CALL FOR PAPERS | Neurophysiology of Tactile Perception: A Tribute to Steven Hsiao

Tactile cues significantly modulate the perception of sweat-induced skin wetness independently of the level of physical skin wetness

Davide Filingeri,1 Damien Fournet,2 Simon Hodder,1 and George Havenith1

1Environmental Ergonomics Research Centre, Loughborough Design School, Loughborough University, Loughborough, United Kingdom; 2Thermal Sciences Laboratory, Oxylane Research, Villeneuve d’Ascq, France

Submitted 11 February 2015; accepted in final form 9 April 2015

Filingeri D, Fournet D, Hodder S, Havenith G. Tactile cues significantly modulate the perception of sweat-induced skin wetness independently of the level of physical skin wetness. J Neurophysiol 113: 3462–3473, 2015. First published April 15, 2015; doi:10.1152/jn.00141.2015.—Humans sense the wetness of a wet surface through the somatosensory integration of thermal and tactile inputs generated by the interaction between skin and moisture. However, little is known on how wetness is sensed when moisture is produced via sweating. We tested the hypothesis that, in the absence of skin cooling, intermittent tactile cues, as coded by low-threshold skin mechanoreceptors, modulate the perception of sweat-induced skin wetness, independently of the level of physical wetness. Ten males (22 yr old) performed an incremental exercise protocol during two trials designed to induce the same physical skin wetness but to induce lower (TIGHT-FIT) and higher (LOOSE-FIT) wetness perception. In the TIGHT-FIT, a tight-fitting clothing ensemble limited intermittent skin-sweat-clothing tactile interactions. In the LOOSE-FIT, a loose-fitting ensemble allowed free skin-sweat-clothing interactions. Heart rate, core and skin temperature, galvanic skin conductance (GSC), and physical (\(w_{body}\)) and perceived skin wetness were recorded. Exercise-induced sweat production and physical wetness increased significantly [GSC: 3.1 \(\mu\)S, SD 0.3 to 18.8 \(\mu\)S, SD 1.3, \(P < 0.01; w_{body}: 0.26\) no-dimension units (nd), SD 0.02, to 0.92 nd, SD 0.01, \(P < 0.01\), with no differences between TIGHT-FIT and LOOSE-FIT (\(P > 0.05\)). However, the limited intermittent tactile inputs generated by the TIGHT-FIT ensemble reduced significantly whole-body and regional wetness perception (\(P < 0.01\)). This reduction was more pronounced when between 40 and 80% of the body was covered in sweat. We conclude that the central integration of intermittent mechanical interactions between skin, sweat, and clothing, as coded by low-threshold skin mechanoreceptors, significantly contributes to the ability to sense sweat-induced skin wetness.

skin; wetness; sweating; mechanoreceptors; tactile

As homeothermic mammals, humans need to maintain their core body temperature within a very narrow range (≈37°C) to ensure optimal cellular and molecular function (Nakamura and Morrison 2007). Because of the variable nature of our surrounding environment, we constantly face the need to automatically and behaviorally thermoregulate, as either core overheating or overcooling can pose a major challenge to our survival (Parsons 2014).

Whether attributable to increases in metabolic heat production (e.g., as a result of exercise) or exposure to hot environments, core overheating is prevented and heat balance maintained by means of sweating (Candas et al. 1979). Evaporative heat loss through sweating plays a critical role in cooling the skin, thus maintaining a favorable core-to-skin gradient for heat losses from the core to the environment (Kondo et al. 1997). Therefore, within environmental conditions that allow full evaporation, the level of skin wetness represents an important parameter to ensure the evaporative efficiency of sweating (Candas et al. 1979).

As a physiological variable, skin wetness (\(w\)) was first introduced by Gagge (1937), who recognized its critical role in the heat balance of the body. Conceptually, \(w\) is defined as the fraction of the body covered by liquid at skin temperature (e.g., sweat), and it represents a physical measure of the degree of wetness involved in the process of evaporation (Gagge 1937). Operationally, \(w\) can be determined as the ratio between \(J\) the difference in water vapor pressure at the skin and in the air and 2 the difference between saturated water vapor pressure at the skin (calculated from skin temperature) and water vapor pressure in the air. \(w\) is usually expressed as a decimal fraction, with 1 representing the upper limit for a fully wet skin and 0.06 representing the minimal value because of insensible perspiration through the skin (Nishi and Gagge 1977).

Since Gagge’s seminal work (1937), the measurement of \(w\) has received great attention, particularly in the context of predicting the body’s heat balance during conditions of increased metabolic heat production (e.g., resulting from exercising muscles) and decreased gradient for heat loss to the environment (e.g., resulting from high ambient temperatures) (Candas et al. 1979; Havenith 2001; Havenith et al. 2013; Nadel and Stolwijk 1973). However, although much is known on the biophysical role of \(w\) in contributing to thermal homeostasis, surprisingly little has been done to elucidate how humans sense wetness on their skin and how the level of “physical” skin wetness relates to the level of “perceived” skin wetness (Montell 2008). This is particularly relevant, as sensing skin wetness has been shown to be critical both for behavioral and autonomic responses (Filingeri and Havenith...
Perceiving changes in both ambient humidity and skin wetness has been shown to impact thermal comfort (Fukazawa and Havenith 2009) and thus the thermoregulatory behavior (Schlader et al. 2010), both in healthy and clinical populations (e.g., individuals suffering from rheumatic pain) (Strusberg et al. 2002). From an autonomic perspective, the degree of skin wetness influences sweat gland function through a progressive suppression of the sweat output (i.e., hidromeiosis) in the presence of wetted skin (Nadel and Stolwijk 1973).

As opposed to insects, in which humidity receptors subserving hygrosensation have been identified and widely described (Tichy and Kallina 2010), humans seem not to be provided with specific receptors for the sensation of wetness (Clark and Edholm 1985; Filingeri 2014). Thus, we seem to “learn” to perceive the wetness experienced when the skin is in contact with a wet surface or when sweat is produced (Bergmann Tiest et al. 2012) through a complex multisensory integration (Driver and Spence 2000) of thermal (i.e., heat transfer) and tactile (i.e., mechanical pressure and skin friction) inputs generated by the interaction between skin, moisture, and (if donned) clothing (Fukazawa and Havenith 2009). This hypothesis has been supported by our previous findings. We have repeatedly shown that the central integration of cold sensations (primarily resulting from theafferent activity of cutaneous cold-sensitive, thinly-myelinated Aβ-nerve fibers) (Darian-Smith 1984) and of tactile inputs (encoded by cutaneous mechano-sensitive Aβ-nerve fibers) (Tsunozaki and Bautista 2009) plays a critical role in the ability to perceive skin wetness (Filingeri et al. 2013, 2014a, 2014b, 2014c). Indeed, we seem to interpret the coldness (i.e., thermal component) and stickiness (i.e., tactile component) experienced when the skin is wet as a signal of the presence of moisture (and thus wetness) on the skin’s surface.

By appraising the central role of coldness and tactile sensory integration, our work has significantly contributed to elucidate the neural bases of the perception of skin wetness (Filingeri et al. 2014b). However, our investigations have so far focused on local skin wetness perceptions as evoked by the passive contact with an external wet stimulus. As a second way of experiencing this perception, skin wetness can also be evoked during the active production of sweat. In this respect, still little is known on the neurophysiological mechanisms underlying sweat-induced skin wetness perception.

To our knowledge, only few studies have investigated how the level of sweat-induced physical skin wetness relates to the level of perceived skin wetness during exercise-induced increases in body temperature (Fukazawa and Havenith 2009; Gerrett et al. 2013; Lee et al. 2011). Interestingly, in all these studies, participants were able to both sense skin wetness as well as discriminate it regionally across their body, despite that they did not experience any cold sensations (as skin temperature was always observed to increase significantly during the exercise protocols). This is contrary to our earlier findings that indicated that, during the static contact with a warm-wet surface (with a temperature warmer than the skin), no local skin wetness is perceived, as no skin cooling and thus no cold sensations are experienced (Filingeri et al. 2015). It could be therefore suggested that, in those conditions of sweat-induced skin wetness (Fukazawa and Havenith 2009; Gerrett et al. 2013; Lee et al. 2011), participants relied more on tactile (i.e., intermittent stickiness and movement of their clothing) than on thermal inputs (i.e., warm sensations) to characterize the perception of wetness across their clothed bodies. This hypothesis could be in line with what was previously shown on a local base (i.e., manual exploration of a wet material) by Bergmann Tiest et al. (2012), who reported that, when thermal cues (e.g., thermal conductance of a wet material) provide insufficient sensory inputs, individuals seem to use mechanical cues (specifically the stickiness resulting from the intermittent adhesion and movement of a wet material to the skin) to aid them in the perception of wetness (Bergmann Tiest et al. 2012). However, because, in the above-mentioned studies (Fukazawa and Havenith 2009; Gerrett et al. 2013; Lee et al. 2011), the mechanical interaction at the skin was neither manipulated nor controlled, any hypothesis on what type of mechano-sensory inputs were used by the participants to characterize their perception of skin wetness remains speculative. To bridge this gap, the aim of this study was therefore to investigate the relationship between 1) the type and magnitude of mechanical interactions between skin, sweat, and clothing and 2) skin wetness perception under conditions of sweat-induced (physical) skin wetness.

Under natural conditions of sweat-induced skin wetness, the intermittent adhesion and movement of clothing on (wet) skin generates specific tactile sensations, which could be key in driving the perception of skin wetness when thermal (cold) cues are limited. Tactile inputs resulting from the mechanical stimulation of hairy skin are encoded by a variety of mechano-receptive units with distinctive adapting properties: 1) slowly adapting myelinated type I Merkel cells (primarily responding to static indentation of the skin) and type II Ruffini endings (primarily responding to skin stretch); 2) rapidly adapting myelinated Pacinian-type units (primarily responding to the initial and final contact of a mechanical stimulus with the skin), hair units (primarily responding to hair deflection), and field units (primarily responding to skin indentation); and 3) intermediate adapting unmyelinated C-tactile units (primarily responding to slow, gentle touch) (Olausson et al. 2010; Vallbo et al. 1995). According to such organizations, it follows that, under conditions of sweat-induced skin wetness and skin-clothing interactions, rapidly adapting myelinated Pacinian-type, hair, and field units could contribute to the perception of skin wetness by responding to the intermittent adhesion and movement of clothing on (wet) skin. The role of rapidly adapting skin mechanoreceptors could be also integrated by the activity of slowly adapting Merkel cells and Ruffini endings, encoding the prolonged adhesion and pressure of wet clothing (i.e., when these become saturated with sweat) on the skin. Therefore, if the sensory integration of such specific tactile cues, as encoded by both rapidly and slowly adapting low-threshold skin mechanoreceptors, was the main driver of the perception of sweat-induced skin wetness, it would be reasonable to hypothesize that limiting the degree of intermittent adhesion, stickiness, and movement of clothing on wet skin would result in decreasing the perception of skin wetness.

In line with the above, we tested the hypothesis that, during an incremental exercise protocol performed under conditions of restricted evaporation of sweat from the skin, given the same level of physical skin wetness, wearing a tight-fitting clothing ensemble (which will limit the degree of intermittent mechanical interaction between skin, sweat, and clothing) will result in a significant reduction in the level of perceived skin wetness.
experimental burns. The overall aim of this investigation was to demonstrate that it is possible to manipulate significantly the level of perceived skin wetness, independently of the level of (sweat-induced) physical skin wetness, thus unveiling the synthetic nature of this complex sensory experience.

Increasing the knowledge on the neurophysiological bases of skin wetness perception has an applied significance. First, because of the critical role of tactile roughness and skin wetness discrimination for precision grip and object manipulation (André et al. 2010), the implications of such findings could be highly relevant for the replication of this unique sensory feature in artificial skin and neuro-prosthetics (Kim et al. 2014). Second, because of the primary role of skin wetness on the development of thermal and clothing discomfort (Gagge et al. 2014), the implications of these findings could be important to support advances in protective (e.g., firefighting) and sport clothing design.

METHODS

Participants

Ten healthy male students [mean age 22.4 yr, SD 2.0; mean height 180.3 cm, SD 5.9; mean body mass 79.6 kg, SD 9.6; mean body surface area (DuBois and DuBois 1916) 2.0 m²; SD 0.1; mean chest circumference 88.4 cm, SD 6.3; mean waist circumference 77.7 cm, SD 7.7; mean arm circumference 25.9 cm, SD 4.3; mean thigh circumference 49.4 cm, SD 4.8; mean maximum oxygen consumption (VO₂max) 52.8 ml·min⁻¹·kg⁻¹, SD 7.3], with minimal terminal hairs (which, on the contrary, will freely allow intermittent mechanical interactions and movement between skin, sweat, and clothing). To limit the amount of moisture evaporation form the skin (and thus skin cooling), a vapor-impermeable, lose-fitting clothing ensemble was worn as a second layer on top of both the loose- or the tight-fitting garments. In this way, by reducing the chances of experiencing skin cooling and thus cold sensations during the exercise protocol, we aimed to isolate the contribution of specific tactile inputs (in the form of repeated, intermittent skin-sweat-clothing interactions) to the perception of sweat-induced skin wetness.

Experimental Protocol

Preliminary session. Participants attended one preliminary session to determine their anthropometrical characteristics and aerobic capacity. Each participant’s body mass and height, as well as chest, waist, arm, and thigh circumferences, were measured and recorded. A submaximal fitness test was then performed to estimate individuals’ aerobic fitness levels (expressed as VO₂max) using the Astrand-Rhyming method (Gordon and Pescatello 2010). The test was completed on a treadmill (Woodway Pps Med; Woodway Incorporated, Waukesha, WI) in a thermo-neutral environment (air temperature: 20°C; relative humidity: 50%) to prevent any thermal strain.

Experimental trials. The preliminary session was then followed by the two experimental trials. The experimental trials differed in terms of the first layer of clothing the participants wore during the exercise protocol, being this composed of either a tight-fitting, long-sleeved top and trousers (Domynos, Oxylane, France; total clothing surface area: 1.5 m²; total clothing weight: 466 g) or a loose-fitting, long-sleeved top and trousers (Domynos; total clothing surface area: 2.3 m²; total clothing weight: 643 g). The tight- and loose-fitting test garments were made up of the same fabrics (85% polyester and 15% elastane) and had an intrinsic local thermal resistance of 0.112 and 0.140 kW/m², respectively. To ensure that the tight-fitting clothing ensemble was in full and maximal contact with the skin over the whole body, a size “small” was used both for top and trousers. On the contrary, to allow free intermittent skin-clothing interactions over the whole body, a size “double extra-large” was used both for the top and trousers of the loose-fitting clothing ensemble. A pressure sensor (PF2 n°37, SIXAXES, Argenteuil, France) was used to measure the pressure applied by the tight-fitting test garments on three different regions (i.e., thigh, chest, and back) of a medium-sized manikin. The resulting pressure configuration for the tight-fitting clothing ensemble was on average 2.5 mmHg (SD 0.2). With regards to the relative distance of the loose-fitting test garments from the body, this was ~5 mm at the chest, ~15 mm at the lower back, ~25 mm at the arm, and ~20 mm at the thigh.

The second, vapor-impermeable layer of clothing was the same for all conditions and was worn during the exercise protocol to limit evaporation of moisture. This consisted of a vapor-impermeable, loose-fitting raglan jacket and trousers (total clothing weight of 427 g). The jacket and trousers were dual layered and 100% polyester. In the front, the fastener was a zipper that closed to the top of the collar. A placket front was used to prevent air exchange through zipper. The sleeve and leg linings had also tight cuffs to prevent air exchange. The fit of this layer of clothing was loose enough to ensure no interference with the movement of the first layer of clothing (particularly with regards to the loose-fitting ensemble). When worn on top of the first layer of tight and loose clothing, this resulted in a total whole-body thermal insulation of 0.213 and 0.234 kW/m², respectively. Testing of clothing thermal properties was performed on a standing thermal manikin (Newton; Measurement Technology Northwest, Seattle, WA) with a uniform skin temperature of 34°C, in a climatic chamber set at a temperature of 20°C with 51% relative humidity.

Both TIGHT-FIT and LOOSE-FIT experimental trials consisted of 30-min instrumentation and stabilization period, followed by a 45-min
incremental walking protocol. This consisted of walking on a treadmill (Woodway Pps Med) at a fixed speed (5 km/h) while the inclination of the treadmill was increased by 2% every 5 min, until a maximum of 16% inclination was reached. This protocol was designed to slowly raise participants’ sweat production and physical skin wetness so that changes in skin wetness perception could be detected with sufficient sensitivity. This was confirmed during extensive piloting performed before testing, which indicated this exercise protocol to be effective in inducing a gradual and progressive increase in participants’ sweat production while maintaining the level of body movement to a minimum. All experimental trials were performed in a climatic chamber set for a thermo-neutral exposure (air temperature: 20°C; relative humidity: 50%). These environmental conditions were chosen so that participants’ thermal, wetness, and comfort sensations would not be primarily influenced by the environment (being neutral), but rather by the way participants perceived their body under the vapor-impermeable jacket.

On experimental days, participants arrived at the laboratory 30 min before the time scheduled for the experimental trial to allow preparation procedures and stabilization. Participants were first asked to void their bladder, and seminude body mass was recorded on a digital scale (Sartorius Yacoila; Sartorius, Gottingen, Germany; precision 0.01 g). They were then instructed to self-insert a rectal thermometer (Grant Instruments, Cambridge, UK) 10 cm beyond the anal sphincter for the measurement of core temperature (Tcore) (1-s intervals). Five iButtons (Maxim, San Jose, CA) were taped to five skin sites on the left side of the body (i.e., cheek, abdomen, upper arm, lower back, and back lower thigh) to record local skin temperature (Tsk) (1-min intervals) to use for the calculation of mean Tsk. Four humidity sensors (MSR Electronics, Seuzach, Switzerland) were fixed to a holder and taped with surgical tape to the four skin sites on the right side of the body (i.e., chest, front arm, lateral lower back, and front thigh) to record local relative humidity (1-min intervals) to estimate local skin wetness. Sensors were located ~2 mm from the skin with the sensor tip not covered by tape. Four pairs of pregelled electrodes were attached to the same four skin sites as above for the measurement of local galvanic skin conductance (GSC) using the MP35 Biopac Systems (MP35; Biopac Systems, Goleta, CA), set to record at 35 Hz and 1-s intervals. The skin conductance was monitored to estimate local sudomotor activity (Vetrugno et al. 2003). Gerrett et al. (2013) have recently proven this measurement to be a reliable indicator of sweat gland activity and intradermal sweat accumulation. Finally, each participant wore a Polar HR monitor (Polar Electro, Kempele, Finland) to record heart rate (HR) at 10-s intervals.

After preparation, and according to the trial, participants wore the first layer of tight- or loose-fitting long-sleeved top and trousers, placed a head band over their forehead (to prevent sweat dripping over the face), and then moved to the treadmill where they started the 45-min walking protocol. During the exercise protocol, participants were asked to rate their thermal, wetness, and comfort sensations at 5-min intervals. Furthermore, as soon as the votes “slightly wet” and “slightly uncomfortable” were reported on the respective wetness and comfort scales, participants were asked to indicate (in the following order): 1) which regions between chest, back, arms, and thighs were perceived as wet; 2) which region was perceived as the wettest; and 3) which region was perceived as the most uncomfortable. To make rating of regional distribution of wetness and discomfort sensations possible, participants were presented a whole-body map (as modified from Lee et al. 2011) with the above-mentioned four regions being highlighted by numbers (range: 1–4).

Upon completion of the 45-min walking protocol, recording of the physiological parameters was stopped, participants removed all clothing and sensors, and seminude body mass was once again recorded. Following testing, all recorded physiological data were averaged over 5-min time slots for further calculations and analysis.

### Measurements and Calculations

Body surface area (m²) for each participant was calculated using individual height (m) and body mass (kg) according to the work of DuBois and DuBois (1916) as follows:

\[
\text{Body surface area} = 0.202 \times (\text{height}^{0.425} \times \text{body mass}^{0.725})(\text{m}^2)
\]

\[ (1) \]

Body mass was measured at the beginning and at the end of each experimental trial to determine gross sweat loss in grams (g).

Mean \( T_{sk} \) (°C) was calculated according to the work of Houdas and Ring (1982) as follows:

\[
\text{Mean } T_{sk} = (T_{\text{cheek}} \times 0.07) + (T_{\text{abdomen}} \times 0.175) + (T_{\text{upper arm}} \times 0.19) + (T_{\text{lower back}} \times 0.175) + (T_{\text{back lower thigh}} \times 0.39)(\text{°C})
\]

\[ (2) \]

Skin wetness (w, no-dimensional unit, nd) is defined as the ratio between the evaporated heat flux from the body caused by regulatory sweating and the maximal evaporative heat flux from the body for a totally wet skin. In this study, local skin wetness was estimated for each of the four body regions (which were monitored with humidity sensors) according to Gagge (1937) as follows:

\[
w_{\text{local}} = \frac{P_{sk} - P_{sk,s}}{P_{sk,s} - P_{a}}(\text{nd})
\]

\[ (3) \]

where \( P_{sk} \) (mmHg) is the water vapor pressure at the skin (measured using humidity sensors), \( P_{sk,s} \) (mmHg) is the water vapor pressure in the air, and \( P_{a} \) (mmHg) is the saturated water vapor pressure at the skin calculated from skin temperature (°C). \( P_a \) was calculated using the following equation:

\[
P_a = \frac{\text{RH}}{100} \times P_{a,s}(\text{mmHg})
\]

\[ (4) \]

where RH is ambient relative humidity (%), and \( P_{a,s} \) (mmHg) is saturated water vapor pressure in the air calculated from ambient temperature (\( T_{amb} \)) (°C) using the following equation (\( \text{exp} \) refers to an exponential function) according to Antoine (1888):

\[
P_{a,s} = 0.1 \times \exp \left( \frac{4030.18}{T_{amb} + 235} \right) \text{(mmHg)}
\]

\[ (5) \]

\( P_{sk} \) and \( P_{sk,s} \) were calculated for each skin site using the above equations and by substituting ambient relative humidity with local relative humidity at the skin (measured using humidity sensors), and \( T_{amb} \) was local skin temperature.

Whole body wetness (\( w_{\text{body}} \)) was then calculated using the following equation based on four measurement sites (i.e., chest, front arm, lateral lower back, and front thigh) (modified from Ramanathan 1964):

\[
w_{\text{body}} = (w_{\text{chest}} \times 0.3) + (w_{\text{upper arm}} \times 0.2) + (w_{\text{lower back}} \times 0.3) + (w_{\text{front thigh}} \times 0.2)(\text{nd})
\]

\[ (6) \]
Finally, mean GSC ($\mu$S) was averaged over the four sites (i.e., chest, front arm, lateral lower back, and front thigh).

**Statistical Analysis**

In the present study, the independent variables were condition (with 2 levels, i.e., TIGHT-FIT vs. LOOSE-FIT) and time (with 10 levels, i.e., 5-min intervals). The dependent variables were HR, $T_{rec}$, mean $T_{sk}$, $w_{body}$, mean GSC, gross sweat losses, and thermal, wetness, and comfort sensations.

Data were first tested for normality of distribution and homogeneity of variance using Shapiro-Wilk and Levine’s tests, respectively. With regards to parametric data such as HR, $T_{rec}$, mean $T_{sk}$, $w_{body}$, and mean GSC, the main effect and interactions of each independent variable were analyzed by two-way repeated-measures ANOVA, with clothing fit and time as repeated-measures variables. When a significant main effect was found, Tukey’s post hoc analyses were performed. Huynh-Feldt or Greenhouse-Geisser corrections were undertaken to adjust the degrees of freedom for the averaged tests of significance. With regards to the gross sweat loss data, these were compared between conditions by means of a paired $t$-test.

Nonparametric data such as thermal, wetness, and comfort sensation scores were analyzed by Wilcoxon signed-ranks tests ($Z$) and by Friedman’s analysis of variance ($\chi^2$). First, the main effect of each independent variable was tested by collapsing the data over condition (2 levels of comparison) and time (10 levels of comparison), respectively. A Wilcoxon signed-ranks test was performed for the 2-level comparison, and a Friedman’s analysis of variance was performed for the 10-level comparison. Interactions between variables were investigated using Wilcoxon signed-rank test (post hoc comparisons).

To investigate the differences in regional wetness perception and discomfort, a frequency-distribution analysis was performed. Frequencies were calculated for the number of times each region was perceived as wet, as the wettest and as the most uncomfortable for each condition (i.e., TIGHT-FIT vs. LOOSE-FIT) and analyzed by a $\chi^2$ test.

Finally, regression analyses were performed to investigate the relationship between indicators of physical wetness (i.e., $w_{body}$ and mean GSC) and perceived wetness, both for TIGHT-FIT and LOOSE-FIT conditions, using data from group means. To choose the appropriate regression model, linear and cubic regression analyses between indicators of physical wetness (i.e., $w_{body}$ and mean GSC) and perceived wetness were performed for each subject both for TIGHT-FIT and LOOSE-FIT conditions. Individual $r^2$ values for both linear and cubic models were statically compared using a paired $t$-test. The regression model to be used for the analysis of group mean data was then chosen according to the variance explained (i.e., models explaining the highest variance were preferred).

In all analyses, $P < 0.05$ was used to establish significant differences. Estimated marginal means and 95% confidence intervals were used to investigate the main effects and interactions of the variables. Observed power was computed using $\alpha = 0.05$. Data are reported as means ± SD. Statistical analysis was performed using IBM SPSS Statistics 19 (IBM, Chicago, IL).

**RESULTS**

**Physiological Parameters**

Figure 1 shows average values for HR, $T_{rec}$, mean $T_{sk}$, $w_{body}$, and mean GSC as recorded during the TIGHT-FIT and LOOSE-FIT trials. All parametric data were found to be normally distributed ($P > 0.05$). No significant main effect of clothing fit (i.e., TIGHT-FIT vs. LOOSE-FIT) was found on HR [$F = 0.16(1, 9), P = 0.7$, $T_{rec}$ [$F = 0.006(1, 9), P = 0.94$], mean $T_{sk}$ [$F = 0.81(1, 9), P = 0.39$], $w_{body}$ [$F = 0.29(1, 8), P = 0.60$], and mean GSC [$F = 0.43(1, 39), P = 0.83$]. Only a significant effect of time was found on the above-mentioned physiological parameters. During the exercise protocol (and similarly between TIGHT-FIT and LOOSE-FIT), participants’ HR was observed to increase significantly from an average

![Figure 1](http://jn.physiology.org/)

Fig. 1. Average values ($n = 10$) for heart rate (A), core (rectal) temperature (B), mean skin temperature (C), whole body skin wetness (D), and galvanic skin conductance (E), as recorded during the TIGHT-FIT and LOOSE-FIT trials. Data are reported as means ± SD. A significant increase in participants’ sweat production (as indicated by galvanic skin conductance) and physical skin wetness (as indicated by whole body skin wetness) can be observed. This was not different between TIGHT-FIT and LOOSE-FIT, thus confirming the effectiveness of the experimental protocol designed in inducing the same level of physical skin wetness during both trials. nd, no-dimension units.
baseline value of 81.8 beats/min (SD 3.3) to a maximum of 151.1 beats/min (SD 5.1) \[ F = 175.8(0.81), P < 0.01 \]; \( T_{\text{ec}} \) increased significantly from an average baseline value of 37.3°C (SD 0.1) to a maximum of 38°C (SD 0.1) \[ F = 106.9(0.81), P < 0.01 \]; mean \( T_{\text{sk}} \) increased significantly from an average baseline value of 0.26 nd (SD 0.02) to a maximum of 0.92 nd (SD 0.01) \[ F = 115.9(0.72), P < 0.01 \]; \( w_{\text{body}} \) increased significantly from an average baseline value of 0.26 nd (SD 0.02) to a maximum of 0.92 nd (SD 0.01) \[ F = 115.9(0.72), P < 0.01 \]; mean GSC increased significantly from an average baseline value of 3.1 \( \mu \)S (SD 0.3) to a maximum of 18.8 \( \mu \)S (SD 1.3) \[ F = 118.7(0.35), P < 0.01 \]. With regard to gross sweat loss, no significant differences were found between the recorded body mass changes for the TIGHT-FIT (mean 728 g, SD 192) and LOOSE-FIT trials (mean 848 g, SD 157) (mean difference = 120 g; 95% CI = −60, 304 g; \( t = 1.48 \); 2-tailed \( P = 0.2 \)).

All in all, these results indicate that the designed protocol was effective in inducing a significant increase in participants’ sweat production (as indicated by mean GSC) and physical skin wetness (as indicated by \( w_{\text{body}} \)), with no differences between TIGHT-FIT and LOOSE-FIT conditions.

**Perceptual Parameters**

Figure 2 shows average values for thermal, wetness, and comfort sensations as recorded during the TIGHT-FIT and LOOSE-FIT trials. No significant main effect of clothing fit (i.e., TIGHT-FIT vs. LOOSE-FIT) was found on thermal (\( Z = 0.97, P = 0.33 \)) and comfort sensations (\( Z = −0.37, P = 0.7 \)). These varied significantly over time (and similarly between TIGHT-FIT and LOOSE-FIT), with thermal sensations going from from \(-0.4 \pm 0.7 \) (label range: neutral to cool) to \(+2.5 \pm 0.7 \) (label range: hot to very hot) \[ x^2(9, n = 20) = 159.8, P < 0.01 \] and thermal comfort going from \(+1.0 \pm 1.5 \) (label range: slightly comfortable) to \(-2.3 \pm 0.8 \) (label range: uncomfortable to very uncomfortable) \[ x^2(9, n = 20) = 159.5, P < 0.01 \].

Contrary to what was observed for thermal and comfort sensations, the clothing fit (i.e., TIGHT-FIT vs. LOOSE-FIT) had a significant effect on skin wetness perception (\( Z = −2.7, P < 0.01 \)), with the TIGHT-FIT trial resulting in overall significantly “less wet” perceptions (median = 0.0; mean = \(-0.2 \pm 1.8 \); 95% CI = \(-0.5, +0.1 \); label range: slightly wet to slightly dry) than the ones recorded during the LOOSE-FIT trial (median = 1.0; mean = \(-0.5 \pm 1.7 \); 95% CI = \(-0.8, −0.1 \); label range: slightly wet to neutral). The effect of clothing fit on skin wetness perception showed a significant interaction with time. Indeed, although during both conditions skin wetness perception increased significantly over time (from a mean value of \(+1.4 \pm 1.4 \) to \(+2.4 \pm 0.5 \); label range: dry to dripping wet) \[ x^2(9, n = 20) = 164.6, P < 0.01 \], during the TIGHT-FIT trial skin wetness perception was significantly reduced 20 min after the exercise was initiated compared with the LOOSE-FIT trial (\( Z = −1.9, P = 0.047 \)) (see Fig. 2C), despite that no differences in indicators of physical wetness (i.e., \( w_{\text{body}} \) and mean GSC) were observed at any point in time between conditions (see Fig. 1, D and E).

The regression analysis performed between indicators of physical wetness (i.e., \( w_{\text{body}} \) and mean GSC) and perceived skin wetness provided further support to the significant effect of clothing fit on skin wetness perception (Fig. 3). In all instances, cubic curve estimations were preferred to linear models, as the former always explained a significantly higher variance in the data.

The relationship between \( w_{\text{body}} \) and perceived skin wetness was found to be statistically significant, both for the TIGHT-FIT (cubic curve estimation; \( P < 0.001; r^2 = 0.99 \)) and LOOSE-FIT trial (cubic curve estimation; \( P < 0.001; r^2 = 0.99 \)). However, and as shown in Fig. 3A, during the TIGHT-FIT trial, this relationship was shifted to the right in the middle part of the curve. This indicated that, when \( w_{\text{body}} \) ranged from \(-0.4 \) to \(-0.8 \) nd (i.e., between 40 and 80% of the total body surface was covered in sweat), skin wetness perception was significantly reduced when wearing tight- as opposed to loose-fitting garments.

The relationship between mean GSC and perceived skin wetness (Fig. 3B) was also found to be statistically significant,
mean GSC ranged from
the TIGHT-FIT trial, this relationship was shifted to the right
both for the TIGHT-FIT (cubic curve estimation; 
trials. Each data point represents group average (n
B
distance and perceived skin wetness (A
A
scribed when they wore loose-fitting clothing.
physical wetness was required to induce the same level of perceived wetness
indicated that, when subjects wore tight-fitting clothing, a higher level of
skin wetness perception showed a statically significant and positive rela-
tionship with the level of physical skin wetness, by manipulating the tactile
sensitivity to wetness and comfort, with regions such as the
arms and thighs being less frequently perceived as wet and uncomfortable during the TIGHT-FIT as opposed to the LOOSE-FIT trial. It is worth mentioning that, during both TIGHT-FIT and LOOSE-FIT trials, the chest and back were among the regions that were more frequently perceived as the wettest, during the LOOSE-FIT trial, the arms were also frequently perceived as the wettest region.

With regard to the region perceived as the most uncomfortable, the χ² analysis indicated that overall, during the TIGHT-FIT trial, the chest was more frequently perceived as the most uncomfortable region (40%), followed by the back (31%), arm (21%), and thigh (8%) (Pearson χ² = 30.2; P < 0.001). During the LOOSE-FIT trial, the chest was overall more frequently perceived as the most uncomfortable region (41%), followed by the chest (25%), arm (23%), and thigh (11%) (Pearson χ² = 24.3; P < 0.001). The time-frequency distribution of how often each region was perceived as the wettest is shown in Fig. 5. A and B. It should be noted that, although, during both TIGHT-FIT and LOOSE-FIT trials, the back and chest were among the regions that were more frequently perceived as the wettest, during the LOOSE-FIT trial, the arms were also frequently perceived as the wettest region.

All in all, these results indicated that, not only did the TIGHT-FIT condition reduce the overall level of perceived skin wetness, independently of the level of physical skin wetness, but also the clothing fit had an effect on the regional sensitivity to wetness and comfort, with regions such as the arms and thighs being less frequently perceived as wet and uncomfortable during the TIGHT-FIT as opposed to the LOOSE-FIT trial. It is worth mentioning that, during both conditions, the torso (i.e., chest and back) was more frequently reported as wetter and as more uncomfortable than the limbs (i.e., arms and thighs).

DISCUSSION
The aim of this study was to investigate the relationship between sweat-induced physical and perceived skin wetness and to test the hypothesis that the level of perceived skin wetness can be significantly modulated, independently of the level of physical skin wetness, by manipulating the tactile interaction between skin, sweat, and clothing.
The outcomes of this study have confirmed this hypothesis. Although, during both TIGHT-FIT and LOOSE-FIT trials, the level of physical wetness \( w_{\text{body}} \) was raised in the same pattern from a minimum of 0.24 nd to a maximum of 0.91 nd (TIGHT-FIT) and from a minimum of 0.27 nd to a maximum of 0.93 nd (LOOSE-FIT) (see Fig. 1D), with average maximal values corresponding to an almost fully wet skin (Nishi and Gagge 1977) and, although the time-dependent increase in the sudomotor activity (as indicated by the mean GSC) was equal between conditions (see Fig. 1E), during the TIGHT-FIT trial, the limited intermittent tactile sensations resulting from restricting the repeated adhesion and movement of clothing on wet skin caused a significant reduction in the overall level of perceived wetness, as well as a significant delay in the onset of skin wetness perception, both at a whole-body (see Fig. 2C) and at a regional level (see Fig. 4).

In summary, and for the first time to our knowledge, these results contribute to provide evidence for the fact that 1) under conditions of sweat-induced skin wetness, if no skin cooling occurs, the perception of skin wetness is primarily driven by specific tactile cues resulting from the intermittent mechanical interaction between skin, sweat, and clothing; 2) by manipulating this mechanosensory interaction (e.g., through a clothing intervention), skin wetness perception can be significantly modulated, independently of the level of physical wetness on the skin.

![Time-frequency distribution (%) of regional wetness perceptions based on the number of times the chest (A), back (B), arms (C), and thighs (D) were reported as being wet at each time point, during the TIGHT-FIT and LOOSE-FIT trials. The frequency of perceived skin wetness shows a significantly delayed onset during the TIGHT-FIT than during the LOOSE-FIT trial for all the regions investigated (*P < 0.05).](image)

![Time-frequency distribution (%) based on the number of times each region among chest, back, arms, and thighs was reported as being the wettest (A and B) and most uncomfortable region (C and D) at each time point, during the TIGHT-FIT and LOOSE-FIT trials. Two main tendencies can be observed here. First, although, during both TIGHT-FIT and LOOSE-FIT trials, the arms and thighs were more frequently perceived as the wettest, during the LOOSE-FIT trial, the arms were also frequently perceived as the wettest region (compare A and B). Second, although, during both TIGHT-FIT and LOOSE-FIT trials, the chest and back were among the regions that were more frequently perceived as the most uncomfortable, during the LOOSE-FIT trial, the thighs were also frequently perceived as the most uncomfortable region (compare C and D).](image)
Physical vs. Perceived Skin Wetness: Whole-Body Level

The novelty and implications of the outcomes of this study are twofold. First, these findings confirm what is expected based on a neurophysiological model of wetness perception that we have recently developed (Filingeri et al. 2014b). That is, to characterize their perception of skin wetness, humans rely on specific somatosensory inputs (i.e., thermal and tactile), which, if artificially manipulated (e.g., through a clothing intervention), can lead to a change in perception, which is independent of its physical components (i.e., the level of physical wetness). Second, these findings expand our understanding of how humans sense skin wetness, not only when passively in contact with cold-dry and cold-wet surfaces (Filingeri et al. 2013, 2014a, 2014b, 2014c), but also when actively producing sweat.

Our previous work on the neurophysiology of wetness perception has demonstrated that, to sense skin wetness, humans rely on the cold and tactile sensations experienced when physically wet, and, in this respect, experiencing coldness seems to be a primary contributor (Filingeri et al. 2013, 2014a, 2014b, 2014c). However, this sensory framework for the perception of wetness was developed within the context of passive skin contacts with wet surfaces, opening the question of what somatosensory cues contribute to the perception of skin wetness when sweat is actively produced by the body and clothing is worn.

The findings of the present study provide mechanistic evidence to suggest that the specific mechanosensory afferent inputs that are generated by the intermittent adhesion and movement of clothing on (wet) skin, which are likely coded by both rapidly and slowly adapting low-threshold skin mechanoreceptors, could strongly contribute to the perception of wetness under conditions of sweat-induced skin wetness and reduced evaporative cooling of sweat from the skin. Indeed, by reducing the degree of intermittent adhesion and stickiness of clothing on wet skin (i.e., one of the tactile components of sweat-induced skin wetness), while increasing the amount of static pressure on the skin, as coded by slowly adapting Merkel cells (Filingeri et al. 2014b).

Recent microneurographic recordings in awake healthy humans have shown that rapidly adapting Pacinian and hair mechanoreceptive units could primarily encode the tactile components of water droplets (0.05 ml) when these are applied on the receptive field of the unit (Marshall and Ackerley 2014), further supporting the key role of these myelinated units in sweat-induced skin wetness perception.

Altogether, the evidence provided in this study contributes to identify the integration of the specific sensory inputs resulting from the intermittent mechanical interaction between skin, sweat, and clothing, as likely and primarily coded by rapidly adapting Pacinian and hair units, as one of the candidate somatosensory mechanisms that could characterize the tactile component of sensing sweat-induced skin wetness.

It deserves mention that inputs from slowly adapting Merkel cells and Ruffini endings, as resulting from the prolonged adhesion and pressure of clothing on the skin (when this becomes saturated with sweat), could also contribute to sensing sweat-induced skin wetness by providing complementary tactile cues. In fact, although they selectively respond to different aspects of skin deformation, the majority of skin mechanoreceptors are activated under most naturalistic contexts of skin-object interactions (e.g., skin, sweat, and clothing), and the central convergence of peripheral mechanical inputs ultimately contributes to our ability to discriminate the type and magnitude of different tactile percepts (e.g., sweat-induced skin wetness) (Saal and Bensmaia 2014). Hence, the possibility that inputs from both rapid and slow skin mechanoreceptors, as occurring under naturalistic conditions of sweat-induced skin wetness, could ultimately contribute to the central integration of such perception cannot be ruled out conclusively.

As well as a potential reduction in the degree of mechanical stimulation of rapidly adapting skin mechanoreceptors, an increased stimulation of those slowly adapting skin mechanoreceptors (e.g., Merkel cells) responding to sustained skin indentation (as induced by the prolonged pressure generated on the skin by the tight-fitting clothing ensemble) could also have contributed to the reduction in sweat-induced skin wetness perception that we observed during the middle part of the TIGHT-FIT trial. In support of the above, we have recently shown that higher levels of static pressure can induce a tactile-mediated attenuation of the perception of local skin wetness (independently of its thermal component, i.e., skin cooling) by generating unfamiliar tactile sensations that are not commonly associated with the way we learn to perceive skin wetness (i.e., low levels of static pressure associated with sweating or immersing a body part into a liquid) (Filingeri et al. 2014c).

The fact that the type and magnitude of mechanical interactions between skin, sweat, and clothing can significantly modulate the perception of wetness is not entirely surprising and could be dependent on the synthetic nature of this complex perception (Bentley 1900). When the skin is exposed to external stimuli, surface textures and properties are usually discriminated based on the amount of skin displacement as well as the rate of movement of the stimuli on the skin (Gwosdow et al. 1986). For example, when in contact with fabrics, the level of skin wetness has been shown to increase the amount of friction within the skin-clothing system, a fact that in turn may alter the
tactile sensations arising from the skin’s mechanical contact with the fabric (Gwosdow et al. 1986).

The fact that the specific tactile sensations arising from the intermittent stickiness and lateral movement of clothing over wet skin could be critical in driving sweat-induced skin wetness perception could also explain why the reduction in skin wetness perception observed during the TIGHT-FIT trial appeared to be time and physical skin wetness dependent (i.e., more pronounced during the middle part of the exercise, when physical skin wetness covered between 40 and 80% of the total body surface). The sudden increase in skin wetness perception observed in the TIGHT-FIT trial when physical skin wetness reached values above 80% of the total body surface could have been indeed caused by an increase in sweat saturation of the tight-fitting ensemble, which likely occurred as a result of near-maximal levels of physical skin wetness. As changes in garment saturation could have in turn altered the friction of the garment, lateral motion, and adhesion to the skin, it would be therefore reasonable to hypothesize that such changes in the behavior of the wet tight-fitting garment (e.g., sustained adhesion to the skin and increased lateral stretch) could have triggered those friction- and stretch-dependent tactile sensations, as coded by slowly adapting Merkel cells and Ruffini endings, which could have a complementary role in driving the perception of skin wetness. Such a change in tactile afferents could have ultimately contributed to the increase in skin wetness perception observed in the TIGHT-FIT trial toward the end of the exercise protocol.

Finally, it deserves mention that, despite skin wetness perception that was significantly modulated by the tight-fitting trial during moderate to high levels of physical skin wetness, such perceptual change did not influence the development of thermal discomfort during the TIGHT-FIT trial (see Fig. 2A). As the level of sweat-induced skin wetness has long been acknowledged to drive thermal discomfort (i.e., the greater the skin wetness, the greater the thermal discomfort), particularly during exposures to hot environments (Gagge et al. 1967), it could therefore be argued that a reevaluation of the role of skin wetness perception per se in driving warm thermal discomfort is needed. In this respect, as no changes in whole-body thermal sensations were recorded at any time point between the TIGHT- and LOOSE-FIT trials, it could be suggested that warm thermal sensations could contribute to the development of thermal discomfort to a larger extent than skin wetness perception.

Physical vs. Perceived Skin Wetness: Regional Level

The limited intermittent tactile inputs resulting from the tight-fitting clothing ensemble significantly reduced the perception of skin wetness, not only at a whole body level, but also regionally. Among the region investigated, the limbs (i.e., arm and thighs) were indeed less frequently perceived as wet during the TIGHT-FIT as opposed to the LOOSE-FIT trial. Interestingly, this finding highlights what seems to be the ability of humans to regionally discriminate their sensation of skin wetness, despite not being provided with specific humidity receptors on the skin.

Within the experimental conditions of this study, we observed that, during both TIGHT-FIT and LOOSE-FIT trials, the back and chest (as opposed to arm and thighs) were overall more frequently perceived as the wettest regions. This is in line with what was observed by Lee et al. (2011), who have shown 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. Also, this outcome seems to be confirmed by the work of Ackerley et al. (2012), who have recently shown that, when wet stimuli with different moisture contents (range: 20–160 µl over a 24-cm² surface) were applied to different body regions, individuals were able to differentiate between moisture levels, with a tendency of the back as being among the most sensitive region to wetness. Finally, we have recently demonstrated that, because of its higher thermal sensitivity to cold, the (lower) back seems to be more sensitive to skin wetness (Filingeri et al. 2014a).

The fact that the torso was more frequently perceived as wetter than the limbs is in apparent contrast with the findings of Fukazawa and Havenith (2009), who reported that this body region presented a lower sensitivity to wetness than the limbs. A potential explanation for these apparently contrasting results could be the differences in the approaches used by these studies, either qualitative (i.e., sensation oriented) or quantitative (i.e., sensitivity oriented).

In the study by Lee et al. (2011) (as well as in the present study), participants’ ability to regionally discriminate skin wetness was tested by analyzing the frequency of wetness scores reported for each body region during conditions of natural sweat distribution (i.e., qualitative approach). This approach considered the subjective perception of wetness as the primary variable for comparing different regions. On the contrary, Fukazawa and Havenith (2009) calculated local w values for which comfort was no longer maintained (during conditions of artificially manipulated sweat distribution). This value was then used as a threshold to compare regional sensitivity (i.e., quantitative approach). This approach considered the sensitivity to wetness (i.e., changes in perception for a given change in the physical w) as the primary variable to be used for comparing different regions.

In light of the above, it is therefore clear that the two types of studies targeted different variables (sensation vs. sensitivity), which, although providing information on regional differences in wetness perception, in fact refer to different components of the relationship between stimulus (e.g., physical w) and resulting sensation (e.g., wetness perception). Indeed, the fact that the torso was perceived as wetter than the limbs [as observed in Lee et al. (2011) as well as in the present study] does not necessarily imply that this region presented higher sensitivity to skin wetness [as shown by Fukazawa and Havenith (2009)]. The more frequent perception of wetness recorded for the torso could just indicate that, in the whole, this region prevailed in terms of the absolute magnitude of the sensation generated by the presence of sweat on the skin. Indeed, in natural conditions (and under higher metabolic rates), owing to its higher sweat rate than the limbs (Smith and Havenith 2011), the torso will prevail in the amount of sweat produced and, potentially, in the sensory inputs (i.e., thermal and tactile) generated as a result of the greater moisture levels produced on this large skin region. Hence, although the limbs could present an intrinsically greater sensitivity to wetness [as shown by Fukazawa and Havenith (2009)], the torso is likely to be overall and more frequently experienced as wetter because of 1) greater sweat production, 2) a resulting greater volume of
moisture on the skin, and 3) a resulting larger number of skin receptors that could be concurrently stimulated and could ultimately contribute to a greater perception of wetness via spatial summation (Kenshalo et al. 1967).

This potential explanation is supported by the findings of Gerrett et al. (2013), who have observed that, despite in conditions of natural sweat distribution the limbs appear to be more sensitive to skin wetness, the overall magnitude of wetness perception and thermal discomfort was ultimately higher for the torso than for the arms and legs. The authors suggested that this area could present higher rates of discomfort and wetness perception as a combination of its intrinsic sensitivity to sweat as well as the amount of sweat effectively present on the skin (Gerrett et al. 2013). As the latter is directly related to local sweat rate, the fact that the torso has been repeatedly shown to have some of the highest sweat rates on the body (Smith and Havenith 2011) could provide further support to the above. Therefore, although the need for mixed experimental approaches (combining qualitative and quantitative measurements) translates into the results of this study being not conclusive, in this context, the hypothesis of the torso being a region that ultimately prevails in regionally driving the perception of wetness appears to be consistent with previous literature.

We conclude that, under conditions of sweat-induced skin wetness, while wearing clothing, if no skin cooling occurs, skin wetness perception is primarily driven by the level of intermittent mechanical interaction between skin, sweat, and clothing, as coded by both rapidly and slowly adapting low-threshold skin mechanoreceptors. The outcomes of this study expand our understanding of the neurophysiological and psychophysical mechanisms underlying humans’ ability to sense wetness on their skin. Interestingly, these mechanisms (i.e., integration of specific thermal and tactile sensory cues) appear to be remarkably consistent regardless of the modality for which skin wetness is experienced, i.e., whether attributable to passive contact with a wet stimulus or to active production of sweat. From a mechanistic standpoint, this could be explained by the fact that, independently of the modality (passive exposure vs. active sweat production), when the skin becomes wet (and clothing is worn), the components necessary for sensing wetness (i.e., skin, moisture/sweat, and external stimulus) and the resulting sensory inputs (i.e., thermal and tactile) will always be the same. In other words, skin wetness perception will always be the result of a central integration of specific thermal and tactile sensory cues generated by the interaction between the skin and the wet stimulus. Therefore, by either assessing or manipulating these sensory cues, skin wetness perception can be confidently predicted also within conditions of sweat-induced wetness. Such findings are of particular applied significance for their implications within the context of artificial touch and skin neuro-prosthetics as well as of protective clothing (e.g., firefighting) design.

ACKNOWLEDGMENTS

Current address D. Filingeri: Faculty of Health Sciences, University of Sydney, Sydney, 2006, Australia.

GRANTS

The present research was done in the context of an industry cofunded PhD. Loughborough University and Oxylane Research provided financial support.

D. Filingeri is supported by an Endeavour Research Fellowship from the Australian Government, Department of Education.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

D. Filingeri, D. Fournet, S.H., and G.H. conception and design of research; D. Filingeri performed experiments; D. Filingeri analyzed data; D. Filingeri wrote first draft of manuscript; D. Filingeri prepared figures; D. Filingeri drafted manuscript; D. Fournet, S.H., and G.H. edited and revised manuscript; D. Filingeri, D. Fournet, S.H., and G.H. approved final version of manuscript.

REFERENCES


REFERENCES


