Sweat gland recruitment following thermal and psychological stimuli

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Abstract
Eccrine sweat glands are present across almost the entire body surface. The distinction between glabrous (hairless) and non-glabrous skin has frequently been used to describe differences in human sudomotor function and, in particular, to help differentiate between the thermal and nonthermal mechanisms that modulate sweat secretion. Indeed, the widely accepted consensus is that psychological (psychogenic) sweating is limited to the glabrous regions, while thermally induced secretion occurs only from non-glabrous surfaces (Iwase et al., 1997). Furthermore, it is frequently assumed that independent central controllers, efferent pathways and different neurotransmitters activate the sweat glands within each of these regions. A recent research focus of the current laboratory has been to evaluate the veracity of these assumptions.

Keywords
stimuli, thermal, sweat, gland, following, psychological, recruitment

Disciplines
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INTRODUCTION

Eccrine sweat glands are present across almost the entire body surface. The distinction between glabrous (hairless) and non-glabrous skin has frequently been used to describe differences in human sudomotor function and, in particular, to help differentiate between the thermal and non-thermal mechanisms that modulate sweat secretion. Indeed, the widely accepted consensus is that psychological (psychogenic) sweating is limited to the glabrous regions, while thermally induced secretion occurs only from non-glabrous surfaces (Iwase et al., 1997). Furthermore, it is frequently assumed that independent central controllers, efferent pathways and different neurotransmitters activate the sweat glands within each of these regions. A recent research focus of the current laboratory has been to evaluate the veracity of these assumptions.

Several recent observations fail to fully support this control model for human eccrine sweating. For instance, extensive mapping of the sudomotor responses (across >50 skin sites) to non-thermal stimulation, unequivocally established the fact that psychological sweating is a generalised, whole-body phenomenon (Machado-Moreira and Taylor, 2007). Furthermore, thermal sweating was not restricted to the non-glabrous surfaces, but was also evident from glabrous sites (Machado-Moreira et al., 2008). These observations led to the hypothesis that it was more probable that a common (central) integration of efferent signals occurred, resulting in various stimuli simultaneously activating sweat glands across the entire body surface, even if separate control centres existed for the modulation of thermal and non-thermal sweating. Accordingly, local variations in sweat gland density, size and sensitivity may perhaps account for observed differences in the regional distribution of thermal and psychological sweating.

In the current experiment, sudomotor responses to thermal and psychological stimulation were examined at the glandular level. The central focus was to identify individual sweat glands recruited following each stimulus, and to see if different glands were being activated.

METHODS

Thermally and psychologically induced sudomotor responses were evaluated from the dorsal surfaces of the hands of ten healthy males (27.8 SD 5.1 y). Subjects were studied during seated rest in a climate-controlled chamber (25-26°C, 50% relative humidity). The thermal stress consisted of passive heating, and included feet immersion in heated water and a water-perfusion suit (water temperature: 43°C). Following the establishment of thermal sweating, the psychological stimulus (mental arithmetic) was applied, and subjects were required to solve as many problems as possible within 10 min. During this task, the thermal load was clamped to prevent further increases in body temperatures. Thus, the psychological stimulus was applied on top of an existing thermal load.
The dorsal hand surface was marked with a rectangular target (2.5 x 4 cm), and this site was prepared with a very thin film of silicone oil containing bromophenol blue (modified from Inoue et al., 1999), and the forearm and hand were secured to prevent motion artefact. Sweat secreted below this oil will form dark-blue droplets, permitting the identification of individual sweat glands from photographs taken from these rectangular zones using a high-resolution camera (Cannon EOS D20) and macro lens (Cannon EF-S60 mm f/2.8 macro USM). Photographs were taken of the rectangular targets at 1-min intervals during both the thermal and psychological stimuli, and these are illustrated in Figure 1 for one individual. From these photographs, a 1-cm² area was identified, and the activated sweat glands within this square were marked for subsequent counting (Adobe Photoshop CS4). The following photographs show sweat gland recruitment at the beginning of passive heating, one minute prior to, and during the psychological stimulation.

Figure 1: Sweat gland recruitment from the dorsal hand surface of one individual during thermal and combined thermal and psychological stimulation.

Sweat secretion from the contralateral dorsal hand surface was evaluated using the ventilated sweat capsule and skin conductance techniques. Local sweat rates were computed at 1-s intervals using a sweat monitor system (Clinical Engineering Solutions, NSW, Australia), while skin conductance was measured using a multi-channel conductance meter (Model SC2000/4-SLC, UFI Morro Bay, CA, USA), with data recorded at 10 Hz. Changes in conductance were derived relative to that measured prior to passive heating, and within the thermoneutral state. This technique is sensitive to changes in sudomotor drive (primary sweat) prior to sweat actually reaching the skin surface. Body core (auditory canal) and skin (eight regions) temperatures were recorded at 5-s intervals, and mean body temperature was derived from these data. Paired Hotelling's T-square tests were used to evaluate thermal and sudomotor responses during the first and last minutes of each experimental phase (thermal and psychological). Alpha was set at the 0.05 level.

RESULTS
The initial passive heat loading provoked significant changes in body temperatures (0.3°C; \(P<0.05\)), accompanied by a mean glandular activation of 186 glands.cm⁻² over ~24 min (range: 15-32 min) of thermal stress, and a significant elevation in skin conductance (Table 1). During the psychological stimulus, significant increases in either body temperatures or sweat rates were not evident relative to the last minute of heating (Table 1; \(P>0.05\)). These data confirm that the
thermal status of these subjects was clamped, and that the psychological stimulation occurred against this stable thermal background.

### Table 1: Sudomotor responses from the dorsal hand, body core and mean body temperatures during thermal and psychological stimuli. Data are means and standard errors of the means. * = all physiological responses were significantly elevated compared to those at the start of passive heating \((P < 0.05)\). † = significantly different from the start of the psychological stimulation \((P < 0.05)\).

<table>
<thead>
<tr>
<th>Physiological variables</th>
<th>Thermal</th>
<th>Thermal + Psychological</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Start</td>
<td>Last min*</td>
</tr>
<tr>
<td>Activated sweat glands (glands.cm⁻²)</td>
<td>0.0 ±0.0</td>
<td>186 ±22</td>
</tr>
<tr>
<td>Change in skin conductance (µS)</td>
<td>0.50 ±0.11</td>
<td>7.06 ±1.04</td>
</tr>
<tr>
<td>Sweat rate (mg.cm⁻².min⁻¹)</td>
<td>0.21 ±0.02</td>
<td>0.66 ±0.10</td>
</tr>
<tr>
<td>Mean body temperature (°C)</td>
<td>35.82 ±0.07</td>
<td>36.40 ±0.08</td>
</tr>
<tr>
<td>Auditory canal temperature (°C)</td>
<td>36.37 ±0.06</td>
<td>36.66 ±0.07</td>
</tr>
</tbody>
</table>

Within the first minute of the mental arithmetic, there was a 4% increase in the number of activated sweat glands, whilst at the end of the psychological stimulation (10 min), the number of activated glands increased 11% relative to that observed from the thermal stimulus alone. These changes represented respective increases in activated gland counts of 7 ±2 glands.cm⁻² and 18 ±4 glands.cm⁻² \((P<0.05)\). Whilst sweat rate changes were evident, there was only a significant change in skin conductance over the course of the psychological stimulation \((P<0.05)\).

### CONCLUSIONS

The current data confirm previous observations that psychological sweat secretion from non-glabrous skin surfaces is elicited when thermal sweating precedes the application of non-thermal stimulation (Machado-Moreira and Taylor, 2007). However, this response is not powerful, and may not be detected when less sensitive techniques are used to evaluate sweating. These observations are inconsistent with the assumption that psychological sweating is restricted to the glabrous skin surfaces. Indeed, both thermal and non-thermal stimuli appear to elicit ubiquitous activations of the eccrine sweat glands.

To the best of our knowledge, no other group has investigated differences in sweat gland recruitment between thermal and non-thermal stimulations. It was anticipated that no further glands would be activated during the psychological challenge. Data presented in Table 1 refute this hypothesis. Indeed, over the course of this stimulation, an average of 18 additional glands.cm⁻² were activated. Given that the dorsal (metacarpal) area is about 113 cm², this represents an added recruitment of 2,031 sweat glands for each hand. Several mechanisms may account for this observation. First, the glandular recruitment pattern may resemble that which occurs during thermal loading. That is, under a sustained load, not all glands are initially activated, but more are recruited as the strain is elevated or becomes more protracted (Randall,
1946). This may be analogous to the recruitment of motor units within skeletal muscle. Second, it is well established that 5-10% of the eccrine glands appear not to participate in thermal sweating. Perhaps these glands lack innervation, but possess some neurotransmitter sensitivity. During a prolonged psychological stimulus, it is possible that neurotransmitter release exceeds receptor binding and metabolism, leading to a transient accumulation within the interstitium, and the activation of normally silent sweat glands. Third, since eccrine sweat glands can be adrenergically activated, the possibility exists that this psychological stimulus was of such a magnitude that adrenaline was released from the adrenal gland, resulting in a systemic recruitment of more sweat glands. Finally, it is possible that different neural pathways exist for thermal and non-thermal activation of a subset of sweat glands. Some of these possibilities are currently being evaluated within the current laboratory.

REFERENCES