



Wetness perception across body sites

Rochelle Ackerley, Johan W Wessberg, Håkan Olausson, Francis M Mcglone

► To cite this version:

Rochelle Ackerley, Johan W Wessberg, Håkan Olausson, Francis M Mcglone. Wetness perception across body sites. *Neuroscience Letters*, 2012, 522 (1), pp.73 - 77. 10.1016/j.neulet.2012.06.020 . hal-01599666

HAL Id: hal-01599666

<https://hal.science/hal-01599666>

Submitted on 3 Oct 2017

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Wetness perception across body sites

Rochelle Ackerley^a, Håkan Olausson^a, Johan Wessberg^a, Francis McGlone^b

^a Department of Physiology, University of Gothenburg, Box 432, Göteborg, SE-40530, Sweden

^b School of Natural Sciences & Psychology, Tom Reilly Building, Liverpool John Moores University, Liverpool, L3 3AF, UK

Corresponding author:

Rochelle Ackerley, Department of Physiology, University of Gothenburg, Box 432, Göteborg, SE-40530, Sweden, e-mail: rochelle.ackerley@gu.se

Abstract

Human skin is innervated with a variety of receptors serving somatosensation and includes the sensory sub-modalities of touch, temperature, pain and itch. The density and type of receptors differ across the body surface, and there are various body-map representations in the brain. The perceptions of skin sensations outside of the specified sub-modalities e.g. wetness or greasiness, are described as ‘touch blends’ and are learned. The perception of wetness is generated from the coincident activation of tactile and thermal receptors. The present study aims to quantify threshold levels of wetness perception and find out if this differs across body sites. A rotary tactile stimulator was used to apply a moving, wetted stimulus over selected body sites at a precise force and velocity. Four wetness levels were tested over eight body sites. After each stimulus, the participant rated how wet the stimulus was perceived to be using a visual analogue scale. The results indicated that participants discriminated between levels of wetness as distinct percepts. Significant differences were found between all levels of wetness, apart from the lowest levels of comparison (20 µl and 40 µl). The perception of wetness did not, however, differ significantly across body sites and there were no significant interactions between wetness level and body site. The present study emphasizes the importance of understanding how bottom-up and top-down processes interact to generate complex perceptions.

Key words: body map; psychophysics; somatosensory; temperature; touch.

Abbreviations: rotary tactile stimulator (RTS), primary somatosensory cortex (SI), secondary somatosensory cortex (SII)

Introduction

Cutaneous sensations result from the stimulation of many different skin afferents including those from touch, temperature, pain and itch receptors, and vary across the body due to differences in the receptor type and density. The body is represented in various ways in the brain, for example, the somatotopical sensory homunculus in the primary somatosensory cortex (SI), where the hands have a much larger representation than input from the back [25]. When the skin is stimulated, a sensation is perceived through processing changes in the firing patterns from peripheral afferents. Skin sensations are rarely composed of just one sensory modality and some sensory receptors are polymodal [16]. Furthermore, perception of the sensation usually occurs from a blend of inputs, for example, when we sense that something is wet, it is typically due to changes in both touch and temperature afferents [2, 30]. There is no evidence to suggest that we have 'wetness' receptors in the skin. Bentley [2] tested the perception of dipping a sheath-covered finger into a liquid; the results showed that the participants at first refused to believe that the finger was not actually wet. When skin is touched, cutaneous mechanoreceptors (e.g. Merkel's disks, Pacinian corpuscles and Ruffini's end organs, and also Meissner's corpuscles in glabrous skin and hair and field receptors in hairy skin [17, 33, 35]) detect a change and information is transmitted to the central nervous system by these fast-conducting, myelinated A-fibre afferents. Slowly-conducting, unmyelinated C-fibre afferents (e.g. C-tactile fibers) in hairy skin also contribute to the touch sensation [22, 34, 36]. Together, these mechanosensitive afferents code for different aspects of touch involved in the perception of a liquid, for example, the location, pressure and duration of a stimulus.

In the thermoreceptive system, there are also a number of different receptors that may contribute in the perception of wetness and changes in absolute and relative temperature can be perceived [29]. From separate experiments by Blix, Goldscheider and Donaldson (see [21] for an overview) it has long been known that thermal sensitivity is punctate and there are many more temperature spots responding to cooling than warming, so the perception of cool is a particularly salient stimulus [1, 6]. Temperature sensing involved in the perception of wetness is typically in the innocuous temperature range i.e. where the skin is not damaged. Normal skin temperature is approximately 33°C [1, 20] and when a wet stimulus is sensed, it is usually due to a decrease in temperature (in combination with a mechanical indentation). Specifically for wetness perception, temperature afferents activated may include thinly myelinated A δ afferent fibres that fire preferentially to skin cooling between 20-30°C [3, 4, 8], unmyelinated C cold afferents that are active below 20°C, but may contribute more to the sense of cold pain [3, 4, 5], and unmyelinated

warm afferent fibres that are active at $>30^{\circ}\text{C}$ [9, 15]. The present study investigates the effects of evaporative cooling of water from the skin (i.e. in the A δ thermoreceptor range), however, in other circumstances, the more extreme, cold unmyelinated fibres may contribute more (e.g. when touching freezing water) or the unmyelinated warm afferents may also contribute (e.g. when in contact with warm water).

There are two mechanisms in which the temperature changes induced from wetness may be perceived: (i) through direct contact with a liquid, which causes a change in skin temperature and (ii) through the evaporation of liquid from the skin (leading to cooling of the skin). The present study is aimed at understanding the ability to perceive the wetness of an object moving across the skin. This has relevance for everyday life, as people will report feeling uncomfortable in wet clothes or when they become sweaty [31, 32]. It is of interest to investigate the neurophysiology behind wetness perception to understand the mechanisms of the contributing sensations and how these can relate to the future design of textiles, particularly for sports-wear and in occupations where protective clothing is important. We hypothesize that participants will discriminate between different amounts of wetness and that due to the differences in cutaneous receptor density there may be topographic differences in the discriminatory abilities.

Materials and methods

The perception of wetness was tested using psychophysical ratings. A total of nine healthy female participants completed the experiment (aged 21-42). Participants were given information about the study, which conformed to local ethical approval and was performed in accordance with the Declaration of Helsinki. Written informed consent was obtained for all participants and they were paid for participation. An automated rotary tactile stimulator (RTS; Dancer Design, Wirral, UK) was used to deliver controlled moving stimuli at a predetermined force, direction and speed to the skin sites, using custom-written scripts in LabVIEW (National Instruments, Austin, TX). The RTS had four radial arms with a smooth, slightly rounded plastic surface at each end (length: 6cm, width: 3cm). Pieces of VELCRO[®] (length: 1 cm, width 3 cm) were stuck on the underside of each plastic surface and on to knitted cotton fabric (cut into pieces of length: 8 cm, width: 3 cm) so that the fabric could be attached securely to the plastic surface. This meant that the fabric covered the whole of the plastic end and could be quickly and easily changed.

In the experiment, the participants wore shorts and a vest top so the different skin sites could be accessed easily, and they were positioned comfortably on a massage table so that the RTS

could be manoeuvred above them to deliver the stimuli. The temperature of the room was set at 24°C and the water used for wetting the fabric was kept at room temperature. The participants wore earplugs to minimize any noise and also glasses with side-shielding so they could only see the screen in front of them, which was used for rating wetness. A micropipette was used to wet a piece of fabric, just before application of the stimulus, with one of four levels of water (20, 40, 80, or 160 µl). Each level of water was applied in a single stroke to the different body parts at a relatively slow velocity of 0.5 cm/s and at a relatively light force of 0.25 N. There were eight body sites under investigation: mid-forehead, and on the left side of the body, the dorsal forearm, palm of hand, collar, shoulder, lower back, ventral thigh, and the mid-ventral leg. The body sites chosen were all relatively flat so that the area of skin contacted by the probe was similar across the conditions. The direction of stimulation on the forehead, collar, shoulder and lower back was from right to left and on the forearm, palm, thigh and leg, the direction was proximal to distal. The wetted fabric was randomly assigned to an arm on the RTS for each trial and the stimuli presentation to the body parts was also randomised. A new piece of fabric was used for each wetness level, body site and participant.

After each stimulus, the participant rated how wet they thought the fabric was with a slider device held in their right hand. A visual analogue scale (VAS) was used with the hand-held slider for ratings. The end anchors of the scale were 'Completely dry' on the left of the screen, which represented a bone dry piece of fabric, and 'Completely wet' on the right side, which represented a dripping wet piece of fabric. There was a minimum of 30 seconds between each stimulus. The participants were informed how to use the scale and what the end-text anchors were before the experiment. They also had a practice run prior to the experiment so that they had an idea of the feel of the stimulation and also how to use the VAS. The output from the RTS provided data on a 0-100 point scale from each participant, for each wetness level and body site. Statistical analyses were conducted using MATLAB (The Mathworks, MA) to calculate significant differences between conditions using a repeated measures analysis of variance (ANOVA) with two variables (wetness: 4 levels of water; body site: 8 levels, representing each site). Where significant main effects were found, a multiple comparison post hoc test using Tukey's least significant difference (alpha sought at $p < 0.05$, $p < 0.01$ or $p < 0.001$) was used to compare between the levels of the variable. Inferential statistics were required to conclude whether any significant differences found in the data were more than the random variability in the population sampled.

Results

The results showed that participants were able to differentiate accurately between the wetness levels and a main effect was found ($F=30.94_{(3, 12)}$, $p<0.001$). Figure 1A shows the differences between the participants' ratings, averaged per wetness level and collapsed over the body site where the stimulus was applied. A multiple comparison post hoc test showed that there were significant differences ($p<0.001$) between all of the levels of wetness, apart from between 20 μl vs. 40 μl ($t=1.819$, $p>0.05$). Ratings were more variable at lower levels of wetness (20 and 40 μl) and less variable at higher levels (80 and 160 μl); this can be seen in the differences in the length of box-and-whisker plots between the minimum and maximum ratings for each wetness level (Figure 1A).

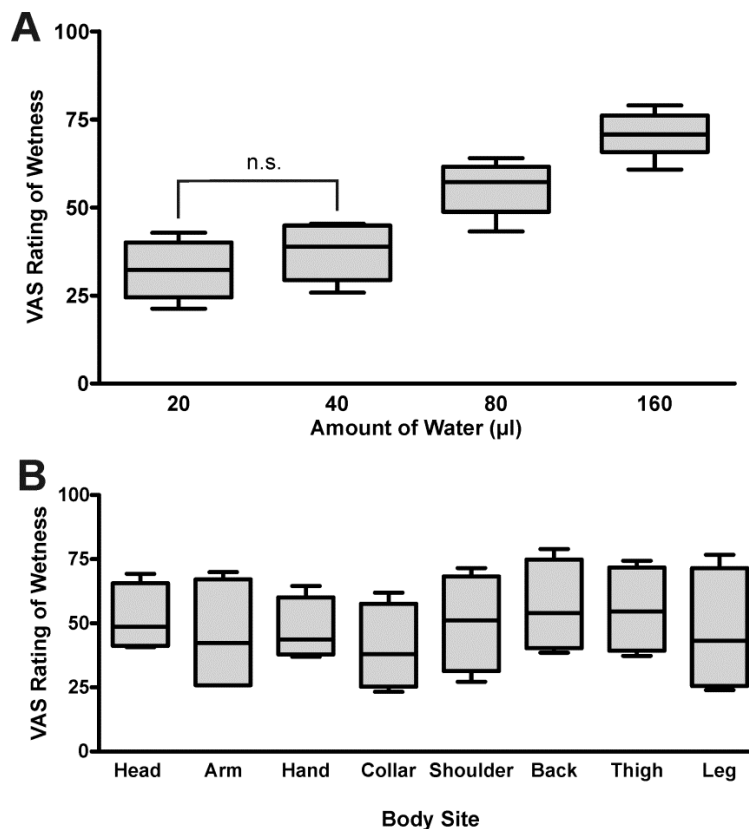


Figure 1: Ratings for wetness over all the participants averaged over (A) wetness level and (B) body site. In (A), the average ratings of wetness are shown for each level of wetness. There was no significant (n.s.) difference between the ratings for 20 and 40 μl , however all other combinations of wetness level were significantly different ($p<0.001$). In (B) the average ratings for wetness are shown per body site. There was no significant main effect of body site. Both graphs show the minimum-to-maximum average ratings in the box and the median value as a line in the middle of the box, with standard error bars. The high variability in the ratings in Figure 1B is due to the averaging over the highly differently rated wetness levels.

Figure 1B shows the participants' ratings averaged over body site and collapsed over the wetness levels. One of the aims of the present study was to determine whether certain body sites were more sensitive to wetness than others. No significant main effect for body site was found ($F=1.64_{(7, 28)}$, $p=0.102$). In general, the collar area was rated as generally lower on wetness, and the lower back and thigh were rated higher than other body parts for wetness (see Figures 1B and 2). The interaction between wetness level and body site was also explored. Figure 2 details the average ratings per wetness level per body site, however, no significant main interaction was found ($F=0.35_{(21, 84)}$, $p=0.996$) and there were no significant interactions between the wetness level and body site.

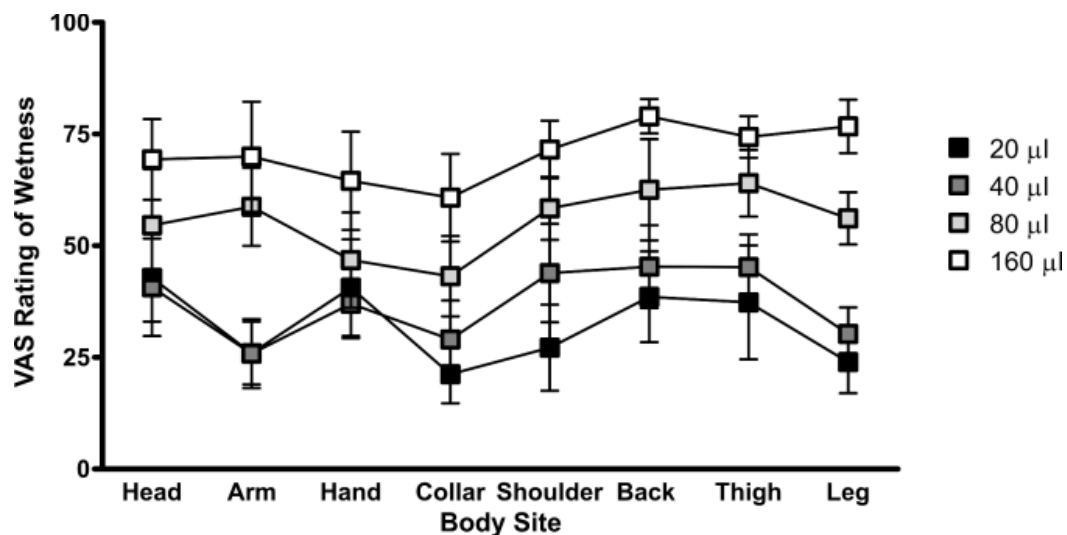


Figure 2: Averages of wetness ratings for all body sites over all levels of wetness. This shows the average ratings for all participants, with standard error bars. There were no significant interactions between wetness level and body site.

Discussion

The present study emphasises the importance of understanding the interaction between the peripheral and central nervous system. Stimulation of the skin by the application of different levels of wetted cloth was perceived through changes detected by pressure receptors (the touch of the wetted cloth) and temperature receptors (from contact of the wetted cloth and the evaporation of residual water from the skin). The results demonstrate that this is a very sensitive system, as participants readily discriminated between very small amounts of wetness. However, there were no significant differences across body sites for wetness perception. Sensitivity to wetness was not increased on the glabrous skin of the palm, which has a much higher density of

myelinated mechanoreceptors, exemplified in two-point discrimination tests as increased discriminatory abilities [37]. This implies that wetness perception was not directly related to a certain type of tactile receptor density. Differences in tactile receptor type and density may nevertheless contribute to the encoding of wetness, however in the present study the tactile stimulus was not difficult to detect. In situations where light forces or minimal duration of tactile contact are used, differences may be found between wetness sensing at glabrous and hairy skin sites, due to the high precision of mechanoreceptive information from glabrous skin that may capture small differences in tactile contact.

In comparison to the distribution of afferents for mechanosensation, the temperature sensing system has a more uniform distribution across the skin, although there are many more receptors for cool sensing [1, 21]. Most studies on thermal perception have been conducted in patients, although studies on healthy adults have shown that the foot is less sensitive in thermal threshold tests than the arm or hand [12, 13, 26]. Less is known on how thermal perception thresholds differ across the whole body. To investigate how cool detection varied across many body sites, we compared data from two sources: a study by Heldestad and Nordh [13] and from reference values in the TSA-II (Medoc, Israel) thermal sensory testing device database. Data from these showed that the detection of cooling occurred at a thermal change of $\sim 1^{\circ}\text{C}$ for most skin sites (e.g. face, neck, upper arm, mid-arm and palm), with lower detection temperatures on the mid-leg (requiring a 2°C change). Furthermore, the upper body, and more proximal skin sites (including the thigh), appeared to be more sensitive to cool than distal sites on the lower half of the body [13]. The present study investigated many different body sites and there were no significant differences in the distribution of wetness perception, although the more proximally located abdomen and thigh may be more sensitive to cooling than other sites. From comparing these wetness and cool sensing data, both appear to show largely similar sensitivities across the body. This suggests that in the present study, the main influence for the perception of wetness came from cool thermoreception and that this has little variation across the body.

At the lowest wetness levels, it was more difficult to judge the wetness of the fabric samples and the ratings were more variable: there was no significant difference for levels of wetness in the ratings between 20 and 40 μl water. From this, there may be a level of wetness that is difficult to discriminate and/or not readily noticed. It is likely that this is signalled by thermoreception, as the participants were able to feel the tactile pressure input, which did not change. Furthermore, relating to the two ways in which thermoreception occurred in the experiment (change in

temperature of the skin on contact and through evaporation), the results point to evaporation as being most important in wetness perception. As the temperature of the stimulus was the same throughout the experiment, we conclude that the difference in the perception of the level of wetness was due to differences in the residual water left on the skin, which evaporated at slightly different rates. These small differences in evaporation rate may be sensed by faster-conducting cool A δ afferents and to some extent a decrease in the firing of warm unmyelinated afferents.

If the skin is saturated with water, evaporation may play a lesser role and the perception will be more limited to the changes in touch coupled with a direct change in temperature. Furthermore, if the liquid contacting the skin is at the same temperature, it may become difficult to perceive wetness as there would only be a change felt in the touch somatosensory modality. However, in everyday life, the senses rarely act alone. The perception of wetness is primarily detected by somatosensory input; however the other senses can play a role in the mediation of the sensation. For example, seeing the input (e.g. the observation that a material is wet) may make the decision about wetness perception much quicker (i.e. you may be able to see if the material is wet). Also, auditory input has been shown to influence tactile perception: previous studies have highlighted the cross-modal influence of audition on somatosensation through attenuating sounds while examining surfaces to change the perception of wetness/dryness and roughness/smoothness of the surface [11, 14].

Afferents relating to touch project to the contralateral SI and secondary somatosensory cortex (SII), but also to the posterior insula [19, 24]. Innocuous thermal stimuli activate the insula cortex, whereas noxious thermal stimuli additionally activate SII [7, 10, 18]. Specifically, these studies have demonstrated bilateral posterior insula activation to innocuous cold stimuli. From these findings, the integration of afferent inputs from mechano- and thermoreceptors, which lead to the perception of wetness, may be due to the convergence of these inputs in the posterior insula, although it is also possible that a network of cortical areas are involved, including the insula, SI and SII and also more frontal areas associated with the more complex processing of somatosensory stimuli [27, 28]. The perception of wetness has implications for everyday situations, for example, it is linked to the detection of sweating and comfort in wearing clothes. People who need to wear protective clothing during physical work (e.g. fire-fighters) may benefit from clothes designed to take into account the neurophysiology of the perception of wetness to improve comfort in strenuous work conditions [23, 38]. Further studies will investigate how touch and temperature combine to determine wetness perception, such as testing different liquids (e.g.

ethanol, which evaporates faster than water) and also the perception of water at different temperatures. Future directions for gaining a better insight into the limits of wetness detection will also include psychophysical tests on the 'just-detectable' level of wetness and investigating the sensitivity of wetness detection to the actual volume of water applied to the skin.

Conclusions

The present study demonstrates that low levels of wetness can be perceived and the amount of wetness can be rated accurately, even though there are no dedicated wetness receptors in the skin. From the results, the differences in the perception of wetness did not relate directly to mechanoreceptor type or density, but were more related to thermoreception. Nevertheless, it is likely that the combination of all touch and temperature receptors activated at a specific skin site send information to the central nervous system where this input is integrated as a 'touch blend' leading to the perception of wetness. From these results, we emphasize the importance of understanding how the peripheral and central nervous system interact to generate complex somatic perceptions from more basic (temperature and touch) sensations.

References

- [1] E.A. Arens, H. Zhang, The Skin's Role in Human Thermoregulation and Comfort, in: N. Pan, P. Gibson (Eds.), *Thermal and Moisture Transport in Fibrous Materials*, Woodhead Publishing Ltd, Cambridge, 2006, pp. 560-602.
- [2] I.M. Bentley, The Synthetic Experiment, *Am. J. Psychol.* 11 (1900) 405-425.
- [3] M. Campero, J. Serra, H. Bostock, J.L. Ochoa, Slowly conducting afferents activated by innocuous low temperature in human skin, *J. Physiol.* 535 (2001) 855-865.
- [4] M. Campero, T.K. Baumann, H. Bostock, J.L. Ochoa, Human cutaneous C fibres activated by cooling, heating and menthol, *J. Physiol.* 587(2009) 5633-5652.
- [5] M. Campero, H. Bostock, Unmyelinated afferents in human skin and their responsiveness to low temperature, *Neurosci. Lett.* 470 (2010) 188-192.
- [6] D. Claus, M.J. Hilz, I. Hummer, B. Neundörfer, Methods of measurement of thermal thresholds, *Acta. Neurol. Scand.* 76 (1987) 288-296.
- [7] A.D. Craig, K. Chen, D. Bandy, E.M. Reiman, Thermosensory activation of insular cortex, *Nat. Neurosci.* 3 (2000) 184-190.
- [8] I. Darian-Smith, K.O. Johnson, R. Dykes, "Cold" fiber population innervating palmar and digital skin of the monkey: responses to cooling pulses, *J. Neurophysiol.* 36 (1973) 325-346.

- [9] I. Darian-Smith, K.O. Johnson, C. LaMotte, Y. Shigenaga, P. Kenins, P. Champness, Warm fibers innervating palmar and digital skin of the monkey: responses to thermal stimuli, *J. Neurophysiol.* 42 (1979) 1297-1315.
- [10] K.D. Davis, C.L. Kwan, A.P. Crawley, D.J. Mikulis, Functional MRI study of thalamic and cortical activations evoked by cutaneous heat, cold, and tactile stimuli, *J. Neurophysiol.* 80 (1998) 1533-1546.
- [11] S. Guest, C. Catmur, D. Lloyd, C. Spence, Audiotactile interactions in roughness perception, *Exp. Brain Res.* 146 (2002) 161-171.
- [12] L.G. Hagander, H.A. Midani, M.A. Kuskowski, G.J.P. Parry, Quantitative sensory testing: effect of site and skin temperature on thermal thresholds, *Clin. Neurophysiol.* 111 (2000) 17-22.
- [13] V. Heldestad, E. Nordh, Quantitative sensory testing: reference data with the 'method-of-limits' at eight body regions, in: V. Heldestad, Methodological aspects and usefulness of Quantitative Sensory Testing in early small fiber polyneuropathy, thesis from Umeå University, Sweden, 2011, Chapter II.
- [14] V. Jousmäki, R. Hari, Parchment-skin illusion: sound-biased touch, *Curr. Biol.* 8 (1998) R190.
- [15] F. Konietzny, H. Hensel, Letters and notes: Warm fiber activity in human skin nerves, *Pflügers Arch.* 359 (1975) 265-267.
- [16] E.A. Lumpkin, M.J. Caterina, Mechanisms of sensory transduction in the skin, *Nature* 445 (2007) 858-865.
- [17] V.G. Macefield, Physiological characteristics of low-threshold mechanoreceptors in joints, muscle and skin in human subjects, *Clin. Exp. Pharmacol. Physiol.* 32 (2005) 135-144.
- [18] C. Maihöfner, M. Kaltenhäuser, B. Neundörfer, E. Lang, Temporo-spatial analysis of cortical activation by phasic innocuous and noxious cold stimuli--a magnetoencephalographic study, *Pain* 100 (2002) 281-290.
- [19] F. McGlone, E.F. Kelly, M. Trulsson, S.T. Francis, G. Westling, R. Bowtell, Functional neuroimaging studies of human somatosensory cortex, *Behav. Brain Res.* 135 (2002) 147-158.
- [20] A. Mehrabyan, S. Guest, G. Essick, F. McGlone, Tactile and thermal detection thresholds of the scalp skin, *Somatosens. Mot. Res.* 28 (2011) 31-47.
- [21] U. Norrsell, S. Finger, C. Lajonchere, Cutaneous sensory spots and the "law of specific nerve energies": history and development of ideas, *Brain Res. Bull.* 48 (1999) 457-465.
- [22] H. Olausson, J. Wessberg, I. Morrison, F. McGlone, A. Vallbo A. The neurophysiology of unmyelinated tactile afferents, *Neurosci. Biobehav. Rev.* 34 (2010) 185-191.
- [23] T. Ohnaka, Y. Tochihara, T. Muramatsu, Physiological strains in hot-humid conditions while wearing disposable protective clothing commonly used by the asbestos removal industry, *Ergonomics* 36 (1993) 1241-1250.

- [24] H. Onishi, M. Oyama, T. Soma, M. Kubo, H. Kirimoto, H. Murakami, S. Kameyama, Neuromagnetic activation of primary and secondary somatosensory cortex following tactile-on and tactile-off stimulation, *Clin. Neurophysiol.* 121 (2010) 588-593.
- [25] W. Penfield, T. Rasmussen, *The Cerebral Cortex of Man*, Macmillan, New York, 1950.
- [26] R. Rolke, R. Baron, C. Maier, T.R. Tölle, R.D. Treede, A. Beyer, A. Binder, N. Birbaumer, F. Birklein, I.C. Bötefür, S. Braune, H. Flor, V. Häge, R. Klug, G.B. Landwehrmeyer, W. Magerl, C. Maihöfner, C. Rolko, C. Schaub, A. Scherens, T. Sprenger, M. Valet, B. Wasserka, Quantitative sensory testing in the German Research Network on Neuropathic Pain (DFNS): standardized protocol and reference values, *Pain* 123 (2006) 231-243.
- [27] E.T. Rolls, The affective and cognitive processing of touch, oral texture, and temperature in the brain, *Neurosci. Biobehav. Rev.* 34 (2010) 237-245.
- [28] E.T. Rolls, J. O'Doherty, M.L. Kringelbach, S. Francis, R. Bowtell, F. McGlone, Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices, *Cereb. Cortex* 13 (2003) 308-317.
- [29] R.J. Schepers, M. Ringkamp, Thermoreceptors and thermosensitive afferents, *Neurosci. Biobehav. Rev.* 33 (2009) 205-212.
- [30] A.H. Sullivan, The perceptions of liquidity, semi-liquidity and solidity, *Am. J. Psychol.* 34 (19023) 531-541.
- [31] M.M. Sweeney, D.H. Branson, Sensorial comfort. Part I: a psychophysical method for assessing moisture sensation in clothing, *Textile Res. Journal* 60 (1990a) 371-377.
- [32] M.M. Sweeney, D.H. Branson, Sensorial comfort. Part II. A magnitude estimation approach for assessing moisture sensation, *Textile Res. Journal* 60 (1990b) 447-452.
- [33] A.B. Vallbo, R.S. Johansson, Properties of cutaneous mechanoreceptors in the human hand related to touch sensation, *Hum. Neurobiol.* 3 (1984) 3-14.
- [34] A. Vallbo, H. Olsson, J. Wessberg, U. Norrskell, A system of unmyelinated afferents for innocuous mechanoreception in the human skin, *Brain Res.* 628 (1993) 301-304.
- [35] A.B. Vallbo, H. Olsson, J. Wessberg, N. Kakuda, Receptive field characteristics of tactile units with myelinated afferents in hairy skin of human subjects, *J. Physiol.* 483 (1995) 783-795.
- [36] A.B. Vallbo, H. Olsson, J. Wessberg, Unmyelinated afferents constitute a second system coding tactile stimuli of the human hairy skin, *J. Neurophysiol.* 81 (1999) 2753-2763.
- [37] S. Weinstein, Intensive and extensive aspects of tactile sensitivity as a function of body part, sex, and laterality, in: D. Kenshalo (Ed.), *The Skin Senses*, Charles C. Thomas, Springfield, IL, 1968, pp. 195-222.
- [38] M.K. White, M. Vercruyssen, T.K. Hodous, Work tolerance and subjective responses to wearing protective clothing and respirators during physical work, *Ergonomics* 32 (1989) 1111-1123.