented were developed assuming left-right symmetry (see Ouzzahra *et al.*, 2012) (44). Regions showing greater skin cooling, colder sensations, more frequent wetness perceptions and more unpleasant sensations are represented in darker colors. The rating scales used by the participants to score their absolute thermal and pleasantness sensations are reported next to the respective body maps. Two main tendencies are shown. First, the regional differences in thermal, wetness and pleasantness sensation present a similar pattern across the torso (e.g. as opposed to the chest, the lateral and lower back appears more sensitive to cold, wetness and thermal displeasure). Second, these sensory patterns seem independent from the regional variations in skin cooling (*i.e.* regions which show greater skin cooling, such as the lateral chest, are not necessarily the ones in which the stimulus was perceived as colder, more often wet or more unpleasant).

Figure 3: Relationship between: (A) thermal (cold) sensation and the frequency of perceived wetness; (B) pleasantness sensation and the frequency of perceived wetness; (C) thermal (cold) sensation and pleasantness sensation. Data are reported as mean for each skin site, collapsed over all conditions, and standard deviation (horizontal and vertical lines). There is a highly significant correlation between the level of coldness experienced and the frequency of perceived wetness (*i.e.* increasing coldness and increasing wetness), the level of pleasure experienced and the frequency of perceived wetness (*i.e.* decreasing pleasantness and

871 increasing wetness), and the level of coldness and pleasure experienced (*i.e.* increasing
872 coldness and decreasing pleasantness).

873 **Table 1:** Significance levels of the multiple comparisons for the 12 skin sites are reported for
874 skin cooling (ΔT_{sk}), thermal (TS), wetness (WP) and pleasantness (PS) sensation.

875 **Table 1 footnote:** * $p < 0.05$; † $p < 0.01$; ‡ $p < 0.001$.

1. Medial chest
(270 mm above the umbilicus)

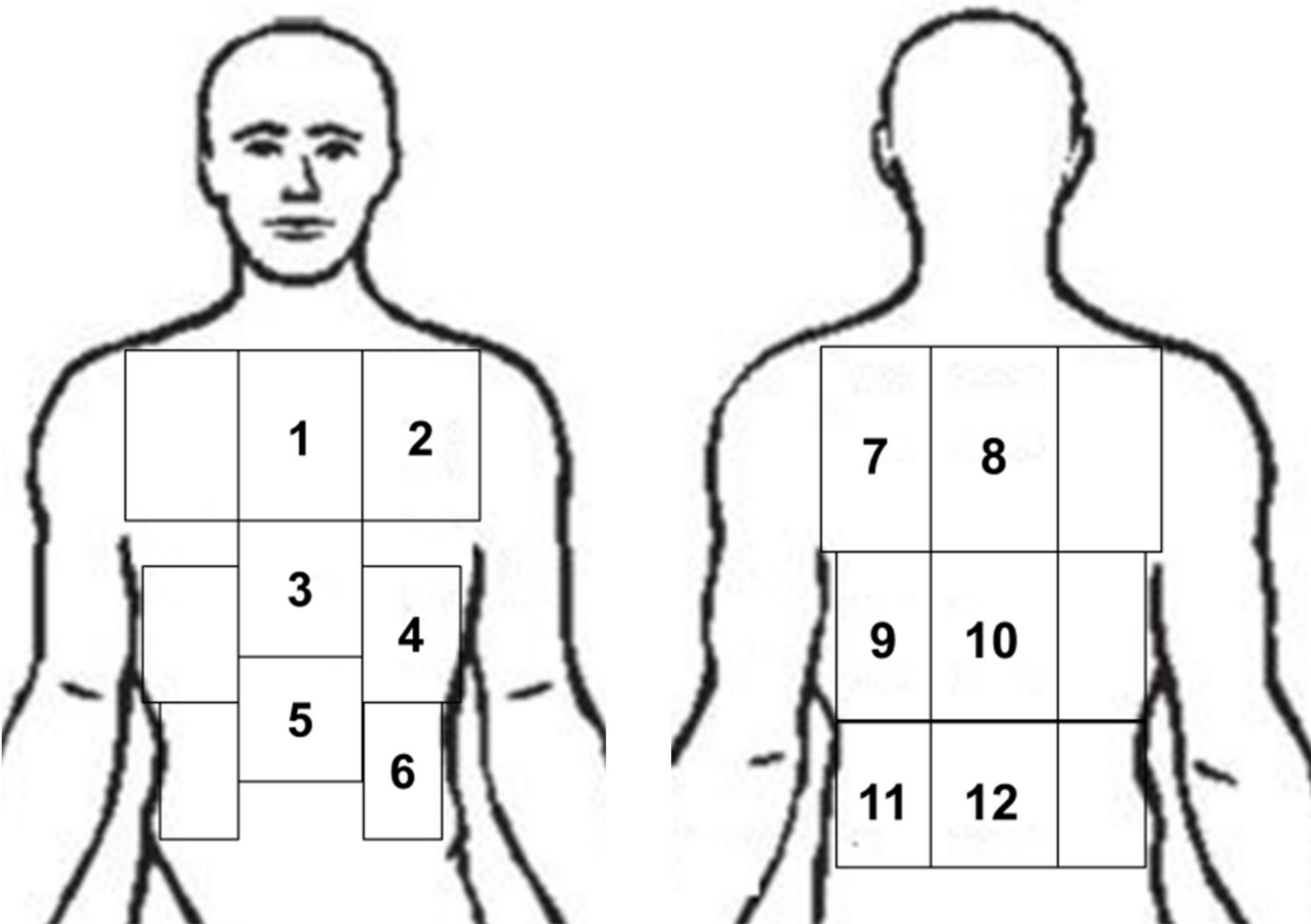
2. Lateral chest
(70 mm above the nipple)

3. Medial upper abdomen
(130 mm above the umbilicus)

4. Lateral upper abdomen
(30 mm below the nipple)

5. Medial abdomen
(30 mm above the umbilicus)

6. Lateral lower abdomen
(45 mm above the anterior superior iliac crest)



7. Lateral upper back
(50 mm above the inferior angle of the scapula)

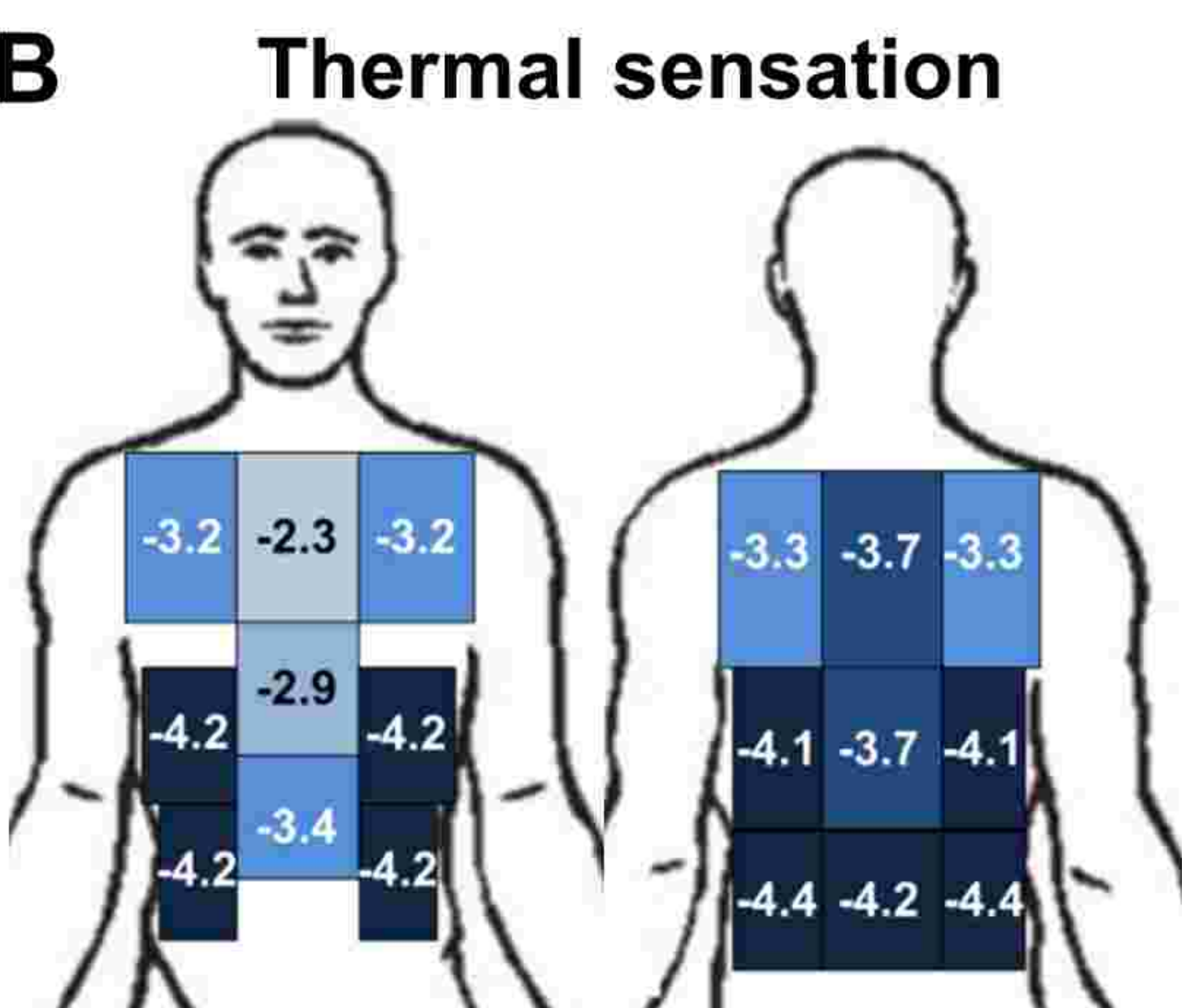
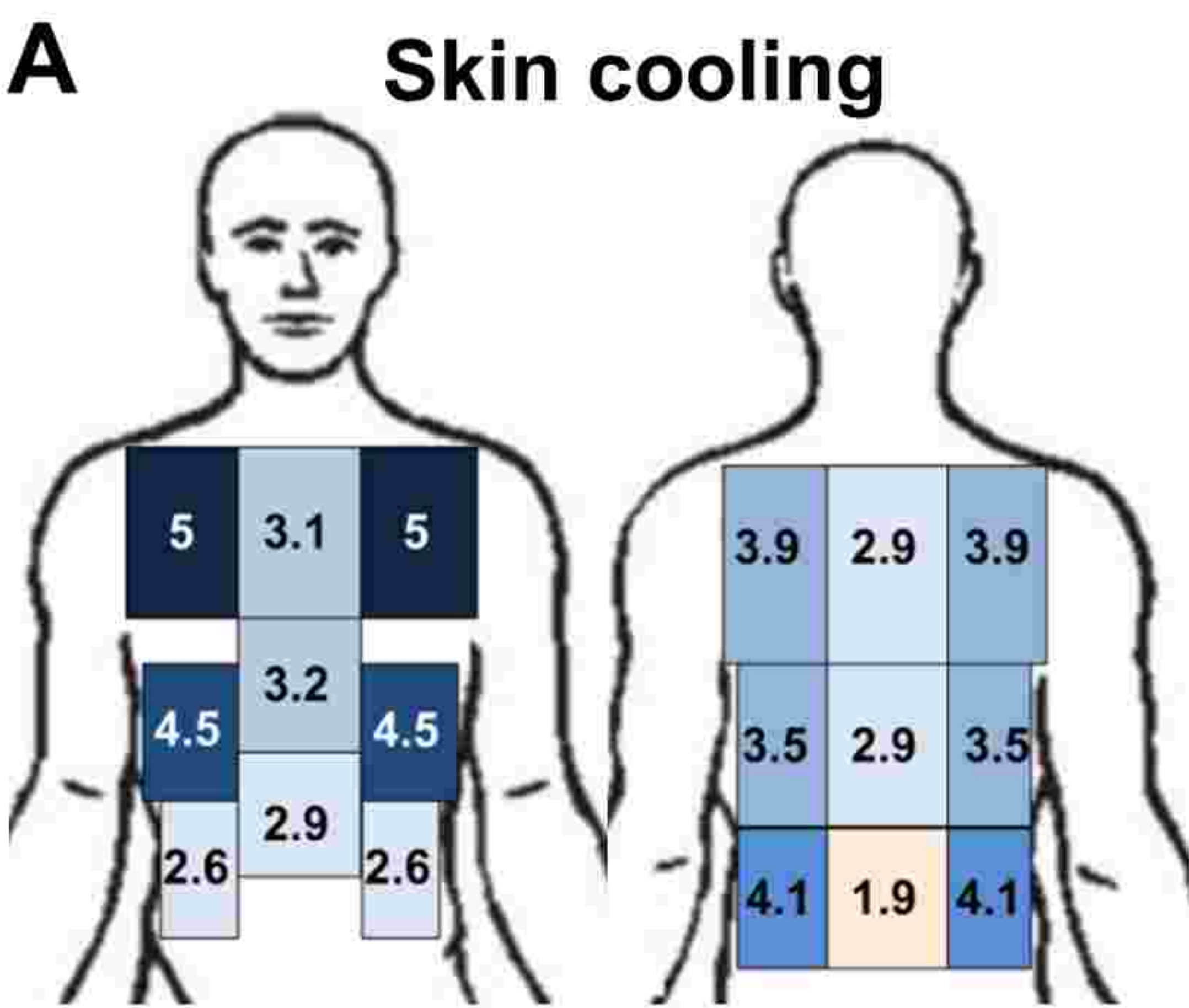
8. Medial upper back
(30 mm medial to 7)

9. Lateral mid-back
(10 mm below the inferior angle of the scapula)

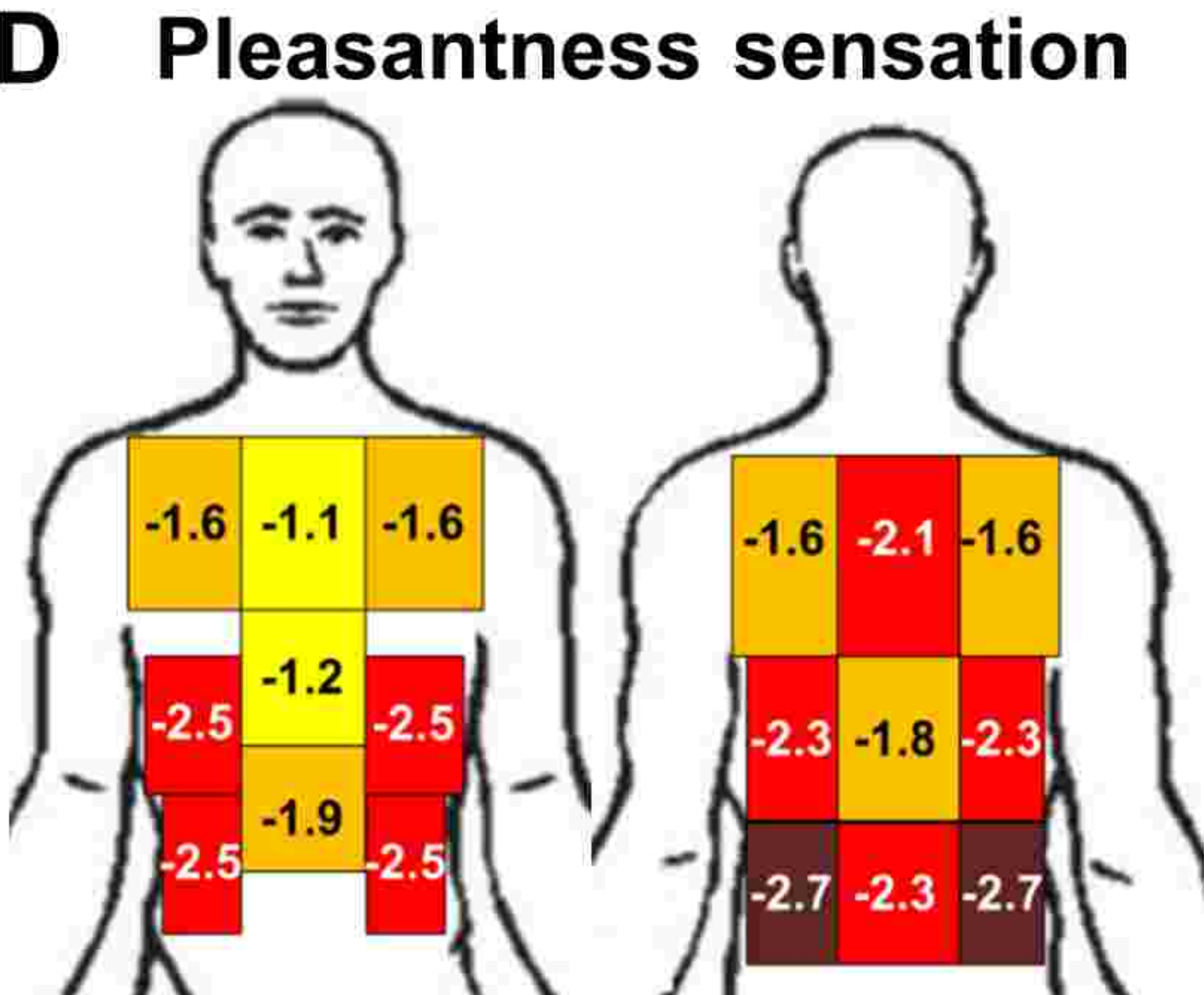
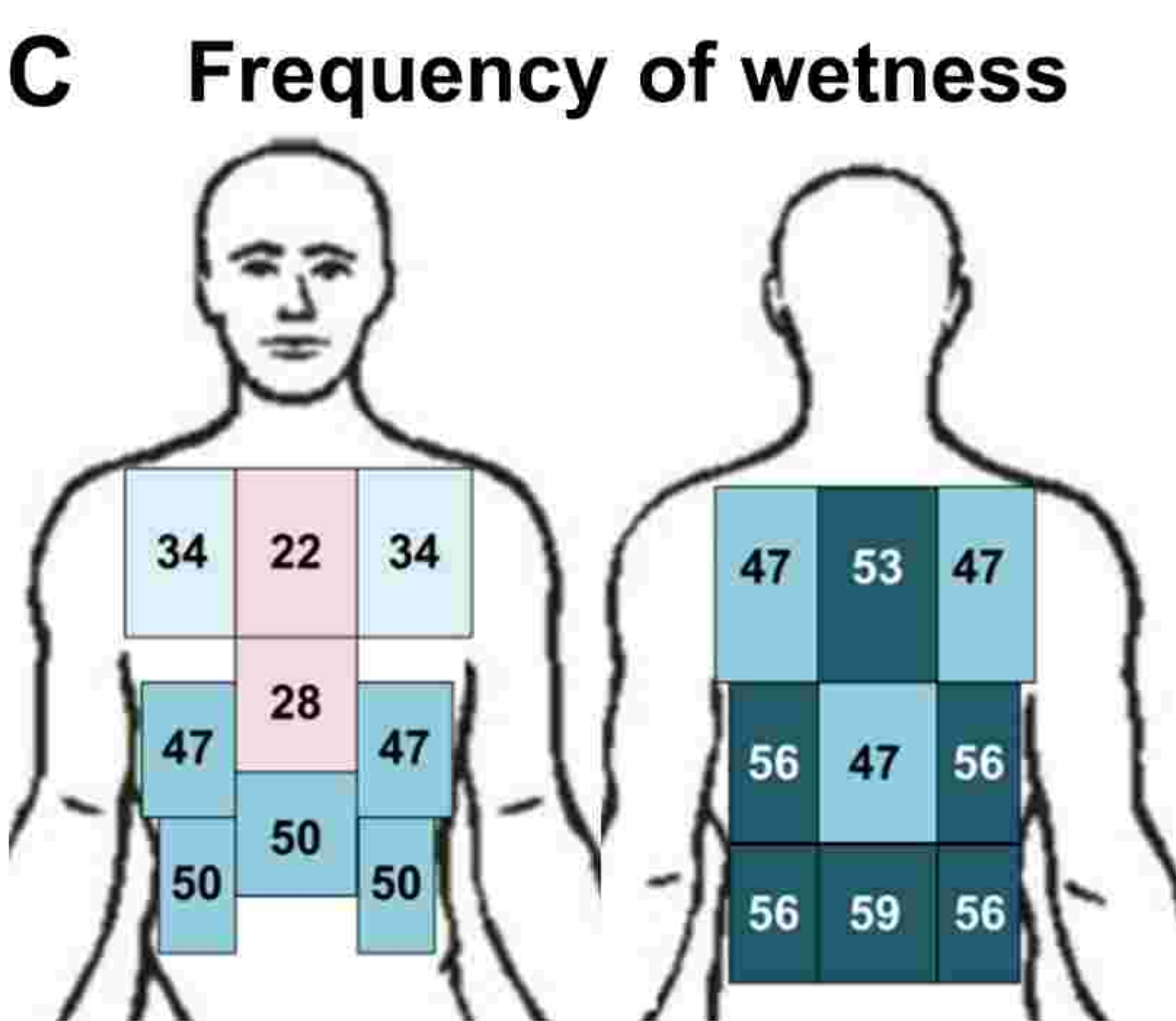
10. Medial mid-back
(30 mm medial to 9)

11. Lateral lower back
(165 mm below the inferior angle of the scapula)

12. Medial lower back
(30 mm medial to 11)

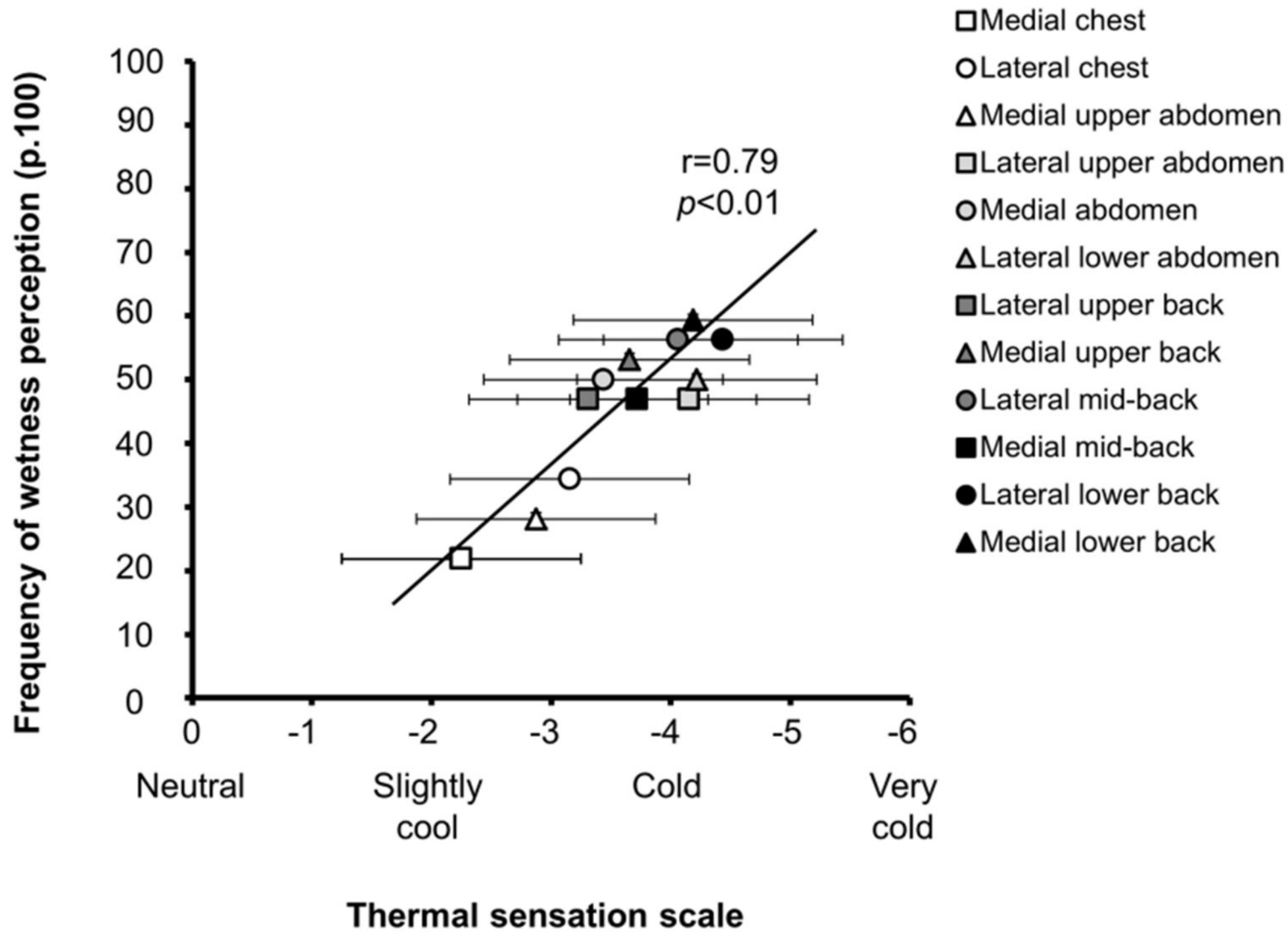


- Thermal scale*
- +4 Warm
 - +3
 - +2 Slightly warm
 - +1
 - 0 Neutral
 - 1
 - 2 Slightly cool
 - 3
 - 4 Cold
 - 5
 - 6 Very cold

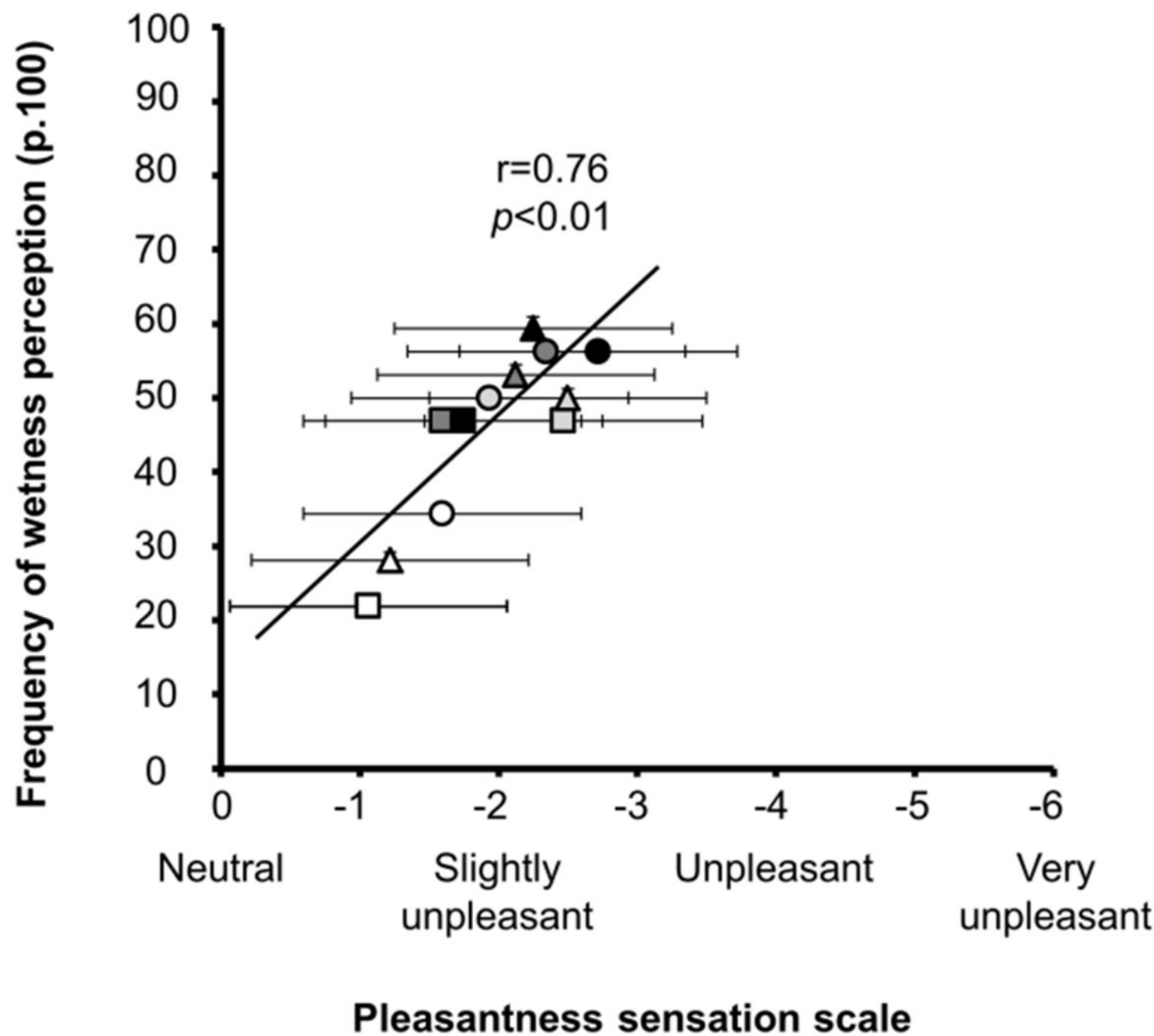


- Pleasantness scale*
- +4 Pleasant
 - +3
 - +2 Slightly pleasant
 - +1
 - 0 Neutral
 - 1
 - 2 Slightly unpleasant
 - 3
 - 4 Unpleasant
 - 5
 - 6 Very unpleasant

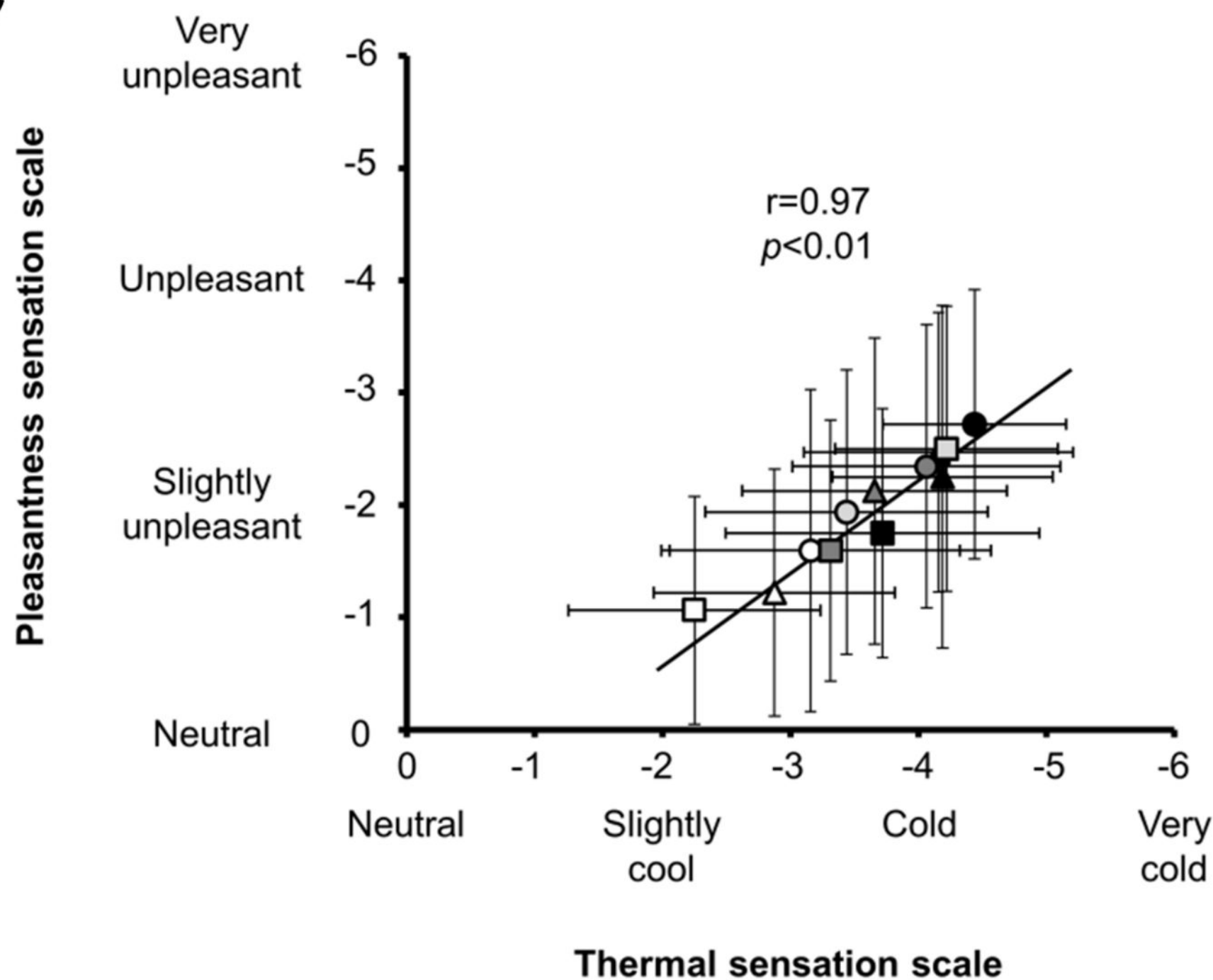
A



B



C



			Front Torso						Back Torso					
			Medial chest (1)	Lateral chest (2)	Medial upper abdomen (3)	Lateral upper abdomen (4)	Medial abdomen (5)	Lateral lower abdomen (6)	Lateral upper back (7)	Medial upper back (8)	Lateral mid-back (9)	Medial mid-back (10)	Lateral lower back (11)	Medial lower back (12)
Front Torso	Medial chest (1)	ΔT_{sk}		†										*
		TS				†		†		†	†	†	†	†
		WP								†			†	*
		PS				†	*	†		†	†		†	†
	Lateral chest (2)	ΔT_{sk}	†		†		†	†	*	*	*	*	*	†
		TS				†		*			*		†	†
		WP												
		PS				*		*						†
	Medial upper abdomen (3)	ΔT_{sk}		†										*
		TS				†		†			†		†	†
		WP								†			†	*
		PS				†		†		*	†		†	†
	Lateral upper abdomen (4)	ΔT_{sk}					*	†			*			†
		TS	†	†	†				*					
		WP												
		PS	†	*	†				*					
	Medial abdomen (5)	ΔT_{sk}		†		*								*
		TS												†
		WP												
		PS	*											
	Lateral lower abdomen (6)	ΔT_{sk}		†		†								
		TS	†	*	†				†					
		WP												
		PS	†	*	†				*					
Back Torso	Lateral upper back (7)	ΔT_{sk}		*									*	†
		TS				*		†					*	†
		WP												
		PS				*		*						†
	Medial upper back (8)	ΔT_{sk}		*		*								†
		TS	†											
		WP	†		*									
		PS	†		*									
	Lateral mid-back (9)	ΔT_{sk}		*										*
		TS	†	*	†									
		WP	†											
		PS	†		†									
	Medial mid-back (10)	ΔT_{sk}		*										
		TS	†											
		WP												
		PS												†
	Lateral lower back (11)	ΔT_{sk}		*			*							†
		TS	†	†	†				*					
		WP	†		†									
		PS												
	Medial lower back (12)	ΔT_{sk}	*	†	*	†			†	*	†		†	
		TS	†	†	†		†		†					
		WP	*		*									
		PS	†	†	†				†			†		