


RESEARCH PAPER

Ageing reduces skin wetness sensitivity across the body

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Abstract

Humans use sensory integration mechanisms to sense skin wetness based on thermal and mechanical cues. Ageing impairs the skin's thermal and tactile sensitivity, yet we lack evidence on whether wetness sensing also changes with ageing. We mapped local skin wetness and temperature sensitivity in response to cold-, neutral- and warm-wet stimuli applied to the forehead, neck, lower back, dorsal foot, index finger and thumb, in 10 Younger (22.4 ± 1.1 years) and 10 Older (58.2 ± 5.1 years) males. We measured local skin temperature and conductance (i.e., a marker of hydration status) at the tested sites, to establish the role of skin's thermal and mechanical parameters in ageing-induced changes in wetness sensing. Irrespective of body site, Older reported overall lower wetness perceptions than Younger across all wet-stimulus temperatures (mean difference: -14.6 mm; 95% CI: $-4.3, -24.9$; $P = 0.008$; $\sim 15\%$ difference). When considering regional wetness sensitivity, the effect of ageing was more pronounced in response to the cold-wet stimulus over the lower back (mean difference Older vs. Younger: -36.8 mm; 95% CI: $-68.4, -5.2$; $P = 0.014$; $\sim 37\%$ difference) and dorsal foot (mean difference: -37.1 mm; 95% CI: $-68.7, -5.5$; $P = 0.013$; $\sim 37\%$ difference). We found no differences between age groups on overall thermal sensations ($P = 0.744$) nor local skin temperature ($P = 0.372$); however, we found that Older presented overall lower skin conductance than Younger (mean difference: $-1.56 \mu\text{S}$; 95% CI: $-0.49, -2.62$; $P = 0.005$), which corresponded to an $\sim 78\%$ reduction in skin hydration. We conclude that skin wetness sensing decreases with ageing primarily due to age-induced changes in skin mechanics and tactile sensitivity.

KEYWORDS

ageing, body temperature regulation, skin, thermoreceptors, wetness

1 | INTRODUCTION

The perception of skin wetness is a fundamental sensory function for humans (Filingeri et al., 2015a) that enables the surrounding environment to be experienced (Filingeri, 2015) as well as objects that encounter the skin such as clothing (Filingeri et al., 2015a). Furthermore, the experience of sweat-induced skin wetness is a well-

known trigger of thermal discomfort (Gagge et al., 1967) and a key contributor to thermoregulatory behaviours (Vargas et al., 2018). In the apparent absence of a putative skin hygroreceptor, humans have developed alternative sensory integration mechanisms to sense skin wetness (Filingeri et al., 2014b), which are underpinned by thermal sensory cues triggered by conductive and evaporative heat transfer in the presence of moisture on the skin (Filingeri et al., 2014a,b, 2015a),

in combination with mechanical cues arising from the movement of moisture across the skin (Filingeri et al., 2014a,c, 2015b).

Ageing is a well-known individual factor affecting the thermal and tactile sensitivity of the skin (Decorps et al., 2014; Guergova & Dufour, 2011), yet to date we lack any empirical evidence on whether wetness sensing also changes with ageing. This is surprising considering that the effects of ageing on thermal and tactile transduction processes, both of which underlie skin wetness perception, have been widely investigated (Decorps et al., 2014; Guergova & Dufour, 2011). For example, it has been repeatedly reported that, when compared to younger adults, the elderly present both greater warm and cold thermal detection thresholds over the hands and feet (Huang et al., 2010; Kenshalo, 1986), as well as a lower magnitude of estimation of thermal sensation from suprathreshold stimuli (Schellen et al., 2010), both of which denote an ageing-induced reduction in skin thermal sensitivity. Age-related differences in thermal sensation have been reported to be non-uniform over the body, with distal regions such as the extremities being more affected than proximal regions such as the forehead (Inoue et al., 2016; Tochihiro et al., 2011). The discriminative aspects of tactile function are also known to decline with age, with the elderly presenting a reduced ability to detect light touch (Bruce, 1980; Thornbury & Mistretta, 1981) and vibrations at different frequencies (Goble et al., 1996; Kenshalo, 1986), as well as the direction of movement (Olausson et al., 1997) and the distance between spatial features across the skin (Dinse et al., 2006; Stevens, 1992; Stevens & Patterson, 1995). While age-induced impairments in thermal and tactile sensitivity develop progressively across the lifespan (Decorps et al., 2014; Guergova & Dufour, 2011), these become more apparent around 60 years of age, likely as a result of changes in the functional (e.g., thermoregulatory) and structural (e.g., changes in dermal collagen) properties of the skin, and of degeneration in the peripheral and central nervous systems (Foster et al., 1976; Verdù et al., 2000; Wickremaratchi & Llewelyn, 2006; Skedung et al., 2018).

Aside from age-induced changes in thermo-tactile sensing, ageing also induces changes in the biophysical properties of the skin, amongst which is a reduction in skin hydration (Verrillo et al., 1998). Changes in skin hydration can alter skin mechanics, and it has been previously reported that variations in the hydration status of the skin can have profound effects on magnitude estimation of roughness perception (Verrillo et al., 1998). Yet, the potential biophysical role of age-induced variations in skin hydration on skin wetness sensing in younger and older adults remains to be established.

Considering the evidence above and the importance of thermal and tactile cues for skin wetness sensing, it would be reasonable to hypothesize that wetness sensing may also change with ageing. Increasing our fundamental understanding of how wetness sensing changes with ageing has important implications for better understanding age-related declines in human thermoregulatory behaviours and thermal comfort (Soebarto et al., 2019). This fundamental knowledge could inform the development of thermo-protective strategies and wearables such as clothing, which take into account the thermal needs and sensory status of older people, in order to optimize their comfort and resilience to hot and cold environmental exposures (Terrien et al., 2011).

New Findings

- **What is the central question of this study?**

Ageing impairs the skin's thermal and tactile sensitivity: does ageing also induce loss of skin wetness sensitivity?

- **What is the main finding and its importance?**

Older adults show an average 15% loss of skin wetness sensitivity, with this sensory deficit being mediated by a combination of reductions in skin's tactile sensing and hydration status. These findings increase knowledge of wetness sensing mechanisms across the lifespan.

The aim of this study was therefore to determine whether younger and older, otherwise healthy individuals differ in their ability to sense warm, neutral and cold wetness across both proximal and distal body regions. We hypothesized that older adults would present reductions in skin wetness sensitivity, which will be more pronounced across distal body regions such as the foot. Furthermore, we hypothesized that reduced wetness sensitivity in older adults may be underlain by differences in the skin's thermo-tactile sensitivity, as well as its biophysical status, between younger and older adults.

2 | METHODS

2.1 | Ethical approval

The testing procedure and the conditions were explained to each participant and they all gave written informed consent for participation. The study was approved by the Loughborough University Ethics Sub-Committee for Human Participants (Ref. no. R18-P083), as well as by the University of Trieste Ethics Committee (Ref. 068_2020H #COVID19#), and testing procedures were in accordance with the *Declaration of Helsinki* (except for registration in a database). All testing took place at Loughborough (UK) across a 4-week testing period between February and March 2020, and in Trieste (Italy) across a 2-week period between February and March 2021.

2.2 | Participants

We performed an a priori sample size calculation based on previously published data (Valenza et al., 2019), using an effect size corresponding to a $15 \pm 8\%$ (mean \pm SD) difference in wetness perception between groups. This value is equivalent to ~ 1.5 cm on the visual analogue scale (VAS) used for wetness scoring, and was considered a meaningful effect size to infer the presence of differences in wetness perception between groups. Such a choice was also motivated by the desire to ensure that any group difference would be much greater than any bias introduced

by measurements errors. We have previously estimated that our experimental procedures can carry measurements errors that could potentially induce up to a ~5% change in perceptual responses (see Valenza et al., 2019); hence, adopting an effect size three times greater than that potentially induced by our measurement errors was deemed appropriate and sufficient for the purpose of this study. The resulting effect size $f = 0.93$, combined with an α -value of 0.05 and a β (power)-value of 0.8, determined a minimum sample of eight participants per group. Accordingly, 10 younger males (Younger; 22.4 ± 1.1 years; age range: 21–24 years; 184.3 ± 4.8 cm; 83.7 ± 12.4 kg) and 10 older males (Older; 58.2 ± 5.1 years; age range: 51–65 years; 177.6 ± 7.3 cm; 78.2 ± 14.5 kg), with no history of cardiovascular, metabolic, neurological and skin-related conditions (e.g., eczema), were recruited from the Loughborough and Trieste areas to take part in the present study. Further inclusion criteria were being of White European ethnicity and non-smoker/vaper. As the independent effect of female hormones and menstrual cycle on wetness sensing is yet to be established, the current investigation focused on a male population only, to minimize biases arising from the interactions between sex, age and hormonal status. Participants were instructed to refrain from (i) performing strenuous exercise in the 48 h preceding testing; (ii) consuming alcohol in the 24 h preceding testing; and (iii) consuming caffeine or food in the 3 h preceding testing. They were also instructed to maintain their normal hydration practices.

2.3 | Experimental design

We used a single-blind psychophysical approach based on a well-established quantitative sensory protocol of skin wetness sensing that we have developed (Filingeri et al., 2014b) to map group differences in regional wetness sensitivity at rest in a thermoneutral environment (ambient temperature: 22.7°C; relative humidity: 37.5%).

All participants took part in one experimental session, during which we performed the same quantitative sensory test at rest. The quantitative sensory test that we used consisted of participants reporting the perceived magnitude of local thermal and wetness perceptions arising from the short-duration (i.e., 5 s) static application of a cold-wet (i.e., 5°C below local skin temperature (T_{sk})), neutral-wet (i.e., equal temperature to local T_{sk}) and warm-wet (i.e., 5°C above local T_{sk}) hand-held temperature-controllable probe (surface area: 1.32 cm², water content: 0.8 ml). Participants reported the magnitude of their local perceptions on two digital VAS for thermal sensation (length 200 mm; anchor points: 0, very cold; 100, neutral; 200, very hot) and wetness perception (length: 100 mm; anchor points: 0, dry; 100, completely wet). This approach allowed us to determine both the independent and combined role of thermal and tactile sensory cues on the resulting wetness perception. This was necessary to establish the potential role of changes in thermo-tactile sensitivity between younger and older adults, which could underlie differences in wetness perception between groups. We used stimuli whose temperatures were relative to the local T_{sk} pre-stimulation (i.e., $\pm 5^\circ\text{C}$ or equal to local T_{sk}) to account for the expected body location-related changes in local

T_{sk} . In this way, we ensured that the same relative thermal stimulus would be applied because the difference between the temperature of a stimulus and that of the skin is an important determinant of the magnitude of a resulting thermal sensation (i.e., the greater the difference, the more intense the sensation) (Darian-Smith, 1984).

We mapped thermal and wetness sensitivity at six different locations over the body: the centre of the forehead (i.e., 5 cm above the pupillary line), the posterior neck (i.e., over the process spinous of cervical 4), the lower lateral back (i.e., over the posterior superior iliac crest), the dorsal foot (i.e., midpoint between the second and third metatarsal joints), the centre of the thumb pad distal phalanx on the dominant hand and the centre of the index pad distal phalanx on the dominant hand. We chose those body regions because (i) they include both proximal and distal regions; (ii) they are generally reported to trigger wet-induced thermal discomfort (e.g., lower back) (Fukazawa & Havenith, 2009); and (iii) there is limited evidence on their intrinsic wetness sensitivity in older males.

To characterize age-related changes in the skin's biophysical status, which could also modulate wetness sensing, we estimated local skin hydration for each age group by means of skin conductance measurements prior to the application of the wet stimuli. Conductance measurements provide for a non-invasive marker of skin hydration of the skin's stratum corneum (Tagami, 2014). Along with local skin conductance, we measured regional variations in local T_{sk} in both groups, to further characterize the biophysical status of aged skin (Verrillo et al., 1998).

As per our previous studies (Filingeri et al., 2014a,b, 2018), all participants were blinded to the nature and application of the stimuli to limit expectation biases, and they were only informed about the location of the stimulation. Furthermore, participants underwent a systematic familiarization and calibration to the testing procedures and perceptual scales prior to testing (Valenza et al., 2019). Participants wore a T-shirt and running shorts during all testing. The same investigator performed all testing, to limit any inter-individual variability arising from the procedures carried out.

2.4 | Experimental protocol

Participants arrived at the laboratory on testing days and underwent preliminary measurements and preparation. They changed into shorts before we assessed their semi-nude body mass on a precision scale (Model 874; Seca GmbH, Hamburg, Germany) and their height on a wall stadiometer. Six skin thermistors (Grant, Cambridge, UK) were taped to locations on the left side of the body (i.e., cheek, upper chest, outer mid lower arm, hand dorsum, anterior thigh and lower lateral back) to record local T_{sk} for the estimation of mean T_{sk} according to the equation (Lund & Gisolfi, 1974):

$$\begin{aligned} \text{mean } T_{sk} = & (\text{cheek } T_{sk} \times 0.14) + (\text{upper chest } T_{sk} \times 0.19) \\ & + (\text{outer mid lower arm } T_{sk} \times 0.11) + (\text{hand dorsum } T_{sk} \times 0.05) \\ & + (\text{anterior thigh } T_{sk} \times 0.32) + (\text{lower lateral back } T_{sk} \times 0.19) \end{aligned}$$

Local T_{sk} was recorded at 2 Hz via a dedicated data acquisition system (USB-Temp; MCCdaq, Norton, MA, USA) and custom-written software (DASYLab; MCCdaq). We used a washable marker to mark the skin sites to be stimulated, and we gently shaved hairy sites to limit any insulative effect of hairiness on heat transfer during the application of the stimuli where needed. Following on this preparation, participants underwent 20 min of resting on a chair to adjust to the environmental conditions. During this time, participants were familiarized with the experimental procedures, and calibrated to the VAS. Calibration procedures consisted of the following. Six stimuli varying in temperature and wetness (i.e., 0.8 ml of water, or dry) were applied to the volar surface of both forearms (i.e., midpoint between wrist and antecubital fossa) in a randomized order, and participants were instructed to associate each stimulus to a specific descriptor on the thermal scale. The stimuli and related descriptors were (i) wet stimulus, 10°C above local skin temperature – scale descriptor: very hot; (ii) wet stimulus, 5°C above local skin temperature – scale descriptor: midpoint between neutral and very hot; (iii) wet stimulus, equal temperature to local skin temperature – scale descriptor: neutral; (iv) dry stimulus, equal temperature to local skin temperature – scale descriptor: neutral; (v) wet stimulus, 5°C below local skin temperature – scale descriptor: midpoint between neutral and very cold; and (vi) wet stimulus, 10°C below local skin temperature – scale descriptor: very cold. During each of the six stimulus applications, participants were instructed to freely determine the level of wetness experienced on the wetness VAS. This procedure ensured that all participants had comparable experiences of the different stimuli and related perceptual anchor points to be used during testing. The forearm was chosen as a 'neutral' calibration site to avoid any priming, given that this region was not going to be tested during the mapping protocol.

Upon termination of calibration, recordings of local T_{sk} was started and continued throughout the testing session. Furthermore, spot measurements of tympanic temperature (T_{tym}) (ThermoScan IRT 6520; Braun, Kronberg, Germany) were taken at this stage in triplicate and used as an indicator of core temperature.

At this point, the quantitative sensory test commenced, lasting 20 min. Depending on the body region to be tested, we first measured local skin conductance of the testing site using a custom-made skin conductance meter, which was applied onto the skin for 5 s, until a steady state conductance reading (μS) was reached. Second, we recorded the local T_{sk} with an infrared thermometer (Spot IR Thermometer TG54; FLIR Systems, Wilsonville, OR, USA). We then determined the temperature of the first wet stimulus (e.g., cold wet, 5°C below local skin temperature) and applied a 100% cotton fabric on the hand-held, round thermal probe (surface area: 1.32 cm²; NTE-2A; Physitemp Instruments LLC, Clifton, NJ, USA), which was then wetted with a pipettor with 0.8 ml of water to ensure its full saturation. Following a verbal warning, the wet stimulus was applied statically on the participant's skin for 5 s, during which the participant was encouraged to rate their very first thermal and wetness perception. Application pressure was not measured but was controlled to be sufficient to ensure full contact, at the same time not resulting in pronounced skin

indentation. Upon acquisition of the perceptual rating, we removed the stimulus, gently dried the skin, and then repeated the same procedure for the other stimuli (e.g., neutral and warm-wet) on the same skin site, before proceeding to the next skin region until completion of the testing session. The order of testing region was counter-balanced between participants and the order of stimuli (e.g., warm vs. neutral vs. cold wet) was counter-balanced between and within participants.

2.5 | Statistical analysis

First, we evaluated differences in thermal status between groups, by analysing the independent effect of age (two levels: Younger vs. Older) on core temperature (T_{core}) and mean T_{sk} , with independent Student's *t*-tests. The T_{core} and mean T_{sk} data used for this analysis were those collected following the 20-min stabilization phase and prior to sensory testing, and were deemed appropriate to provide an indication of steady-state thermal state at the start of the quantitative sensory test. (Note, for mean T_{sk} this was the 60-s average of the last minute of the 20-min stabilization phase.) Furthermore we evaluated differences in the skin biophysical status between age groups, by analysing the independent and interactive effect of age (two levels: Younger vs. Older) and body region (six levels) on baseline local T_{sk} (i.e., prior to application of wet stimuli) and skin conductance, with two-way mixed ANOVAs.

Second, we evaluated differences in wetness perception across the whole body between groups, by analysing the independent and interactive effect of age (two levels: Younger vs. Older) and stimulus temperature (three levels: cold, neutral, warm) on wetness perceptions collapsed over body region (i.e., mean perception of the six regions tested for each participant), with a two-way mixed ANOVA. This analysis allowed us to establish the generalized effect of ageing on wetness sensing over the whole body, and its interaction with the stimulus temperature. Evaluating the interaction between age and stimulus temperature on wetness sensing over the whole body was particularly important, as it could provide evidence on whether basic wetness sensing mechanisms (i.e., cold-wet stimuli induce greater wetness, whereas warm-wet stimuli suppress the perception of wetness) change with age. Furthermore, we evaluated differences in thermal sensation across the whole body between groups, by analysing the independent and interactive effect of age (two levels: Younger vs. Older) and stimulus temperature (three levels: cold, neutral, warm) on thermal sensations collapsed over body region (i.e., mean perception of the six regions tested for each participant), with a two-way mixed ANOVA. This analysis allowed us to establish whether a generalized reduction in thermal sensitivity to both warmth and cold occurred between age groups.

Third, we evaluated differences in local wetness perception between groups, by analysing the independent and interactive effect of age (two levels: Younger vs. Older) and body region (six levels), separately for each stimulus (i.e., cold-wet, neutral-wet, warm-wet), on regional wetness perceptions, with a two-way mixed ANOVA. This analysis allowed us to establish whether the effect of ageing on

wetness sensing would be more evident on specific body regions and as a result of specific temperature stimuli. Furthermore, we evaluated differences in local thermal sensation between groups, by analysing the independent and interactive effect of age (two levels: Younger vs. Older) and body region (six levels) separately for each stimulus (i.e., cold-wet, neutral-wet, warm-wet) on regional thermal sensation, with a two-way mixed ANOVAs.

In the event of statistically significant main effects or interactions, *post hoc* analyses were conducted with Sidak's test. Normality testing using the Shapiro–Wilk test was performed for all datasets. Data are reported as the means, SD and 95% confidence intervals (CI). Observed power was computed using $\alpha = 0.05$. Statistical analysis was performed using Prism, version 8.0 (GraphPad Software Inc., La Jolla, CA, USA).

3 | RESULTS

3.1 | Incomplete datasets

Due to impact and constraints resulting from the COVID-19 pandemic, we were able to collect full datasets (i.e., thermoregulatory, biophysical and perceptual data) for all 10 younger participants but for only six older participants. These 16 participants were tested at Loughborough University. The remaining four older participants were tested at the University of Trieste, and we were able to collect only T_{tymp} , local T_{sk} and perceptual data, as the Trieste laboratory was not equipped with the skin conductance meter. Accordingly, the analyses of participants' skin conductance were based on $n = 10$ for Younger and $n = 6$ for Older. All other analyses were based on $n = 10$ for both groups. The experimental protocol and data collection procedures were standardized between the Loughborough and Trieste laboratories and we found no significant differences in all measures between the Older participants tested at those two testing sites.

3.2 | Participants' thermal status and skin biophysical status

Participants' T_{tymp} was significantly different between groups (mean difference: $+0.30^\circ\text{C}$; 95% CI: $+0.09, +0.51$; $P = 0.008$) with Younger presenting a higher T_{tymp} ($36.7 \pm 0.3^\circ\text{C}$) than Older ($36.4 \pm 0.1^\circ\text{C}$). Regarding mean T_{sk} , we found no statistically significant difference (mean difference: $+2.3^\circ\text{C}$; 95% CI: $-0.5, 5.0$; $P = 0.099$) between Younger ($32.7 \pm 1.4^\circ\text{C}$) and Older (mean T_{sk} : $30.4 \pm 1.4^\circ\text{C}$).

Baseline local T_{sk} varied significantly across body regions ($F_{5,70} = 13.9$; $P < 0.001$), with no differences between Younger and Older ($F_{1,14} = 0.85$; $P = 0.372$). Specifically, we observed a pattern of decrease in local T_{sk} from the forehead, to the centre of the body, to the extremities in both groups (Figure 1).

Skin conductance varied significantly as a function of age ($F_{1,68} = 8.490$; $P = 0.005$) but not of body region ($F_{1.5,20.2} = 0.69$; $P = 0.472$). Specifically, Older presented overall lower skin conductance than Younger (mean difference: $-1.56 \mu\text{S}$; 95% CI:

$-0.49, -2.62$), thereby indicating the presence of lower skin hydration across all regions tested (Figure 2). The mean value of Younger skin conductance collapsed over body region was $1.96 \pm 0.89 \mu\text{S}$, whereas the mean value of Older skin conductance collapsed over body region was $0.40 \pm 0.21 \mu\text{S}$; accordingly, the mean difference between Younger and Older overall skin conductance corresponded to $\sim 78\%$.

3.3 | Ageing effects on wetness perception and thermal sensation across the whole body

When considering wetness sensing, we found a significant effect of age ($F_{1,18} = 8.8$; $P = 0.008$) and of stimulus temperature ($F_{1.6,29.5} = 30.1$; $P < 0.0001$), but no age–stimulus interaction ($F_{2,36} = 0.2$; $P = 0.831$), on wetness perceptions collapsed over body region (Figure 3a). Specifically, Older presented with overall lower wetness perceptions than Younger across all wet stimuli temperatures (mean difference Older vs. Younger: -14.6 mm ; 95% CI: $-4.3, -24.9$; $P = 0.008$; corresponding to $\sim 15\%$ difference). Yet, both groups experienced the cold-wet stimulus as wetter than the neutral-wet (mean difference cold-wet vs. neutral-wet: $+11.9 \text{ mm}$; 95% CI: $+5.2, +18.6$; $P = 0.0005$; corresponding to $\sim 12\%$ difference), and the warm-wet (mean difference cold-wet vs. warm-wet: $+23.1 \text{ mm}$; 95% CI: $+13.8, +32.4$; $P < 0.0001$; corresponding to $\sim 23\%$ difference) (Figure 3a). All in all, these results indicated that, when considering generalized wetness sensing across the whole body, Older presented lower sensitivity than Younger across the temperature continuum tested.

When considering thermal sensing, we found a significant effect of stimulus temperature ($F_{1.6,28.8} = 109$; $P < 0.0001$), but not of age ($F_{1,18} = 0.1$; $P = 0.744$), and no age–stimulus interaction ($F_{2,36} = 0.6$; $P = 0.544$), on thermal sensations collapsed over body region (Figure 3b). Specifically, both groups experienced the cold-wet stimulus as colder than the neutral-wet (mean difference cold-wet vs. neutral-wet: -34.7 mm ; 95% CI: $-45.8, -23.6$; $P < 0.0001$), and the warm-wet stimulus as warmer than the neutral-wet (mean difference warm-wet vs. neutral-wet: $+49.6 \text{ mm}$; 95% CI: $+32.6, +66.6$; $P < 0.0001$) (Figure 3b).

3.4 | Ageing effects on local wetness perception and thermal sensation: cold-wet stimulus

When considering local cold-wetness sensing, we found a significant effect of body region ($F_{5,90} = 3.23$; $P = 0.001$), age ($F_{1,18} = 6.39$; $P = 0.021$) and of the interaction age–body region ($F_{5,90} = 2.81$; $P = 0.021$). Specifically, we found that cold-wetness sensing varied significantly across the body in both age groups, with the dominant index finger pad presenting some of the most intense wetness perceptions, whereas the dorsal foot presented some of the least intense (mean difference: $+25.9 \text{ mm}$; 95% CI: $+3.0, +48.9$; $P = 0.015$; corresponding to $\sim 26\%$ difference) (Figure 4d); yet, Older generally perceived the same cold-wet stimulus as less wet than Younger (mean difference: -16.4 mm ; 95% CI: $-30.1, -2.8$; corresponding to $\sim 16\%$

FIGURE 1 Body maps of baseline local T_{sk} . Body maps of pre-stimulation local T_{sk} in Younger ($n = 10$) and Older males ($n = 10$). Numerical data represent group means. Symbols denote statistical differences between regions at $P < 0.05$ (note: no main effect of age was found). α : different from forehead; β : different from back of neck; γ : different from lower back; δ : different from hand thumb pad; ϵ : different from index finger pad; ω : different from dorsal foot

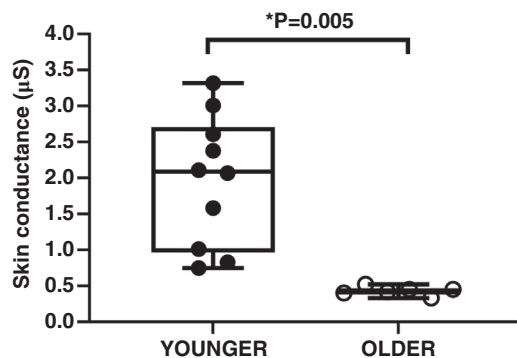
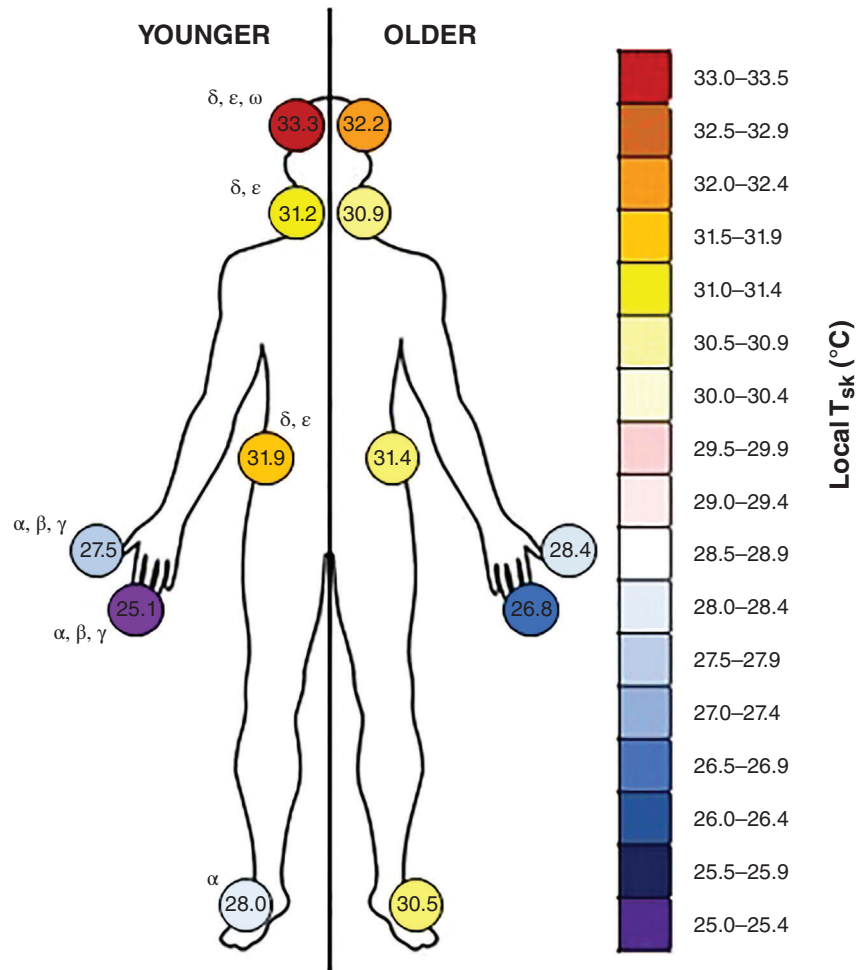


FIGURE 2 Ageing effect on skin conductance. Box and whisker plots and individual data (Younger, $n = 10$; Older, $n = 6$) for skin conductance data collapsed over body region (six sites tested). *Main effect of age ($P < 0.05$)

difference), with this ageing effect being particularly evident over the lower back (mean difference Older vs. Younger: -36.8 mm; 95% CI = $-68.4, -5.2$; $P = 0.014$; corresponding to $\sim 37\%$ difference) and dorsal foot (mean difference Older vs. Younger: -37.1 mm; 95% CI = $-68.7, -5.5$; $P = 0.013$; corresponding to $\sim 37\%$ difference) (Figure 4d).

When considering local thermal sensing, we found no main effect of age ($F_{1,18} = 0.49$; $P = 0.490$), nor of body region ($F_{3,90} = 2.3$; $P = 0.071$). However, we found a significant interaction age–body region ($F_{5,90} = 4.0$; $P = 0.002$). Specifically, we found that Older presented significantly less intense cold sensations on specific body regions, such as the forehead (mean difference Older vs. Younger: -27.8 mm; 95% CI: $-51.5, -4.1$; $P = 0.024$; corresponding to $\sim 14\%$ difference) and the dorsal foot (mean difference Older vs. Younger: -43.7 mm; 95% CI: $-77.7, -9.7$; $P = 0.015$; corresponding to $\sim 22\%$ difference) (Figure 4a).

3.5 | Ageing effects on local wetness perception and thermal sensation: neutral-wet stimulus

When considering local neutral wetness sensing, we found a significant effect of age ($F_{1,18} = 7.8$; $P = 0.012$), but not body region ($F_{5,90} = 0.61$; $P = 0.694$), nor of any interaction age–body region ($F_{5,90} = 0.49$; $P = 0.782$). Older generally perceived the same neutral wet stimulus as less wet than Younger (mean difference: -14.1 mm; 95% CI: $-24.7, -3.5$; corresponding to $\sim 14\%$ difference), with no specific regional patterns (Figure 4e).

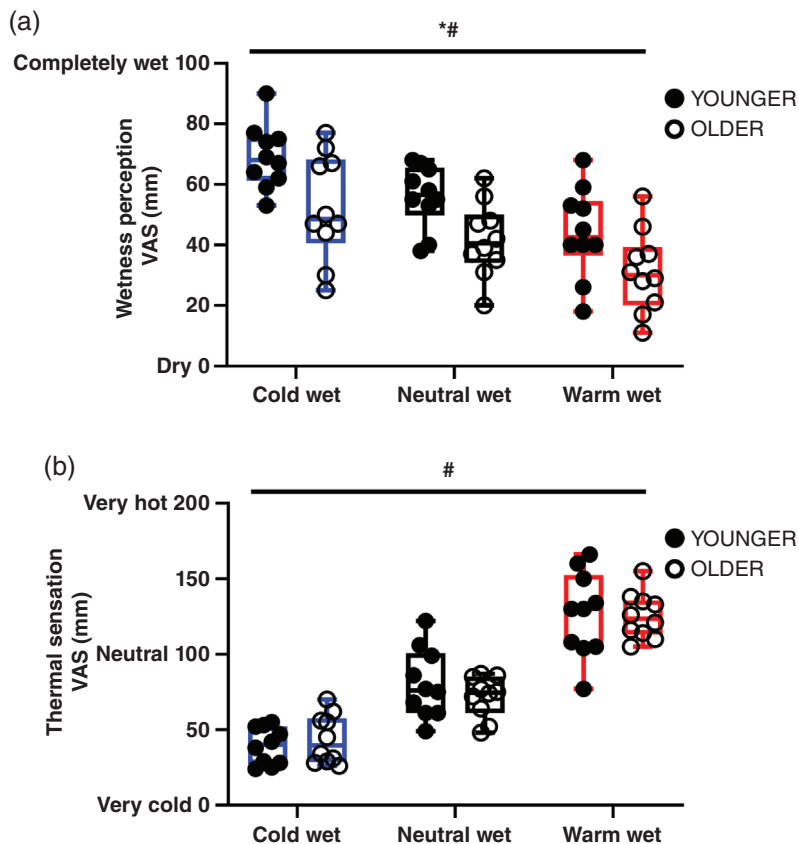


FIGURE 3 Ageing effects on wetness perception and thermal sensation across the whole body. Box and whisker plots and individual data ($n = 10$ per group) for wetness perceptions (a) and thermal sensations (b) arising from the application of the cold-wet, neutral-wet and warm-wet stimuli, in Younger and Older males. Data are collapsed over body region. *Main effect of age ($P < 0.05$); #main effect of stimulus temperature ($P < 0.05$)

When considering local thermal sensing (Figure 4b), we found no effect of age ($F_{1,18} = 1.03$; $P = 0.323$), nor body region ($F_{5,90} = 1.7$; $P = 0.141$). Although there was a trend for both groups to present slightly colder thermal sensations than the 'Neutral' descriptor located at the 100th mm of the 200-mm VAS, mean thermal sensations (collapsed over body region) for both groups were within a reasonable range from 'Neutral' (i.e., Older: 71.9 ± 5.1 mm; Younger: 80.4 ± 12.7 mm). This confirmed that the neutral-wet stimulus triggered minimal thermosensory cues.

3.6 | Ageing effects on local wetness perception and thermal sensation: warm-wet stimulus

When considering local warm-wetness sensing, we found a significant effect of body region ($F_{5,90} = 3.67$; $P = 0.004$) and age ($F_{1,18} = 4.29$; $P = 0.053$), but no interaction age–body region ($F_{5,90} = 0.77$; $P = 0.572$) (Figure 4f). Specifically, we found that warm-wetness sensing varied significantly across the body in both age groups, with the dominant index finger pad presenting some of the most intense wetness perceptions, whereas the dorsal foot presented some of the least intense (mean difference dominant index finger pad vs. dorsal foot: $+28.9$ mm; 95% CI: $+7.7, +50.2$; $P = 0.001$; corresponding to $\sim 29\%$ difference); yet Older generally perceived the same warm-wet stimulus as less wet than Younger (mean difference: -13.0 mm; 95% CI: $-26.2, +0.2$; corresponding to $\sim 13\%$ difference), with no specific regional patterns (Figure 4f).

When considering local warm thermal sensing, we found no effect of body region ($F_{3,5,63,0} = 1.70$; $P = 0.168$) nor age ($F_{1,18} = 0.01$; $P = 0.917$) (Figure 4c).

4 | DISCUSSION

The aim of this study was to determine whether younger and older, otherwise healthy, individuals differ in their ability to sense warm, neutral and cold wetness across both proximal and distal body regions. In relation to our first hypothesis, our findings indicate that older adults presented a generalized $\sim 15\%$ reduction in wetness sensitivity across all tested body regions and temperature stimuli (see Figure 3a). Interestingly, this ageing effect was more pronounced for specific body region and stimulus temperatures, such that cold-wetness sensing reached a 37% reduction in the older individuals when cold-wet stimuli were applied to both the lower back and the dorsal foot (see Figure 4d). In relation to our second hypothesis, we did not find any overarching differences in thermal sensing between the age groups; yet, we found a clear age effect on skin biophysics, such that the older individuals presented with a mean $\sim 78\%$ reduction in skin hydration across the body regions tested. Taken together, our findings indicate that older male individuals aged ~ 60 years experience loss of skin wetness sensitivity across both proximal and distal body parts, and that this sensory deficit is likely mediated by ageing-induced changes in hydration-dependent skin mechanics and tactile, but not thermal, sensitivity.

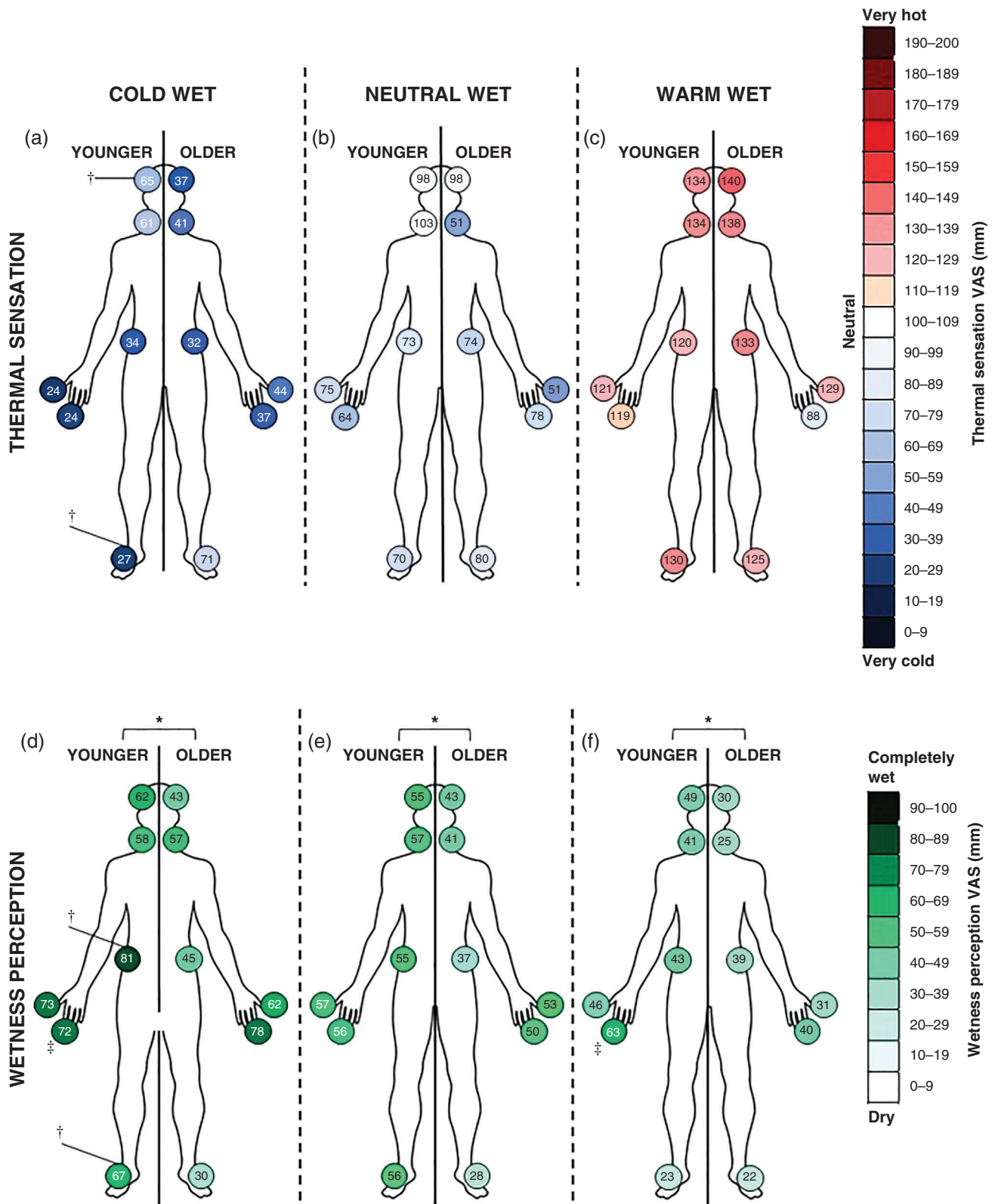


FIGURE 4 Body maps of thermal sensations and wetness perceptions in Younger and Older adults. Body maps of thermal sensations and wetness perceptions in Younger ($n = 10$) and Older males ($n = 10$) resulting from the application of the cold-wet (a, d), neutral-wet (b, e), and warm-wet stimuli (c, f). Numerical data represent group means. Symbols denote statistical differences between regions at $P < 0.05$. *Main effect of age; †interaction age \times region, whereby age groups differ at specific body regions; ‡main effect of body region, whereby index finger pad is different from dorsal foot

The first novel finding of this study is that skin wetness sensing appears to decline with ageing and across the temperature continuum of wet stimuli that the skin is likely to encounter, that is, from warm- to neutral- to cold-wet (see Figure 3a). Yet, despite this clear ageing effect, we found that older individuals retained an approach to wetness sensing that resembled that of younger individuals, which is aligned with our previously proposed neurophysiological model of skin wetness sensing (Filingeri et al., 2014b). Specifically, we found that both younger and older individuals perceived the cold-wet stimulus as wetter than the neutral- and warm-wet ones, despite all stimuli presenting the same moisture (i.e., 0.8 ml) (see Figure 3a). This perceptual behaviour is well predicted by our neurophysiological model of wetness, as we have repeatedly shown that irrespective of the physical presence of moisture on the skin, activation of cold-sensitive A-type skin thermoreceptors will trigger the neural representation of a typical wet stimulus (hence a perception of wetness), which is often associated with cooling sensations (Filingeri et al., 2014b, 2015b). Accordingly, humans are more likely to perceive cold-wet (and cold-dry) (Filingeri et al., 2013) stimuli as wetter than equally wet warm and neutral stimuli (Filingeri et al., 2014b). Our current findings clearly indicate that older individuals retain such perceptual behaviour, where cold-wet stimuli are perceived as wetter than neutral and warm wet ones; yet it appears that ageing shifts wetness sensitivity downwards (see Figure 3a). This observation may suggest that the central mechanisms that allow us to discriminate skin wetness (i.e., perceptual inference based on the neural representation of a typical wet stimulus) (Filingeri et al., 2014b) are maintained at least until ~60 years of age, and that skin wetness sensory loss with ageing may therefore occur secondary to peripheral changes to sensory transduction and skin biophysics.

With regards to skin thermo-tactile sensitivity, we know that skin wetness sensing relies on the optimal integration of thermal and tactile cues arising from the interaction of moisture on the skin, and that the relative importance of thermal versus tactile sensing changes with the wet stimulus temperature (i.e., neutral- and warm-wet sensing relies more on tactile than thermal cues than does cold-wet sensing) (Filingeri et al., 2014b). In this respect, we found that older individuals presented a lower thermal sensitivity than younger participants only during the application of the cold-wet stimulus to the forehead and dorsal foot (see Figure 4a). During the application of the neutral- and warm-wet stimulus, there were no differences in thermal sensitivity between groups, despite the older group presenting significantly lower wetness sensitivity to both these stimuli (see Figure 4e, f). This observation indicates that ageing-induced loss in peripheral cold sensing played a limited role in the observed reductions in wetness sensing in the older cohort. Indeed, had thermal sensing played a primary role in the observed reductions in wetness sensing in the older group, we would have expected the older group to also present a lower warm sensitivity; yet this was not the case. As previously mentioned, our experimental model allows us to identify the relative contribution of thermal versus tactile cues in wetness sensing. Specifically, comparison of wetness perceptions arising from the neutral-wet stimulus with those arising from cold- and warm-wet ones provides evidence on the contribution

of tactile cues, resulting from the mechanical adhesion of the wet surface to the skin in the absence of thermal cues (i.e., as the stimulus has temperature equal to the local skin temperature) (Bergmann Tiest et al., 2012), to the perception of wetness. When considering both our whole body (Figure 3a) and regional (Figure 4e) analyses, we found that wetness sensing was significantly reduced in the older group during the neutral-wet stimulation. Accordingly, we believe that this evidence is indicative of the likely contribution of an ageing-induced reduction in tactile sensing of the skin, which in turn could have led to the recorded lower wetness perceptions in the older group.

It is well known that ageing induces functional and anatomical changes to the skin that heavily impact on tactile transduction processes (Decorps et al., 2014; Guergova & Dufour, 2011). Our biophysical data clearly indicate that, when one considers relevant parameters for wetness sensing such as skin temperature and hydration status, the largest effect of ageing was evident in an ~78% reduction in the hydration of older participants' skin (see Figure 2), given that local T_{sk} did not differ between groups (see Figure 1). We know that changes in skin hydration can alter the mechanical properties of the skin, and it has been previously reported that variations in the hydration status of the skin can have profound effects on magnitude estimation of roughness perception (Verrillo et al., 1998). Skin hydration levels decrease with age (Südel et al., 2005), and this was confirmed in the current study. This reduction in skin hydration is caused by the thinning of the epidermis and dermis and by the decline in its mechanical strength. Furthermore, a decrease in the number of cutaneous blood vessels, nerve endings and connective tissues (collagen and elastin) contribute to this problem (Kottner et al., 2013). These biophysical changes reduce the ability of the skin to retain moisture, control temperature as well as sense the surrounding environment (Haroun, 2013). Consequently, dry skin is frequently associated with rough, flaky texture, which could also diminish the intensity of mechanical afferents, reducing the sensation felt by the participants (Norman, 2003). Based on this evidence, we believe it is reasonable to suggest that the large reduction in skin hydration recorded in our older participants could have played a significant role in modulating the mechanical properties of aged skin, and consequently the tactile transduction processes that would have underlain our older participants' ability to detect wet stimuli. This would have been particularly relevant during conditions of neutral- and warm-wet stimulations, as the latter scenarios are heavily reliant on tactile cues for wetness estimation (Filingeri et al., 2014b). Hence, the second novel finding of this study is that changes in wetness sensing with ageing are likely mediated by biophysical changes in skin status that impact on mechanical and tactile transduction processes important for optimal skin wetness estimation. This observation is fundamentally relevant, as it opens the way to the intriguing hypothesis that skin hydration levels can modulate local skin wetness sensing, such that an optimal level of moisture in the skin is required to provide optimal sensory inputs during interaction with moisture. This hypothesis is supported by evidence indicating that the perception of roughness varies with skin hydration levels (Verrillo et al., 1998).

4.1 | Limitations and experimental considerations

There are several limitations to the current study. First, some biophysical parameters, such as skin hydration, were collected in only some of the Older group, and therefore our analysis had lower power. Yet, the differences identified were large enough to provide confidence in the interpretation of our results. Second, our findings are limited to the effects of ageing in males, as no females were tested. As sex-related differences in wetness sensing exist (Valenza et al., 2019), future studies should consider whether ageing interacts with sex in modulating wetness sensing.

5 | CONCLUSION

We provide initial evidence that, despite retaining similar neuro-sensory mechanisms of wetness sensing to their younger counterparts, older males aged ~60 years experience a generalized loss of skin wetness sensitivity across the temperature continuum. This sensory deficit appears to be mediated by age-induced changes in skin mechanics and tactile sensitivity. Our findings increase our fundamental understanding of wetness sensing mechanisms across the lifespan, which has important implications for characterizing age-related declines in human thermoregulatory behaviours and thermal comfort. Furthermore, this fundamental knowledge could inform the development of thermo-protective strategies and wearables such as clothing which consider the thermal needs and sensory status of older people, to optimize their thermal comfort and resilience.

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COMPETING INTERESTS

The authors report no conflict of interest.

AUTHOR CONTRIBUTIONS

C.W., A.B. and D.F. conceived and designed the work. C.W., A.B.S. and K.F. acquired the data. A.V., A.B., and D.F. analysed and interpreted the data. A.V. and D.F. drafted the manuscript and all authors revised the manuscript critically for intellectual content. All authors approved the final version of the manuscript and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

DATA AVAILABILITY STATEMENT

All perceptual data supporting the results in this paper are reported as Supporting information for online publication.

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REFERENCES

- Bergmann Tiest, W. M., Kusters, N. D., Kappers, A. M. L., & Daanen, H. A. M. (2012). Haptic perception of wetness. *Acta Psychologica*, 141, 159–163. <https://doi.org/10.1016/j.actpsy.2012.07.014>
- Bruce, M. F. (1980). The relation of tactile thresholds to histology in the fingers of elderly people. *Journal of Neurology, Neurosurgery, and Psychiatry*, 43, 730–734. <https://doi.org/10.1136/jnnp.43.8.730>
- Darian-Smith, I. (1984). Thermal sensibility. In: *Handbook of physiology, Section 1, The nervous system, Vol. III, Sensory processes*, American Physiological Society (pp. 879–913). <https://onlinelibrary.wiley.com/doi/10.1002/cphy.cp010319>
- Decorps, J., Saumet, J. L., Sommer, P., Sigaud-Roussel, D., & Fromy, B. (2014). Effect of ageing on tactile transduction processes. *Ageing Research Reviews*, 13, 90–99. <https://doi.org/10.1016/j.arr.2013.12.003>
- Dinse, H. R., Kleibel, N., Kalisch, T., Ragert, P., Wilimzig, C., & Tegenthoff, M. (2006). Tactile coactivation resets age-related decline of human tactile discrimination. *Annals of Neurology*, 60, 88–94. <https://doi.org/10.1002/ana.20862>
- Filingeri, D. (2015). Humidity sensation, cockroaches, worms, and humans: Are common sensory mechanisms for hygrosensation shared across species? *Journal of Neurophysiology*, 114, 763–767. <https://doi.org/10.1152/jn.00730.2014>
- Filingeri, D., Fournet, D., Hodder, S., & Havenith, G. (2014a). Body mapping of cutaneous wetness perception across the human torso during thermo-neutral and warm environmental exposures. *Journal of Applied Physiology*, 117, 887–897. <https://doi.org/10.1152/jappphysiol.00535.2014>
- Filingeri, D., Fournet, D., Hodder, S., & Havenith, G. (2014b). Why wet feels wet? A neurophysiological model of human cutaneous wetness sensitivity. *Journal of Neurophysiology*, 112, 1457–1469. <https://doi.org/10.1152/jn.00120.2014>
- Filingeri, D., Fournet, D., Hodder, S., & Havenith, G. (2015a). Tactile cues significantly modulate the perception of sweat-induced skin wetness independently of the level of physical skin wetness. *Journal of Neurophysiology*, 113, 3462–3473. <https://doi.org/10.1152/jn.00141.2015>
- Filingeri, D., & Havenith, G. (2015). Human skin wetness perception: Psychophysical and neurophysiological bases. *Temperature*, 2, 86–104. <https://doi.org/10.1080/23328940.2015.1008878>
- Filingeri, D., Redortier, B., Hodder, S., & Havenith, G. (2013). The role of decreasing contact temperatures and skin cooling in the perception of skin wetness. *Neuroscience Letters*, 551, 65–69. <https://doi.org/10.1016/j.neulet.2013.07.015>
- Filingeri, D., Redortier, B., Hodder, S., & Havenith, G. (2014c). Thermal and tactile interactions in the perception of local skin wetness at rest and during exercise in thermo-neutral and warm environments. *Neuroscience*, 258, 121–130. <https://doi.org/10.1016/j.neuroscience.2013.11.019>
- Filingeri, D., Redortier, B., Hodder, S., & Havenith, G. (2015b). Warm temperature stimulus suppresses the perception of skin wetness during initial contact with a wet surface. *Skin Research & Technology*, 21, 9–14. <https://doi.org/10.1111/srt.12148>
- Filingeri, D., Zhang, H., & Arens, E. A. (2018). Thermosensory micromapping of warm and cold sensitivity across glabrous and hairy skin of male and female hands and feet. *Journal of Applied Physiology*, 125, 723–736. <https://doi.org/10.1152/jappphysiol.00158.2018>
- Foster, K. G., Ellis, F. P., Doré, C., Exton-Smith, A. N., & Weiner, J. S. (1976). Sweat responses in the aged. *Age and Ageing*, 5, 91–101. <https://doi.org/10.1093/ageing/5.2.91>
- Fukazawa, T., & Havenith, G. (2009). Differences in comfort perception in relation to local and whole body skin wettedness. *European Journal of Applied Physiology*, 106, 15–24. <https://doi.org/10.1007/s00421-009-0983-z>

- Gagge, A., Stolwijk, J., & Hardy, J. (1967). Comfort and thermal sensations and associated physiological responses at various ambient temperatures. *Environmental Research*, 1, 1–20. [https://doi.org/10.1016/0013-9351\(67\)90002-3](https://doi.org/10.1016/0013-9351(67)90002-3)
- Goble, A. K., Collins, A. A., & Cholewiak, R. W. (1996). Vibrotactile threshold in young and old observers: The effects of spatial summation and the presence of a rigid surround. *Journal of the Acoustical Society of America*, 99, 2256–2269. <https://doi.org/10.1121/1.415413>
- Guergova, S., & Dufour, A. (2011). Thermal sensitivity in the elderly: A review. *Ageing Research Reviews*, 10, 80–92. <https://doi.org/10.1016/j.arr.2010.04.009>
- Haroun, M. T. (2003). Dry skin in the elderly. *Geriatrics & Aging*, 6, 41–44.
- Huang, H. W., Wang, W. C., & Lin, C. C. K. (2010). Influence of age on thermal thresholds, thermal pain thresholds and reaction time. *Journal of Clinical Neuroscience*, 17, 722–726. <https://doi.org/10.1016/j.jocn.2009.10.003>
- Inoue, Y., Gerrett, N., Ichinose-Kuwahara, T., Umino, Y., Kiuchi, S., Amano, T., Ueda, H., Havenith, G., & Kondo, N. (2016). Sex differences in age-related changes on peripheral warm and cold innocuous thermal sensitivity. *Physiology & Behavior*, 164(Pt A), 86–92.
- Kenshalo, D. R. S. (1986). Somesthetic sensitivity in young and elderly humans. *Journal of Gerontology*, 41, 732–742. <https://doi.org/10.1093/geronj/41.6.732>
- Kottner, J., Lichtenfeld, A., & Blume-Peytavi, U. (2013). Maintaining skin integrity in the aged: A systematic review. *British Journal of Dermatology*, 169(3), 528–542. <https://doi.org/10.1111/bjd.12469>
- Lund, D. D., & Gisolfi, C. V. (1974). Estimation of mean skin temperature during exercise. *Journal of Applied Physiology*, 36, 625–628. <https://doi.org/10.1152/jappl.1974.36.5.625>
- Norman, R. A. (2003). Xerosis and pruritus in the elderly: Recognition and management. *Dermatologic Therapy*, 16(3), 254–259. <https://doi.org/10.1046/j.1529-8019.2003.01635.x>
- Olausson, H., Norrsell, U., Gothner, K., & Wallin, B. G. (1997). Directional sensibility for quantification of tactile dysfunction. *Muscle & Nerve*, 20, 1414–1421.
- Schellen, L., van Marken Lichtenbelt, W. D., Loomans, M. G., Toftum, J., & de Wit, M. H. (2010). Differences between young adults and elderly in thermal comfort, productivity, thermal physiology in response to a moderate temperature drift and a steady-state condition. *Indoor Air*, 20, 273–283. <https://doi.org/10.1111/j.1600-0668.2010.00657.x>
- Skedung, L., El Rawadi, C., Arvidsson, M., Farcet, C., Luengo, G. S., Breton, L., & Rutland, M. W. (2018). Mechanisms of tactile sensory deterioration amongst the elderly. *Scientific Reports*, 8, 5303. <https://doi.org/10.1038/s41598-018-23688-6>
- Soebarto, V., Zhang, H., & Schiavon, S. (2019). A thermal comfort environmental chamber study of older and younger people. *Building and Environment*, 155, 1–14. <https://doi.org/10.1016/j.buildenv.2019.03.032>
- Stevens, J. C. (1992). Aging and spatial acuity of touch. *Journal of Gerontology*, 47, P35–P40. <https://doi.org/10.1093/geronj/47.1.P35>
- Stevens, J. C., & Patterson, M. Q. (1995). Dimensions of spatial acuity in the touch sense: Changes over the life span. *Somatosensory & Motor Research*, 12, 29–47.
- Südel, K. M., Venzke, K., Mielke, H., Breitenbach, U., Mundt, C., Jaspers, S., Koop, U., Saueremann, K., KnuBmann-Hartig, E., Moll, I., & Gercken, G. (2005). Novel aspects of intrinsic and extrinsic aging of human skin: Beneficial effects of soy extract. *Photochemistry and Photobiology*, 81(3), 581–587. <https://doi.org/10.1562/2004-06-16-RA-202.1>
- Tagami, H. (2014). Electrical measurement of the hydration state of the skin surface in vivo. *British Journal of Dermatology*, 171, 29–33. <https://doi.org/10.1111/bjd.13245>
- Terrien, J., Perret, M., & Aujard, F. (2011). Behavioral thermoregulation in mammals: A review. *Frontiers in Bioscience*, 16, 1428–1444. <https://doi.org/10.2741/3797>
- Thornbury, J. M., & Mistretta, C. M. (1981). Tactile sensitivity as a function of age. *Journal of Gerontology*, 36, 34–39. <https://doi.org/10.1093/geronj/36.1.34>
- Tochihara, Y., Kumamoto, T., Lee, J. Y., & Hashiguchi, N. (2011). Age-related differences in cutaneous warm sensation threshold in human males in thermoneutral and cool environments. *Journal of Thermal Biology*, 36, 105–111. <https://doi.org/10.1016/j.jtherbio.2010.11.007>
- Valenza, A., Bianco, A., & Filingeri, D. (2019). Thermosensory mapping of skin wetness sensitivity across the body in young males and females at rest and following maximal incremental running. *Journal of Physiology*, 597, 3315–3332. <https://doi.org/10.1113/JP277928>
- Vargas, N. T., Chapman, C. L., Johnson, B. D., Gathercole, R., & Schlader, Z. J. (2018). Skin wettedness is an important contributor to thermal behavior during exercise and recovery. *American Journal of Physiology, Regulatory, Integrative and Comparative Physiology*, 315, R925–R933. <https://doi.org/10.1152/ajpregu.00178.2018>
- Verdù, E., Ceballos, D., Vilches, J. J., & Navarro, X. (2000). Influence of aging on peripheral nerve function and regeneration. *Journal of the Peripheral Nervous System*, 5, 191–208. <https://doi.org/10.1111/j.1529-8027.2000.00026.x>
- Verrillo, R. T., Bolanowski, S. J., Checkosky, C. M., & McGlone, F. P. (1998). Effects of hydration on tactile sensation. *Somatosensory & Motor Research*, 15, 93–108.
- Wickremaratchi, M. M., & Llewelyn, J. G. (2006). Effects of ageing on touch. *Postgraduate Medical Journal*, 82, 301–304. <https://doi.org/10.1136/pgmj.2005.039651>

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