University of Southampton

Faculty of Environmental and Life Sciences

School of Health Sciences

Evaluating the role of female body morphology and maturation on local sweating mechanisms to guide innovation in sportswear design

by

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Thesis for the degree of Doctor of Philosophy

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University of Southampton

Abstract

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Doctor of Philosophy

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Human body temperature regulation relies on integrated feedback and feedforward processes that maintain cellular function during thermal challenges. After behavioural adjustments, the production and evaporation of sweat from the skin surface is the primary mechanism for heat dissipation during exercise and heat stress.

Females undergo unique anatomical, physiological, and hormonal changes across their lifespan (e.g., puberty, menstrual cycle, pregnancy, menopause), which influence body morphology (e.g. breast size) and thermoregulatory function, yet they remain under-represented in exercise thermoregulation research. This thesis aims to advance our fundamental understanding of how females regulate local sweating and thermal perception during exercise in the heat, and how developmental and hormonal transitions that shape morphology (e.g., breast development, puberty) affect these responses. The applied goal is to provide evidence that supports sports apparel design reflecting female diversity, moving beyond male-centric standards and drawing on the expertise and research capabilities of project co-funder Nike.

The first experimental campaign investigated the impact of varying breast surface area in adulthood on local sweat rates (LSR), thermal and wetness perception and skin mechanics. The results showed larger breasts have significantly reduced heat activated sweat gland density and LSR, and significantly greater skin stiffness in the upper breast, which meaningfully reduces following exercise in the heat. However, variation in breast size does not appear to impact thermal and wetness sensitivity across the breast, or tactile sensitivity in the lower breast region. The second experimental campaign investigated the impact of pubertal development on patterns of LSR and whole-body thermal perception. It was found that during puberty, LSR across the torso (i.e. chest, abdomen, upper and lower back), but not the limbs (hand, thigh, shin), increased linearly with age, due to age-dependent increases in sweat output per gland. Changes in regional mapping of LSR became apparent and meaningful (i.e. 2-fold difference) at age 14-15 or Tanner stage 3 in girls. The results also indicated that perceptions of temperature, wetness and thermal comfort during exercise in the heat did not differ across age-groups.

Together, these findings provide novel, fundamental evidence that female hormonal and morphological development can shape local sweating, perceptual, and skin mechanics in the heat. This thesis delivers the first integrated characterisation of breast-specific sweating, perceptual sensitivity, and mechanical properties, and the first detailed mapping of the transition from child-like to adult-like regional sweating patterns in girls. These insights address key gaps in female-centred thermophysiology and offer empirical data to improve sportswear and bra design, refine thermoregulatory models, and guide user-centred product development for female children and adults. Collectively, this work establishes a foundational evidence base that advances understanding of female thermoregulation and supports female comfort, health, and exercise participation in warmer environments.

Table of Contents

Table of Contents 3
Table of Tables 7
Table of Figures 8
Research Thesis: Declaration of Authorship 12
Acknowledgements 15
Definitions and Abbreviations 16
Publications 17
Chapter 1 Introduction and Research Motivation 20
1.1 Research context 20
1.2 Industry motivation: Applications to sport apparel design for females 21
1.2.1 Apparel during puberty 21
1.2.2 Sports bras 22
Chapter 2 Literature Review 24
2.1 Human heat balance 24
2.2 Autonomic thermoregulation 27
2.2.1 Regulation of skin vasomotor responses 29
2.2.2 Regulation of sudomotor responses 30
2.2.3 Biophysical determinants of autonomic thermoregulation 32
2.3 Behavioural thermoregulation 36
2.3.1 The human skin 37
2.3.2 Thermal sensitivity 39
2.3.3 Tactile sensitivity 40
2.3.4 Wetness perception 41
2.4 Sex differences in human thermoregulation 42

2.5 Female-specific factors and their impact on autonomic and behavioural thermoregulation 44

2.5.1 Female body morphology variations 44

2.5.2 Female hormonal development during puberty 46

2.5.3 Sweating during puberty 50

2.5.4 Skin temperature during puberty 54

2.5.5 Perceptual sensitivity during puberty 56

2.5.6 Anatomy of the female breast 58

2.5.7 Thermophysiology of the female breast 59

2.5.8 Perceptual sensitivity of the female breast 60

2.5.9 Mechanical properties of female breast 64

2.6 Summary of the literature review and conclusions 65

Chapter 3 Aims and Objectives 67

Chapter 4 Experimental Methodology 70

- **Ethics 71**
- **Thermometry, calorimetry and hygrometry 72**
  - Core temperature 72
  - Tympanic temperature 73
  - Skin temperature 73
  - Partitional calorimetry 75
  - Local sweat rates 78
  - Sweat gland density 79
- **Skin mechanics 81**
  - Skin properties 81
    - MyotonPro 81
    - Optical coherence tomography (OCT) 81
  - 3D Scanner 82

- **Perceptual assessment 83**
  - Psychometric scales 83
  - Sensory threshold estimation 85

Chapter 5 Experimental Study 1: The effect of female breast surface area on heat-activated sweat gland density and output 86

- **Abstract 86**
- **Introduction 87**
- **Materials and methods 88**
- **Results 96**
- **Discussion 101**
- **Conclusion 105**

Chapter 6 Experimental Study 2: The effect of female breast surface area and exercise on breast skin stiffness and tactile sensation . 106

- **Abstract 106**
- **Introduction 107**
- **Materials and methods 109**
- **Results 114**
- **Discussion 120**
- **Conclusion 124**

Chapter 7 Experimental Study 3: The effect of female breast surface area on cutaneous thermal sensation, wetness perception, and epidermal properties 125

- **Abstract 125**
- **Introduction 126**
- **Materials and methods 128**
- **Results 135**

- **Discussion** **141**
- **Conclusion** **146**

Chapter 8 Experimental Study 4: The maturation of regional sweating patterns from childhood to young adulthood in females **147**

- **Abstract** **147**
- **Introduction** **148**
- **Materials and methods** **149**
- **Results** **155**
- **Discussion** **163**
- **Conclusion** **168**

Chapter 9 Industrial Placements – Nike World HQ **169**

9.1 Determining wind speeds for thermal manikin testing of apparel innovations. **170**

9.2 Executive Summary of Nike Impact – Dr Grant Simmons **171**

Chapter 10 Conclusions, Applications & Further Research Directions ... **175**

- **Thesis summary** **175**
- **Original contributions to knowledge** **176**
  - Breast size variations 177
  - Puberty 179
- **Applications of the findings** **180**
- **Recommendations for future research** **181**
- **Conclusions** **183**

Chapter 11 Appendices **184**

Appendix A Participant Information Sheet – Study 2 .... **184**

Table of Tables

Table 2-1. The key characteristics of clothing affecting ergonomics. 27

Table 2-2. Sweat gland types; structure and function (Sato, 1983; Sato, 1977; Kuno, 1956, Szabo, 1958) 31

Table 2-3. Autonomic thermoregulation sex differences and their consequences. 43

Table 2-4. Tanner stages of development.. 47

Table 2-5. The number of sweat glands per sq. cm of the skin (Kawahata, 1939). 59

Table 3-1. Summary of the methods and parameters employed within the experimental chapters. 71

Table 5-1. Participant demographics (n=22). BMI = body mass index; BSA= body surface area; BrSA= breast surface area. 89

Table 5-2. Mean values, standard deviation (SD), minimum and maximum values of evaporative requirement for heat balance in W/m^2 (E_{req}), whole body sweat loss (WBSL), core temperature change (ΔT_{core}), heart rate, run speed and run time measured during the submaximal run in the heat. Split by bra size and finishers (n = 16) and non-finishers (n = 6)... 97

Table 5-3. Multiple regression model for changes in local sweat rate at the breast (n = 16). *p < 0.05. 101

Table 6-1. Participant demographics (n=20); BrSA= breast surface area. 110

Table 6-2. Descriptive statistics of skin stiffness and tactile sensitivity parameters at all test sites, as a function of bra size group, pre- and post-exercise 115

Table 7-1. Participant demographics (n = 21). Mean, minimum and maximum values. BrSA = breast surface area. BSA = body surface area.. 130

Table 7-2. Pearson correlation coefficients and p-values between epidermal properties with thermal sensation and wetness perception at all skin sites. *p < 0.05. 141

Table 8-1. Anthropometric, heat exchange and exercise intensity during exercise (*n*=28)...... 157

Table of Figures

Figure 2-1. A schematic representation of the autonomic responses triggered by changes in body temperature. CNS: Central nervous system. 28

Figure 2-2. Basic sweat gland structure. The eccrine gland is comprised of a secretory coil and a sweat duct opening on the skin surface. The apocrine gland sits in the subcutaneous fat layer with a secretory duct that opens into a hair follicle. Reprinted with permission from Hu et al. (2018). 31

Figure 2-3. Example by Notley et al. (2020) of physical models (three cubes; A, B, and C) to illustrate the influences of variations in morphology and composition on passive heat exchange. Cubes were heated in a stirred water bath (40°C) to a common central (core) temperature and then cooled in a second water bath (20°C). [A] Time-dependent changes in central temperature in each object. [B] Cooling rate of each cube over a 5°C temperature range (30°C to 25°C), as bolded in Panel A. [C] Dimensions and thermal properties of each cube. Cubes A and B (both beeswax) differed only in size. Cubes A and C differed only in composition, with cube C being made of plasticine. Reprinted with permission from Notley et al. (2020) 33

Figure 2-4. Example of exercise prescription methods (H_{prod} or $\%VO_{2peak}$) to allow for unbiased investigations of changes in core temperature (Tc), whole body sweat rate (WBSR), and local sweat rate (LSR) of a girl, boy, adult female, and adult male. By standardizing the work rate to investigate one variable, the H_{prod} and $\%VO_{2peak}$ required to investigate another variable differs between individuals due to physical differences in body size and fitness. Reprinted with permission from Topham et al. (2022). 35

Figure 2-5. Schematic representation of receptors in human skin. Reprinted with permission from Carlson (2018). 38

Figure 2-6. Female serum concentrations (n = 456) of oestradiol (E2) and oestrone (E1) by age, stratified by Tanner stages T1–T5: T1, n = 178; T2, n = 71; T3, n = 69; T4, n = 95; and T5, n = 43. Number of adolescents post-menarche (filled circles), n = 112. Reprinted with permission from Frederiksen et al. (2019). 48

Figure 2-7. Median regional sweat rates ($g.m^{-2}.h^{-1}$) of girls after moderate intensity (60% HR_{max}) treadmill exercise in the heat (30°C, 40% RH). Reprinted with permission from Arlegui et al. (2021). 53

Figure 2-8. Median regional sweat rates ($g.m^{-2}.h^{-1}$) of adult females after moderate intensity (60% VO_{2max}) treadmill exercise in the heat (26°C, 45% RH). Reprinted with permission from Smith and Havenith (2012). 53

Figure 2-9. Female front skin temperature maps showing median skin temperatures for each age group at different timepoints of the experimental protocol. Reprinted with permission from Arlegui (2022). 56

Figure 2-10. Increasing finger surface area increased tactile thresholds, i.e. reduced tactile sensitivity in males (blue) and females (red). Reprinted with permission from Peters et al. (2009) - Copyright © 2009 Society for Neuroscience 0270-6474/09/2915756-06. 62

Figure 2-11. Thermal sensitivity maps across the breast from [A] Luo et al. (2020) (Luo et al., 2020) demonstrating more homgenous distribution and [B] Valenza et al. (2023) showing more heterogenous distribution. Reprinted with permission from both authors. 63

Figure 3-1. A summary of the PhD project research aims. 69

Figure 4-1. Core temperature reader device collecting data whilst the participant runs on a treadmill in the climate chamber. 72

Figure 4-2. Thermal image using the infra-red camera... 75

Figure 4-3. Participant performing exercise in the climate chamber with breath-by-breath analysis to calculate metabolic energy expenditure. 77

Figure 4-4. Technical absorbent patch [A] in saturated and unsaturated states, [B] affixed to the skin using a waterproof film dressing. 79

Figure 4-5. Scanned iodine patches demonstrating differences in sweat gland density. [A] 254 glands (28 glands/cm^2), [B] 226 glands (25 glands/cm^2)... 80

Figure 4-6. MyotonPRO device with J-shaped probe.. 81

Figure 4-7. [A] Annotated 2D-OCT scan of the breast skin. [B] 3D surface roughness scan with scale. 82

Figure 4-8. Breast scan from which breast surface area could be measured. 83

Figure 4-9. Overview of the Likert and Visual Analogue scales used for thermal sensation and wetness perception assessments. The length of the lines for the Visual Analogue scales were 100mm. 84

Figure 4-10. Von Frey monofilaments used to measure tactile thresholds 85

Figure 5-1. Schematic of experimental design. 91

Figure 5-2. Absorbent patch and iodine paper contact locations; above nipple, below nipple, bra triangle. 3x3cm patches. 94

Figure 5-3. Relationship between breast surface area and evaporative requirement for heat balance (in W/m^2) for [A] all participants (n=22; used in sweat gland density analysis) and for [B] the full 45-minute trial finishers (n=16; used in LSR analysis). 99

Figure 5-4. Relationship between sweat gland density (n = 22) [A, B], LSR (n = 16) [C, D] and output per gland (n = 16) [E, F] in 2 locations [breast average, bra triangle] relative to breast surface area. 100

Figure 6-1. Schematic of experimental design. 111

Figure 6-2. Relationship between breast surface area and skin stiffness at rest at [A] 3 cm above the areola, [B] the superior areola border, [C] the inferior areola border and [D] 3 cm below the areola. *Significant correlation ($p < 0.05$). 117

Figure 6-3. Relationship between breast surface area and tactile sensitivity thresholds at rest at [A] the nipple, [B] the areola edge and [C] 3 cm below the areola. 118

Figure 6-4. The main effect of [A] test site and [B] exercise on skin stiffness in the 'finishers' (n = 15). *Significant difference ($p < 0.05$). 119

Figure 6-5. The effect of [A] test site and [B] exercise on tactile sensitivity thresholds in the 'finishers' (n = 15). Presented as median and 95% CI. *Significant difference ($p < 0.05$).120

Figure 7-1. Schematic of experimental design and tested sites across the breast and bra triangle. 132

Figure 7-2. [A] Annotated 2D-OCT scan of the breast skin. [B] 3D surface roughness scan with scale. 134

Figure 7-3. Relationships between breast surface area and 4 stimuli (cold-thermal [A], cold-wet [B], hot-thermal [C], hot-wet [D]) at 4 skin sites (above nipple [i], nipple [ii], below nipple [iii], bra triangle [iv]) (n = 21). 137

Figure 7-4. Mean (n = 21) cold-thermal (A), hot-thermal (B), cold-wet (C) and hot-wet (D) sensitivity for the 4 locations tested. Statistically significant multiple comparisons are pictured (*p < 0.05). (E) Coefficient of variations (%) at each test site for cold-thermal (CT), cold-wet (CW), hot-thermal (HT) and hot-wet (HW) sensations. 138

Figure 7-5. Relationships between breast surface area and epidermal measurements (epidermal thickness [A], surface roughness [B]) at 3 skin sites (above nipple [i], below nipple [ii], bra triangle [iii]) (n = 21). 139

Figure 7-6. Mean (n = 21) [A] epidermal thickness, [B] surface roughness at the 3 skin sites. Statistically significant comparisons are pictured (*p < 0.05). [C] Coefficient of variations (%) at each test site for epidermal thickness and surface roughness. 140

Figure 8-1. Schematic of experimental design. Preliminary session (left) and experimental session (right)... 154

Figure 8-2. Relationship between age and local sweat rate at the torso sites (bra triangle [A], abdomen [B], upper back [C], lower back [D]) and the extremities (hand [E], thigh [F], shin [G]) (n = 28). 159

Figure 8-3. Relationship between age and [A] heat activated sweat gland density (HASGD), and [B] sweat output per gland at the bra triangle (n = 9)....................................... 160

Figure 8-4. The effect of age [A] and tanner stage [B] on grouped local sweat rates (extremities vs. torso). Presented as mean and SD. *Significant difference between sites (p ≤ 0.05). 161

Figure 8-5. Box plots displaying thermal sensation [A], wetness perception [B] and thermal comfort [C] measured at 4 time points and grouped by age. Data presented as median (diamond symbol), interquartile range (box) and min/max (error bars)...... 162

Figure 9-1. Nike World Headquarters, including the LeBron James Innovation Centre that houses the NSRL. 169

Figure 9-2. Male and female thermal manikins in the climate chamber. 171

Figure 9-3. Climate chamber equipped with VICON motion capture. 173

Figure 10-1. A summary of the PhD project key take home messages................................... 176

List of Accompanying Materials

DATASETS

Dataset - Chapter 5, 6, 7 - The effect of female breast surface area on thermoregulation, skin mechanics and perception. https://doi.org/10.5258/SOTON/D3910

Dataset - Chapter 8 - The maturation of regional sweating patterns from childhood to young adulthood in females. https://doi.org/10.5258/SOTON/D3909

Research Thesis: Declaration of Authorship

Print name: Hannah Blount

Title of thesis: Evaluating the role of female body morphology and maturation on local sweating mechanisms to guide innovation in sportswear design

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
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6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

    - **Blount, H**. (2025). Does breast size matter? The thermoregulatory, perceptual and mechanical properties of the breast. Experimental Physiology, 1–3. https://doi.org/10.1113/EP092441
    - **Blount, H**., Valenza, A., Ward, J., Caggiari, S., Worsley, P. R., & Filingeri, D. (2024). The effect of female breast surface area on heat-activated sweat gland density and output. Experimental Physiology, 109, 1330–1340. https://doi.org/10.1113/EP091850
    - **Blount, H.,** Valenza, A., Ward, J., Caggiari, S., Worsley, P. R., & Filingeri, D. (2024). The effect of female breast surface area on skin stiffness and tactile sensitivity at rest and following exercise in the heat. Experimental Physiology, 109, 1698–1709. https://doi.org/10.1113/EP091990
    - **Blount, H**., Valenza, A., Ward, J., Caggiari, S., Worsley, P. R., & Filingeri, D. (2024). The effect of female breast surface area on cutaneous thermal sensation, wetness

perception and epidermal properties. Experimental Physiology, 1–13. https://doi.org/10.1113/EP092158

Signature: HANNAH BLOUNT **Date:** 10/02/2026

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Definitions and Abbreviations

LSR .... Local sweat rate

WBSR .... Whole body sweat rate

HASGD .... Heat-activated sweat gland density

HR .... Heart Rate

VO_{2max} .... Maximal oxygen uptake

M .... Rate of metabolic energy production ($W \cdot m^{-2}$)

Wk .... Rate of mechanical work ($W \cdot m^{-2}$)

E .... Rate of evaporative heat loss ($W \cdot m^{-2}$)

R .... Rate of radiative heat loss ($W \cdot m^{-2}$)

C .... Rate of convective heat loss ($W \cdot m^{-2}$)

K .... Rate of conductive heat loss ($W \cdot m^{-2}$)

S .... Rate of heat storage ($W \cdot m^{-2}$)

H_{prod} .... Rate of metabolic heat production

E_{req} .... Evaporative requirement for heat balance

T_{core} .... Core temperature

T_{skin} .... Skin temperature

T_{tym} .... Tympanic temperature

BRSA .... Breast surface area

BSA .... Body surface area

BMI .... Body mass index

GnRH .... Gonadotropin-releasing hormone

FSH .... Follicle-stimulating hormone

LH .... Luteinizing hormone

IUD .... Intrauterine device

OCT .... Optical coherence tomography

RH .... Relative humidity

Publications

Blount, H., Koch Esteves, N., Ward, J., Simmons, G.H., Worsley, P. R., & Filingeri, D. (2026). The maturation of regional sweating patterns from childhood to young adulthood in females. *Accepted for publication in Experimental Physiology*.

Blount, H., Ward, J., James, P.A.B., Worsley, P. R., Filingeri, D., & Koch Esteves, N. (2026). Understanding the Impact of Heatwaves on UK Care Homes: A National Survey of Staff Experiences, Challenges, and Adaptation Strategies. Preprint in medRxiv. https://doi.org/10.64898/2026.03.24.26349157. *Under review in BMJ Public Health*.

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Valenza, A., **Blount, H.**, Ward, J., Merrick, C., Wootten, R., Dearden, J., Wildgoose, C., Bianco, A., Buoite-Stella, A., Filingeri, V. L., Worsley, P. R., & Filingeri, D. (2025). Skin wetness perception across body sites in children and adolescents aged 7–16 years old. *Experimental Physiology*, 1–9. https://doi.org/10.1113/EP092691

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CONFERENCE PROCEEDINGS

Blount H, Valenza A, Ward J, Caggiari S, Worsley P, Simmons G, Filingeri D. The effect of female breast surface area on heat-activated sweat gland density and output - size matters! *Physiology 2023, The Physiological Society,* 10 -12 July 2023, Harrogate, UK. *Oral Presentation.*

Blount H, Valenza A, Ward J, Caggiari S, Worsley P, Simmons G, Filingeri D. The impact of female breast surface area on cutaneous thermal, wetness and tactile sensitivity. *The Festival of Touch,* 4 - 7 July 2023, Marseille, France. *Poster Presentation.*

Blount H, Valenza A, Ward J, Caggiari S, Worsley P, Filingeri D. The impact of female breast surface area on skin stiffness and tactile sensitivity at rest and following exercise. *ICEE 2024,* 3 – 7 June 2024, South Korea. *Poster Presentation.*

Blount H, Valenza A, Ward J, Caggiari S, Worsley P, Filingeri D. The impact of female breast surface area on skin stiffness and tactile sensitivity at rest and following exercise. *WiSEAN,* 26 – 27 June 2024, Portsmouth, UK. *Poster Presentation.*

Blount H, Koch Esteves N, Ward J, Simmons G, Worsley P, Filingeri D. The maturation of sweating across the body from childhood to young adulthood in females. IUPS, 10 – 14 September 2025, Frankfurt, Germany. *Poster Presentation.*

INVITED TALKS

Invited speaker: University of Oregon, Eugene, Oregon, USA – November 2023: In person presentation on 'The effect of female breast surface area on heat-activated sweat gland density and output'.

Invited speaker: British Association for Sport and Exercise Sciences (BASES) Webinar – December 2024: Online presentation on my research relating to breast size, thermoregulation, skin mechanics and perception: 'Beyond the Standard Fit: Breast Health and Bra Design for Women in Physically Demanding Occupations'.

Invited Speaker: Brock University, St. Catharines, Canada - July 2025: In person presentation on 'The maturation of sweating across the body from childhood to young adulthood in females'

Invited Speaker: US Army Research Institute of Environmental Medicine, Natick, Massachusetts, USA - July 2025: In person presentation on the industrial work from 3-month secondment at Nike.

AWARDS

2025 Doctoral College Research Awards – University of Southampton

Competitive prize awarded for outstanding academic performance and academic achievement within the School of Health Sciences.

Chapter 1 Introduction and Research Motivation

1.1 Research context

Exercise is a key determinant of health and quality of life (Lavie & Milani, 1995; Teoman et al., 2004), making increased uptake and accessibility essential to counter rising sedentary behaviour and obesity worldwide (WHO, 2021). Yet maintaining female participation in sport and exercise across the lifespan remains challenging. Despite major advances in gender equality in sport over the past five decades, dropout rates among females remain disproportionately high, particularly during puberty (Howard, 2024; Slater & Tiggemann, 2010; Zarrett et al., 2020) and among those with larger breasts (Brown et al., 2014; McGhee & Steele, 2020).

Fundamentally, females experience a series of unique hormonal, morphological, and physiological transitions across the lifespan that can influence participation and comfort in exercise settings. Puberty, the menstrual cycle, pregnancy, the post-partum period, and menopause are all associated with marked changes in body morphology (e.g. breast development), thermoregulation, and thermal sensitivity (Lei et al., 2019; Smallcombe et al., 2021; Wade et al., 2010). Despite these known differences, females remain vastly underrepresented in thermoregulatory research (Filingeri, Blount, & Valenza, 2024), with only ~12% of participants in such studies being female over the last decade (Hutchins et al., 2021). This knowledge gap is problematic, as sex-based differences exist in thermal perception, sweat distribution, and behavioural responses to heat stress (Greenfield et al., 2023; Kaciuba-Uscilko & Grucza, 2001; Vargas et al., 2019).

From an applied perspective, participation in sport and exercise depends heavily on the design and function of sports apparel, which provides protection, support, and comfort. Excess sweat and inadequate moisture management in apparel are frequently reported as major sources of thermal discomfort, irritation, and reduced confidence. However, current clothing design principles remain largely based on male morphology and physiology, often neglecting the unique needs of females (Goldman, 2006; Parsons, 2007; Wilfling et al., 2022). These factors represent critical barriers to lifelong sport participation that demand deeper physiological and design-based understanding. To produce effective sportswear that aids thermoregulation and comfort, it is essential to first understand the physiological and perceptual needs of the wearer such as their body morphology (e.g. consider differences in breast size amongst women) and hormonal development (e.g. consider female development during puberty). Generating this foundational knowledge can enable apparel manufacturers to design garments that better manage sweat, improve thermal comfort, and reduce key barriers to participation, such as breast discomfort and overheating.

1.2 Industry motivation: Applications to sport apparel design for females

The aim of this thesis was to inform sports apparel design that better reflects the needs of the female body at different stages of the lifespan and moves beyond traditional male-derived design standards. This PhD was co-funded by Nike Inc., the largest sports apparel manufacturer in the world, and the Engineering and Physical Sciences Research Council (EPSRC). This industry-academic partnership provided a direct avenue for the application of this Thesis' findings to inform apparel innovation that improves wear comfort and performance, ultimately helping to keep women active throughout their lifespan. In alignment with the EPSRC's Health Technologies Strategy, which emphasises research that supports long-term health, wellbeing, and disease prevention, this work contributes foundational knowledge relevant to promoting physical activity in women. Due to this partnership, and the influence that the fundamental knowledge gained throughout this PhD could have on product, the research focussed on understanding the mechanisms underlying local sweat production across the breast and during pubertal development - two characteristic yet understudied female-specific scenarios, with potential for considerable impact.

1.2.1 Apparel during puberty

Research has shown that up to 65% of girls drop out of sport as they reach puberty, with almost half of the girls questioned avoiding exercise due to their breasts and 73% of girls feeling uncomfortable in their body shape and image, leading to a fear of being judged (Women In Sport, 2022). Focus groups have shown several themes are at play when considering why girls see a decline in exercise participation during adolescence, such as, sport not being seen as 'cool' or feminine, an increase in opportunities for other social activities, increased school work in high school, the opportunity to play a range of sports declines and finally, clothing and body image (Slater & Tiggemann, 2010). Sports clothing can have large psycho-social and physiological impacts during puberty. Body image concerns of sports kit, including sexualisation, fear of "masculinisation", and "appearance" during sport when looking red-faced and sweaty play a considerable role in girls' high dropout rates (Howard, 2024; Slater & Tiggemann, 2010; Zarrett et al., 2020). Yet clothing is a necessity, and clothing that supports the wearer to feel comfortable and confident is also a necessity to ensure that this does not act as a barrier to exercise participation at a time during development when several other social pressures are evident.

Little is known about the stages of thermoregulatory development (sweating and perception) during puberty. To better support pubertal females remaining active during this challenging life phase, there is a need to understand the thermoregulatory changes that occur to better inform girls sports apparel design through improved sweat management and insulation.

1.2.2 Sports bras

The average breast size in the UK and Australia is increasing (Mintel Group, 2001). Females with larger breasts have greater issues of breast motion, inducing pain and other negative health outcomes (upper limb, neck, back and head pain) (McGhee et al., 2013; White et al., 2015). During dynamic exercise, the breasts tend to move in a 3D sinusoidal pattern relative to the torso (McGhee & Steele, 2020). This displacement has shown to significantly correlate with exercise-induced breast discomfort (Gehlsen & Albohm, 1980; Lorentzen & Lawson, 1987; Scurr et al., 2010). Females with larger breasts have greater breast displacement than those with smaller breasts, and as a result see greater levels of discomfort (Lawson & Lorentzen, 1990). This can limit a female's ability and desire to participate in physical activity, explaining why the majority of females deem sports bras a necessity (Brown et al., 2014). As well as issues of short-term discomfort due to breast movement, greater breast displacement has also shown to increase breast skin strain and have negative implications on breast health (Norris et al., 2020). Greater mechanical skin strain is also thought to be related to breast ptosis (sag) in later life and can manifest as striae distensae (Devillers et al., 2010). Thus, further highlighting the need for effective breast support. As such, it is unsurprising that 86% of females deem sports bras to be an essential piece of equipment during exercise (Brown et al., 2014).

The necessity of females to wear a sports bra, as well other required layers of clothing, reduces the air movement near the skin, insulating the body and reducing the ability to evaporate sweat (Brotherhood, 2008; Liu et al., 2022). If sweat cannot evaporate, the body's effectiveness at reducing skin temperature is reduced as well as radiant and convective heat transfer (Havenith, 1999; Havenith et al., 2002). This reduction in heat loss efficiency due to clothing is exacerbated when clothing fits tightly (commonly the case in sports bras) as it reduces the exchange of air beneath the clothing (Caravello et al., 2008). Furthermore, a build-up of sweat between the skin and clothing increases friction during movement which generates heat and further elevates T_{skin} thus reducing thermal comfort (Liu et al., 2022). This effect may be more prominent in larger breasted females, who see greater breast displacement.

The limited understanding of breast-specific thermoregulation, sensory perception, and dynamic breast mechanics related to breast size constrains evidence-led design. To better support females remaining active, particularly those with larger breasts, there is a need to characterise breast motion, heat and sweat responses, and associated discomfort, to inform sports bra design that optimises both mechanical support and thermal comfort.

To summarise, female participation in exercise is shaped by physiological change, body morphology, and the interaction between the body and sports apparel across the lifespan. Limited understanding of female-specific thermoregulation, sweat responses, and sensory perception - particularly during puberty and in relation to breast size - constrains evidence-led apparel design and contributes to discomfort and reduced participation. The following literature review therefore examines current evidence in this field to identify key knowledge gaps and justify the research undertaken in this thesis.

Chapter 2 Literature Review

A literature review was carried out to evaluate the current research investigating the complex demands of female thermal physiology during puberty and across variations in the extent of breast development. This literature review firstly aimed to summarise our contemporary understanding of human heat balance and clothing ergonomics, and the underlying autonomic and behavioural mechanisms that regulate body temperature. This was followed by a more focussed narrative review on sex differences and female-specific thermoregulation which aimed to achieve the following objectives:

1. To critically evaluate how female-specific factors, such as breast development and hormonal maturation, may impact on autonomic and behavioural thermoregulatory mechanisms.
2. To identify knowledge gaps on how modulators of female thermoregulation (e.g. body morphology and hormonal development) may impact sport apparel comfort and performance during exercise.

A structured literature search was conducted to identify relevant research examining female thermoregulation and the implications of sports apparel design for comfort and participation. Searches were performed across multiple electronic databases including PubMed, Scopus and Web of Science. Search terms were developed iteratively based on the research aims and combined using Boolean operators. Key concepts included: female thermoregulation, sex differences, sweating, thermal perception, puberty and adolescence, breast biomechanics, breast motion and discomfort, sports bras, sports apparel, clothing microclimate, moisture management, and exercise heat stress. These terms were combined using operators such as AND and OR to refine results (e.g. female AND thermoregulation AND exercise; breast motion AND sports bra; puberty AND sweating).

2.1 Human heat balance

Humans need to maintain their internal body temperature around 37℃ despite considerable changes to their external environment (Hardy, 1961). A stable thermal condition helps to ensure optimal cellular function as overheating (core temperature [T_{core}] > 38.5℃) or overcooling (T_{core} < 36℃) can pose a considerable challenge to our survival (Gisolfi et al., 2000). The variability of our surrounding environment requires constant autonomic and behavioural thermoregulatory changes to maintain our internal body temperature in dynamic balance (McArdle et al., 2010).

For humans to maintain a stable core temperature, a heat balance exists by which heat production and inputs must be balanced by heat outputs. The conceptual heat balance equation expresses the dynamic equilibrium required between heat loss and gain from the body (Parsons, 2007):

$$M - Wk = E + R + C + K + S$$

Where:

M = rate of metabolic energy production ($W \cdot m^{-2}$)

Wk = rate of mechanical work ($W \cdot m^{-2}$)

E = rate of evaporative heat loss ($W \cdot m^{-2}$)

R = rate of radiative heat loss ($W \cdot m^{-2}$)

C = rate of convective heat loss ($W \cdot m^{-2}$)

K = rate of conductive heat loss ($W \cdot m^{-2}$)

S = rate of heat storage ($W \cdot m^{-2}$)

The metabolic rate (M) provides energy for mechanical work (Wk). The net difference between these (M – Wk) is always positive and represents the amount of energy released by the body as heat. To achieve heat balance, thus no heat storage (S = 0), the heat generated by the body has to equal the heat released by the four main avenues of heat loss: evaporation (E), radiation (R), convection (C), and conduction (K). When net heat gain occurs, heat storage becomes positive, and body temperature will increase. When net heat loss occurs, heat storage is negative, and this results in a decrease in body temperature (Parsons, 2007).

Humans have evolved to use clothing as a means of supporting thermoregulation, extending their ability to maintain heat balance and withstand both heat and cold stress. Clothing acts as a barrier to heat and moisture transfer from the body to the environment. This can be protective against extreme heat or cold, however it can also limit heat loss pathways and limit heat exchange during activity. Clothing itself and the boundary layer of air it encloses can impact dry and evaporative heat loss, as evidenced by these equations (Havenith, 1999):

$$\textbf{Dry heat loss} = \frac{(t_{sk} - t_a)}{I_T}$$

Where:

t_{skin} = skin temperature

t_a = air temperature

I_{tot} = clothing insulation, including air layers

$$\textbf{Evaporative heat loss} = \frac{(p_{sk} - p_a)}{R_e}$$

Where:

p_{sk} = skin vapour pressure

p_a = air vapour pressure

R_e = clothing vapour resistance, including air layers

Different characteristics of clothing that may impact heat balance are outlined in Table 2-1 (Bishop et al., 2014). Dry heat transfer through clothing is mainly due to conduction and radiation. For most clothing, the volume of air enclosed within the fabric and between the garment and skin is greater than the volume of the fibres, such that insulation is largely dependent on the thickness of the material (i.e. the enclosed air layer) or the fit of the garment (i.e. loose or tight) (Havenith, 1999). For materials of a standard permeability, thickness plays a major role in insulation and vapour resistance. However, reduced permeability will retard sweat evaporation increasing the water vapor pressure in the micro-environment thus slowing the rate of evaporation and heat dissipation from the skin.

Regarding fit, loose-fitting clothing allows for dynamic air exchange thus facilitates convection or evaporation which helps keep the microclimate next to the skin cooler. In contrast tightly fitting clothing tends to trap air within the boundary layer, thus restricts that dynamic air exchange and has more of an insulative effect. Indeed, all these characteristics interact with one another to create an overall ergonomic effect.

Table 2-1. The key characteristics of clothing affecting ergonomics.

Clothing characteristic	Impact
Weight	Effects the energy cost of movement to move the additional weight
Resistance to movement	↑ Restriction = ↑ energy required to move
Clothing insulation	Effects the micro-environment. ↑ insulation = ↓ heat transfer rate
Clothing permeability	Effects the micro-environment. ↓ permeability = ↓ sweat evaporation rate
Clothing reflectivity	Effects the heat gain. ↑ reflective exterior = ↓ heat gain
Percent of body surface area covered	↑ body surface covered = ↑ barrier for heat exchange
Fit	Effects air pumping / exchange
Fabric	Moisture transfer, thickness, and comfort can impact evaporation, heat exchange and thermal comfort

To achieve a state of heat balance, humans regulate their body temperature via autonomic and behavioural mechanisms, which will be discussed in the sections below.

2.2 Autonomic thermoregulation

Thermoreceptors are temperature sensitive neurons located in the periphery (i.e., skin) and centrally (i.e., brain, spinal cord, and viscera) in the human body (Nakamura, 2011). These neurons respond to thermal changes in their receptive fields and send afferent information to various areas of the central nervous system (e.g., midbrain, pons and medulla oblongata) in response to temperature stimuli (i.e., warm or cold). The pre-optic hypothalamus is widely accepted to be the central thermal controller (Romanovsky, 2007). In response to afferent stimuli, this area sends commands to peripheral thermo-effectors, which trigger autonomic responses to maintain body temperature despite environmental challenges. Autonomic thermoregulatory responses primarily consist of changes to vasomotor tone (i.e. vasoconstriction and vasodilation), sudomotor activity (i.e. sweating) and activation of shivering and non-shivering thermogenesis (Nakamura, 2011) (Figure 2-1). For example, as core temperature drops, neural drive to heat gain effectors is increased and heat loss is inhibited (Mekjavic & Eiken, 2006) through vasoconstriction of peripheral blood vessels and closing of arteriovenous anastomoses, thus reducing heat loss from the body via convection, conduction and radiation. When core temperature increases, heat gain centres are inhibited (Mekjavic & Eiken, 2006) and heat loss mechanisms activated allowing heat loss from the skin to environment through vasodilation of peripheral blood vessels, such that heat is lost via radiation and condution (Armstrong & Armstrong, 2000). If this heat loss is insufficient, sweating is stimulated to allow heat loss through the most effective channel of evaporation. The autonomic thermoregulatory responses pertaining to changes in vasomotor tone and sudomotor responses are discussed in further detail below (See 2.2.1 and 2.2.2).

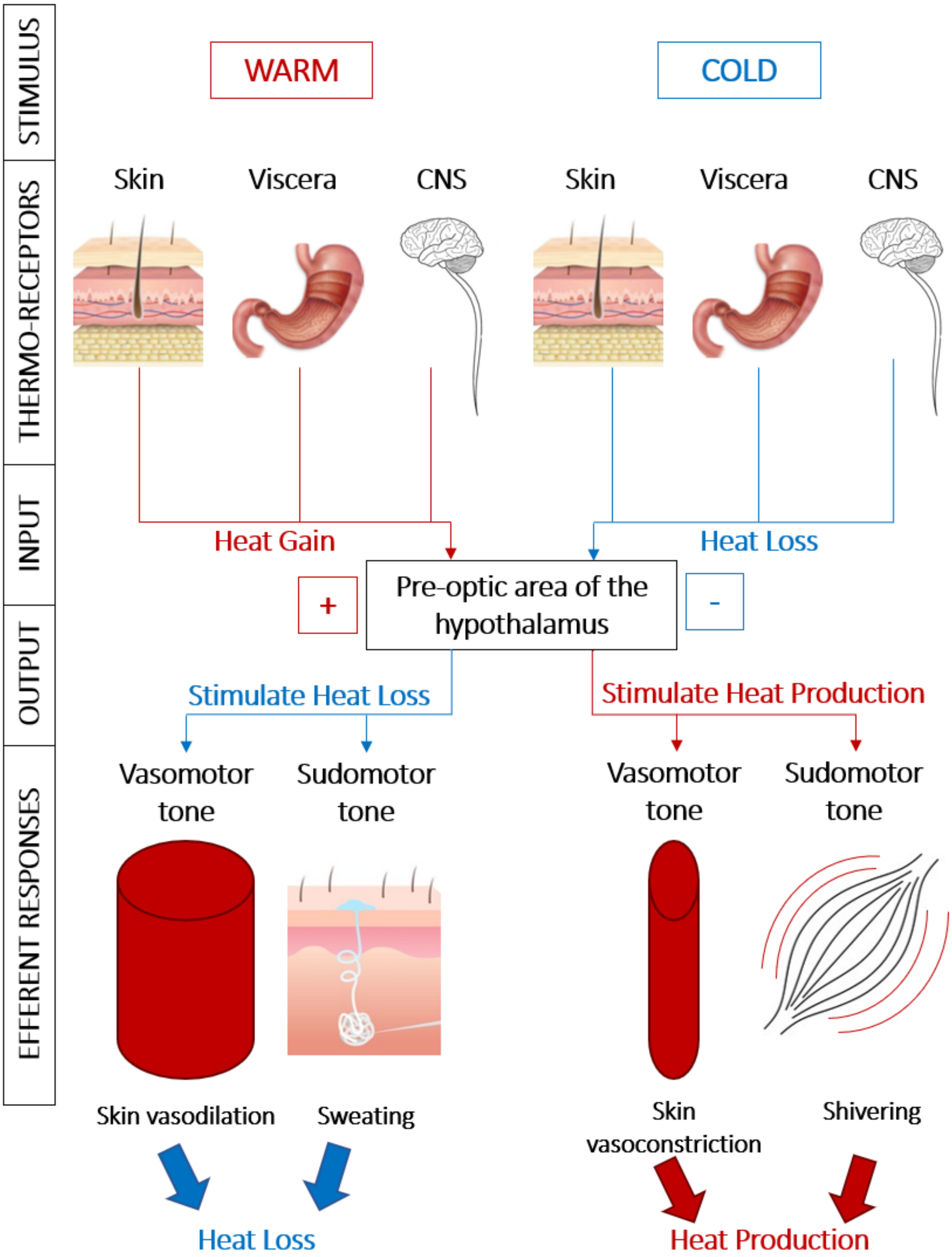


Figure 2-1. A schematic representation of the autonomic responses triggered by changes in body temperature. CNS: Central nervous system.

2.2.1 Regulation of skin vasomotor responses

The control of skin blood flow through vasomotor adjustments is vital for the maintenance of a stable body temperature and homeostasis (Parsons, 2014). Resting skin blood flow in thermoneutral conditions is maintained at around 250 mL/min with minimal physiological exertion (Charkoudian, 2003). When the core temperature fluctuates from its stable point (~37°C), either above or below specific thresholds, autonomic responses controlled by the pre-optic area are activated (Mekjavic & Eiken, 2006).

In response to drops in body temperature, heat loss from the body is limited through vasoconstriction. Vasoconstriction is a progressive response; whereby skin blood flow is reduced to keep the warmer blood near the core and vital organs. The intensity of the vasoconstriction is regulated by the intensity of the cold stimulus until a minimum plateau of skin blood flow occurs, after which no further constriction takes place (Holowatz & Kenney, 2010).

Conversely, in response to rises in body temperature, heat loss from the body is initially facilitated through vasodilation (Parsons, 2014). The cardiovascular system can increase peripheral blood flow as high as 6-8 L/min (Rowell, 1974) - enabling greater heat loss via convection, conduction and radiation from the skin. The vasodilation response is biphasic in nature (Charkoudian, 2003). This is an initial rapid reflex response occurring in the first 3-5 minutes of heating which is supposedly mediated by the co-transmission of acetylcholine and other potential unknown neurotransmitters from sympathetic cholinergic vasodilator nerves (Charkoudian, 2003; Holowatz & Kenney, 2010). Then there is a secondary, slower vasodilation phase which plateaus after ~25-30 min (Minson et al., 2001).

If the heat loss requirements exceed the capacity of vasomotor changes, then the sweat glands are stimulated to initiate the production of sweat, in order to augment heat loss via evaporation. This shift from dry heat exchange via vasomotor adjustments to evaporative cooling via sudomotor activation represents the second major autonomic thermoeffector pathway engaged during heat stress.

Together, vasomotor and sudomotor responses work congruently to regulate body temperature; however, their effectiveness is not solely determined by neural control. The capacity of these systems to dissipate heat is also shaped by the physical characteristics of the individual and the biophysical properties of heat exchange. The following section (2.2.2) examines the regulation of sudomotor responses in detail, before Section 2.2.3 considers the biophysical determinants that ultimately modulate the net effectiveness of these autonomic mechanisms.

2.2.2 Regulation of sudomotor responses

Evaporation of sweat is the body's main method of heat dissipation during exercise in heat and/or exposure to hot environments (Brotherhood, 2008; Havenith, 1999; Havenith et al., 2008). This is most apparent when the ability to evaporate sweat is limited. For example, individuals wearing insulating clothing and equipment (McLellan et al., 2013) or those with disorders such as anhidrosis (Sato et al., 1989) can see sharp rises in body core temperatures during exercise and heat stress.

Once the capacity of the vasomotor response to maintain a stable T_{core} is exceeded, sweat glands are stimulated to initiate and/or increase sweat production and thus heat loss through evaporation. The evaporation of sweat requires energy, in the form of heat from the skin surface, causing sweat to change from a liquid to gas. This process requires 2430 joules per gram ($J \cdot g^{-1}$) of water at 30 ºC (Gibson & Charmchi, 1997). The evaporation of sweat from the skin surface causes the cooling of the skin and the blood close to the periphery. The cooled blood then circulates more centrally in the body, thus maintaining a positive gradient from core to skin for heat loss (Parsons, 2014).

It is estimated that there are between 2-5 million sweat glands over the body with large inter-individual variation in relation to age and race (Kuno, 1956; Szabo, 1958). Three main types of sweat glands exist: apocrine, eccrine and apoeccrine (Table 2-2). By 8 months of development, eccrine sweat glands have developed such that they resemble those of adults (Sato, 1977) (Figure 2-2). Then, from the age of 2, the number of active sweat glands does not alter with age (Kuno, 1956; Szabo 1958), thus sweat gland density (SGD) decreases with skin expansion during growth. Sweat gland density is important as the maximum attainable whole body sweat rate is determined by the number of activated glands and the output per gland (Buono & Connolly, 1992).

Table 2-2. Sweat gland types; structure and function (Sato, 1983; Sato, 1977; Kuno, 1956, Szabo, 1958)

Gland type	Body location	Sweat quantity	Main stimulus
Eccrine	Full body surface	↑↑	Thermal
Apocrine	More restricted regions associated with hair follicles: - Forehead - Axilla - Palmar - Plantar - Pubic regions	↑	Psychological
Apoeccrine (hybrid gland)	Axilla	↑↑↑ 10 x eccrine gland	Thermal + psychological

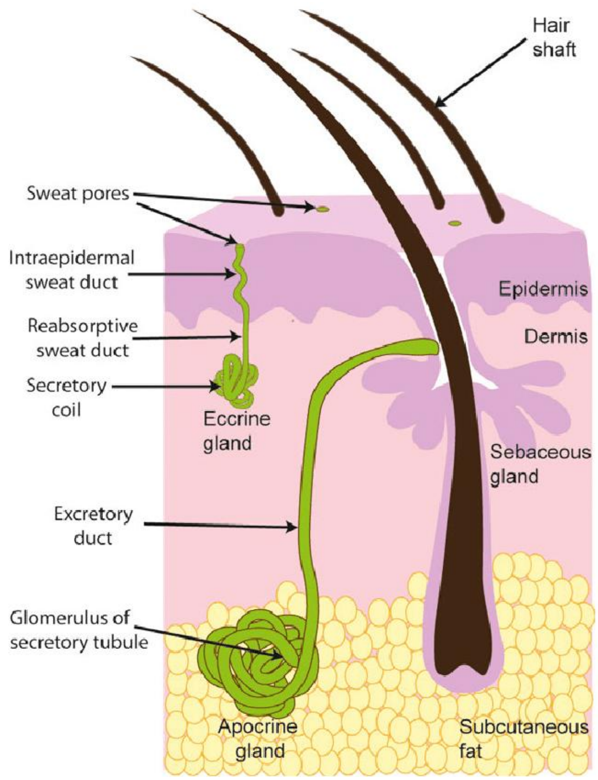


Figure 2-2. Basic sweat gland structure. The eccrine gland is comprised of a secretory coil and a sweat duct opening on the skin surface. The apocrine gland sits in the subcutaneous fat layer with a secretory duct that opens into a hair follicle. Reprinted with permission from Hu et al. (2018).

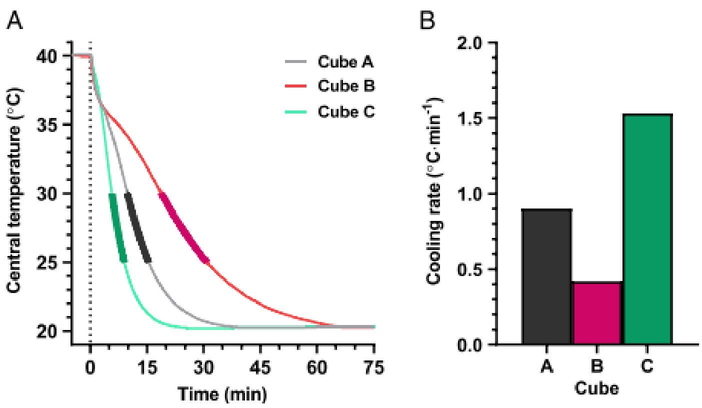
Importantly, although sweating represents a primary autonomic avenue for heat dissipation, the effectiveness of this sudomotor function is ultimately constrained by biophysical factors that determine whether secreted sweat can evaporate. These include the available body surface area for evaporation, the thermal gradient between the skin and environment, and differences in body morphology that influence heat storage. Thus, even if two individuals generate similar sweat outputs, the resultant cooling can differ substantially depending on their anthropometry or the environmental context.

Accordingly, to interpret sudomotor responses accurately - particularly when comparing groups that differ in age, sex, or body size - it is necessary to account for these biophysical determinants of heat exchange. The following section outlines these passive biophysical factors that interact with autonomic thermoeffector activity to determine the net effectiveness of sweating and overall heat balance.

2.2.3 Biophysical determinants of autonomic thermoregulation

In the prescription of exercise for thermoregulatory studies, especially those investigating sweat rates, failure to account for differences in body morphology and size can considerably confound the interpretation of findings (Jay & Cramer, 2015). Heat dissipation is largely dependent on biophysical modulators of sweat production and its evaporation, and the available body surface area for dry and evaporative heat exchange. Whilst we often consider thermoregulatory function and individual differences in relation to the effectiveness of thermoeffector responses that actively facilitate heat loss, it is also necessary to consider that the body is a passive vessel of heat exchange that transfers heat with the environment in relation to its mass, surface area, composition, and the thermal and vapor-pressure gradients between the skin and environment (Notley et al., 2020). As such, when exposed to the same ambient conditions, variation in physical characteristics between individuals (i.e. body surface area [BSA], BSA:mass, body fat %) will play a role in heat exchange, thus the rate of heat loss or storage.

The heat storage capacity of an object is a function of its volume (mass), whereas heat exchange is surface-area dependent. Therefore, the ratio between BSA and mass partially determines the rate of heat storage and exchange. Human heat exchange is highly complex (Gagge & Nishi, 2011), yet it is possible to consider a simplified version of heat exchange based on an objects shape and size, exemplified by Notley et al. (2020). In their example of 3 cubes, two cubes (cubes A and B) have identical composition, but differing size (Figure 2-3). The third cube, cube C, is equal size to cube A, but is comprised of different materials to reflect the divergent thermal properties of adipose (cube A; beeswax) and muscle tissue (cube C; plasticine), thus causing cube C to have a higher density and lower heat capacity than cube A (Figure 2-3). All cubes are heated to a uniform internal temperature (40°C) using a stirred water bath before being plunged into a cooler water bath (20°C). When considering cube A and B, although cube B had a larger mass and surface area, cube A had the faster cooling rate (0.4°C·min^{-1} vs 0.9°C·min^{-1}; Figure 2-3), due to its smaller size, and thus, higher specific surface area. Put in the context of humans, a girl aged 8 (mass, 33kg; BSA, 1.15m^2; BSA:mass, 0035m^2/kg) would have a lower mass and BSA but higher BSA:mass than a young woman aged 18-25 (mass, 70kg; BSA, 1.80m^2; BSA:mass, 0.026m^2/kg), thus when a thermal gradient exists for heat gain (i.e. ambient temperature higher than the skin), children would gain more heat per unit mass. However, thermal properties of tissue (e.g. muscle and fat) can also alter convective heat transfer. For example, considering cube A and C, cube C cools more rapidly than cube A (1.5°C·min^{-1} vs 0.9°C·min^{-1}; Figure 2-3), due to its higher density and thermal conductivity, but lower specific heat capacity. Body adiposity and muscularity is generally higher in adults than children thus can have an impact on rates of dry heat transfer.



C

	Cubes		
	A	B	C
Mass (g)	61	207	107
Density (kg·m^{-3})	960	960	1678
Conductivity (W·m^{-1}·°C^{-1})	0.35	0.35	0.65
Heat capacity (kJ·kg^{-1}·°C^{-1})	3.200	3.200	1.354
Dimensions (cm)	4x4x4	6x6x6	4x4x4
Surface area (cm^2)	96	216	96
Specific surface area (cm^2·g^{-1})	1.57	1.04	0.90

Figure 2-3. Example by Notley et al. (2020) of physical models (three cubes; A, B, and C) to illustrate the influences of variations in morphology and composition on passive heat exchange. Cubes were heated in a stirred water bath (40°C) to a common central (core) temperature and then cooled in a second water bath (20°C). [A] Time-dependent changes in central temperature in each object. [B] Cooling rate of each cube over a 5°C temperature range (30°C to 25°C), as bolded in Panel A. [C] Dimensions and thermal properties of each cube. Cubes A and B (both beeswax) differed only in size. Cubes A and C differed only in composition, with cube C being made of plasticine. Reprinted with permission from Notley et al. (2020)

As evidenced by the example above, isolating the independent effect of sex and/or maturation on thermoregulatory responses to heat stress is convoluted because of differences in physical characteristics between individuals. However, recent research has shown that unbiased investigations of whole body sweat rates (WBSR), local sweat rates (LSR) and T_{core} changes between individuals of different morphology can be made by prescribing exercise at a fixed rate of absolute evaporative requirements for heat balance (E_{req}: W), E_{req} scaled per unit body surface area (W/m^2), and metabolic heat production scaled to body mass (H_{prod}; W/kg), respectively (Cramer & Jay, 2014, 2016, 2019; Gagnon et al., 2013; Jay & Cramer, 2015). Through the removal of the influence of these basic physical confounders, one can better isolate the effect of the independent variable under investigation (i.e., sex, biological maturation) (Figure 2-4).

E_{req} is the sum of metabolic heat production and dry heat exchange (where a positive value indicates dry heat gain and a negative value indicates dry heat loss) (Cramer & Jay, 2015; Gagnon et al., 2013). In studies where the principal aim of an investigation is to examine differences in sweating rates, either whole body or local, ambient conditions can be set to limit the temperature gradient between the skin and environment, thus limiting the avenue for dry heat exchange. In this context, E_{req} would then be largely equitable to H_{prod}. For example, to investigate differences in WBSR, one would prescribe exercise at a fixed E_{req} in W, or if the ambient conditions minimised dry heat exchange, exercise could be prescribed at a fixed H_{prod} in W (Cramer & Jay, 2015; Gagnon et al., 2013). In contrast, a fixed WBSR in individuals with a smaller BSA (e.g., females and children) will result in higher LSR (mg/cm^2/min) (Morris et al., 2013). Therefore, to allow for unbiased comparisons of steady-state LSR, exercise must be prescribed at a fixed E_{req} in W/m^2 or H_{prod} in W/m^2 if the ambient conditions are appropriate (Cramer & Jay, 2014, 2015) (Figure 2-4). Finally, a change in T_{core} is primarily dictated by heat storage per unit body mass (Cramer & Jay, 2014, 2016). Therefore, in individuals differing in body mass, such as a child vs an adult, to elicit the same level of heat storage, thus T_{core} change, exercise should be prescribed in H_{prod} in W/kg (Figure 2-4).

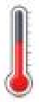
Variable	H_{prod} / Intensity	12 yrs 42 kg 1.51 m 1.33 m² 45 mL·kg⁻¹·min⁻¹	13 yrs 48 kg 1.64 m 1.50 m² 50 mL·kg⁻¹·min⁻¹	29 yrs 60 kg 1.65 m 1.65 m² 45 mL·kg⁻¹·min⁻¹	25 yrs 75 kg 1.80 m 1.90 m² 55 mL·kg⁻¹·min⁻¹
 **T_c change**	**$W \cdot kg^{-1}$**	**8.0**	**8.0**	**8.0**	**8.0**
	W	340	380	480	600
	$W \cdot m^{-2}$	260	250	290	315
	$\% VO_{2peak}$	55	52	55	48
 **WBSR**	$W \cdot kg^{-1}$	8.0	7.1	5.7	4.5
	W	**340**	**340**	**340**	**340**
	$W \cdot m^{-2}$	260	230	210	180
	$\% VO_{2peak}$	55	49	44	31
 **LSR**	$W \cdot kg^{-1}$	8.0	8.1	7.2	6.6
	W	340	390	430	490
	$W \cdot m^{-2}$	**260**	**260**	**260**	**260**
	$\% VO_{2peak}$	55	52	53	41

Figure 2-4. Example of exercise prescription methods (H_{prod} or $\%VO_{2peak}$) to allow for unbiased investigations of changes in core temperature (Tc), whole body sweat rate (WBSR), and local sweat rate (LSR) of a girl, boy, adult female, and adult male. By standardizing the work rate to investigate one variable, the H_{prod} and $\%VO_{2peak}$ required to investigate another variable differs between individuals due to physical differences in body size and fitness. Reprinted with permission from Topham et al. (2022).

Autonomic thermoregulation is a powerful process yet is limited by physiological (sweating capacity and maximal vasodilation and vasoconstriction) and biological constraints (age and anthropometric characteristics). Humans are still able to maintain a thermal balance during exposure to environmental extremes due to behavioural thermoregulation. Without this, autonomic responses alone could not ensure survival (Romanovsky, 2007).

2.3 Behavioural thermoregulation

Thermal homeostasis is primarily based on behavioural thermoregulation and secondarily on autonomic and endocrine mechanisms (Attia, 1984). Behavioural thermoregulation aims to avoid impending thermal stress and acts to maintain heat balance and prevent activation of energy consuming autonomic responses (Flouris & Schlader, 2015). This can present simply as seeking shade on a hot day (Parsons, 2007) or changing posture and donning or doffing clothing (Schlader et al., 2010) to maintain thermal comfort. During exercise, the most obvious and effective behavioural response is to reduce the rate of external work (Flouris & Schlader, 2015).

Thermal comfort is defined as the “state of mind that expresses satisfaction with the surrounding environment” whereas thermal sensation is defined as “the perception of a given peripheral stimulus resulting from the stimulation of peripheral and central thermoreceptors” (ASHRAE, 1997). Thermal comfort is a product of the combined interaction of physical, physiological, and psychological factors which require information from thermal sensations to provide this sense of comfort, thus influence behaviour. Physical factors driving thermal comfort include environmental characteristics e.g. temperature or humidity (Parsons, 2007). Physiological drivers refer to the autonomic responses driven by thermal sensation (Flouris, 2011). Psychological factors relate to an individual’s perception of comfort in their thermal environment based on their internal environment, personal experiences and affective judgement (De Dear, 2011)

One of the essential underlying mechanisms to successfully manage thermal behaviour and comfort is that of skin sensitivity to temperature and wetness. Sensory experiences facilitate the enjoyment of many aspects of daily life but also aid humans to sense threats imposed by the external environment, such as environmental threats (e.g. ambient temperature and humidity), and to sense interactions with objects that contact the skin, such as clothes. Environmental threats or interactions with clothing, which may cause discomfort, are sensed by specialised nerve endings in the skin (e.g. thermoreceptors and mechanoreceptors) and can be mitigated through changes in behavioural thermoregulation (e.g. donning / doffing / rearranging clothing). It is human skin sensitivity that dictates behavioural thermoregulatory control (Mekjavic et al., 2021; Schlader et al., 2011). It is also skin sensitivity that is a primary factor in the feeling of comfort of sportswear, for example, which feeds into exercise uptake and maintenance of an active lifestyle (Wilfling et al., 2022).

Behavioural thermoregulation is therefore the first line of defence against thermal strain and operates through the continuous integration of sensory information arising from the skin.

Because these behavioural choices depend fundamentally on how thermal and tactile cues are detected and interpreted, an understanding of the skin and its sensory receptors is essential. The following section outlines the structure and functional properties of human skin as the medium through which thermal, tactile, and wetness sensations are generated.

2.3.1 The human skin

The skin is the largest organ of the human body, with its structure being divided into three layers; the epidermis, the dermis and subcutaneous tissue (Figure 2-5) (Parsons, 2014). The epidermis is divided into five strata. The most superficial layer of the epidermis, the stratum corneum, consists of 15–20 layers of dead anucleated cells, named corneocytes. The deepest strata contain the region in which the keratinocytes (main epidermal cells) proliferate and slowly progress through the strata. The other cell types include melanocytes, producing the colour pigment, melanin, Langerhan cells responsible for immune response and Merkell cells that provide tactile sensation. Beneath the epidermal layer one finds the dermis which contains blood and lymphatic vascular systems, sweat glands and nerve endings at varying depths. The fibroblasts produce extracellular matrix components, collagen, elastin and hydrophilic proteoglycans, which vary within the dermal layers. Beneath the dermis lies a layer of subcutaneous tissue, a fibro-fatty layer loosely connected to the dermis, which varies considerably with anatomical site, age, gender, race, endocrine and nutritional status of the individual and acts to insulate the musculature below (Arens & Zhang, 2006).

Functionally, the skin plays vital roles in sensation, homeostasis and protection (Schepers & Ringkamp, 2010). The highly organised skin is designed to allow gas/fluid transport across its surface and maintain the internal thermal homeostasis, via the sweat glands and blood vessels. Other functions include protection of underling tissues and organs, excretion, immunity and synthesis of vitamin D (Pasparakis et al., 2014). However, the external environment can be detrimental to these functional roles when the skin is exposed to a range of insults, which may be mechanical, physical, biological and chemical in nature. Yet human skin is an anisotropic, nonlinear viscoelastic, loading history–dependent material thus is resilient to a range of insults (Joodaki & Panzer, 2018).

The structure of skin supports its role in thermoregulation (sensory, vasomotor and sudomotor responses) (Arens & Zhang, 2006). Cutaneous sensation of different modalities is sensed through several specific receptors in the skin. Receptors are grouped according to the nature of the stimuli that activates them, i.e., thermoreceptors (receptive to temperature), mechanoreceptors (receptive to tactile pressure or distortion), nociceptive (receptive to pain) (Figure 2-5). Cutaneous sensation also varies across body locations due to the density and sensitivity of different receptors in those areas (Gerrett et al., 2014; Myles & Binseel, 2007). For example, regarding warm thermal sensation, Gerrett et al. (2014) found thermal sensation to be greatest at the head and torso, and with lower sensitivity at the extremities. Whereas cold sensitivity was found to be greatest at the lateral abdomen and mid back (Ouzzahra et al., 2012).

As discussed, the structure of the skin underpins its role in thermoregulation through its sensory, vasomotor and sudomotor capabilities. These sensory functions form the basis of how humans detect environmental threats, evaluate comfort, and initiate behavioural strategies to maintain thermal balance. Because thermal comfort and behavioural responses arise from the perception of thermal, mechanical, and wetness-related stimuli, the next sections examine each of these sensory modalities in turn.

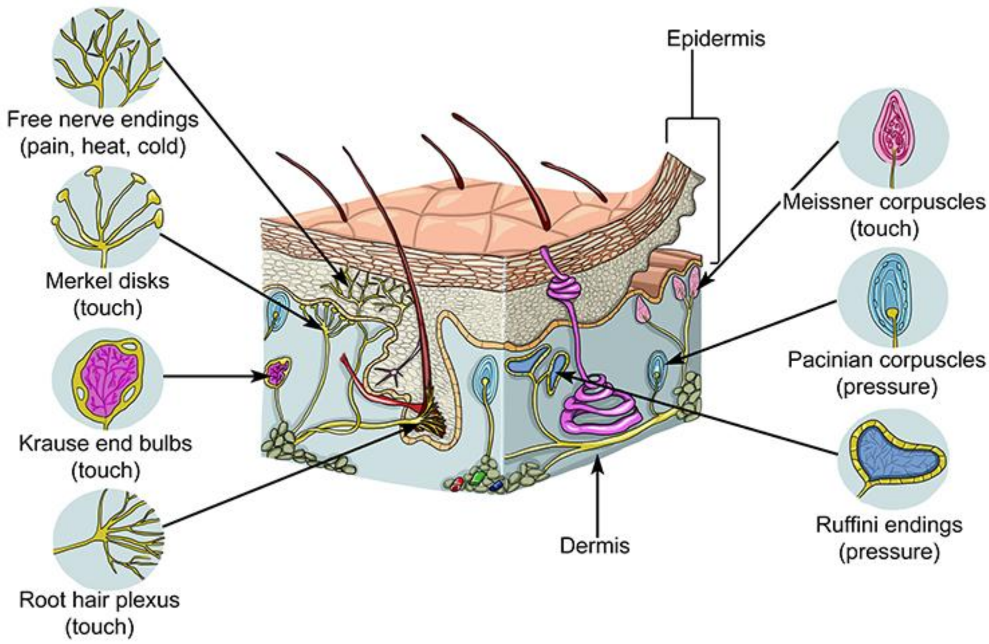


Figure 2-5. Schematic representation of receptors in human skin. Reprinted with permission from Carlson (2018).

2.3.2 Thermal sensitivity

The complex neural network that encompasses the human thermoregulatory system consists of various interconnected feedback loops. Our ability to detect temperature changes is due to the presence of strategically located thermosensitive neurons, known as thermoreceptors (Parsons, 2014). Thermoreceptors are free nerve endings located in the periphery (i.e. skin) and centrally (i.e. brain, spinal cord and viscera) that transduce, encode, and transmit thermal information along afferents that project into the superficial dorsal horn of the spinal cord. The output neurons of this then project into the hypothalamus and brainstem (Craig, 2011). Thermoreceptors are classified depending on their response to thermal stimuli; warm and cold receptors work over different temperature ranges and differ in their number and firing rate (Nakamura, 2011). The distribution of thermoreceptors is not uniform across the body. Cold fibres tend to be located further towards the periphery, are more superficial to the skin surface and are activated between 15-38℃, with a transient response that peaks between 23-28℃. In contrast, warm fibres tend to be located more centrally in the body, thus tend to be found slightly deeper in the skin and are activated around 33℃ and peak between 40-43℃ (Schepers & Ringkamp, 2010). This is due to the greater threat to survival being posed by overheating, as we have an upper survival T_{core} limit of >40.5℃ in contrast to our lower limit of <32℃. Skin properties and requirements can lead to considerable variation in the location and distribution of thermoreceptors which in turn, plays a large role in determining thermal sensation (Davoodi et al., 2018). This can explain the regional differences in thermal sensitivity across the body and the potential impact of growth or skin surface area changes.

Local and whole-body thermal sensation refers to the perception experienced by an individual in response to a temperature stimulus and is one of the main sensory modalities of the skin (Hensel, 1981; Schepers & Ringkamp, 2010). Several factors influence the degree of thermal sensation. Firstly, the magnitude and rate of temperature change govern neural firing rates which in turn influences the degree of perceived thermal sensation (Arens et al., 2006; Flouris & Schlader, 2015); the greater the difference between skin temperature and a stimulus, the greater the degree of thermal sensation. Furthermore, thermal sensation has been shown to be influenced by the surface area exposed to a given stimulus due to the phenomenon known as spatial summation (Courtin et al., 2023); the larger the surface area of skin exposed to a thermal stimulus, the greater the magnitude of perceived sensation due to activation of a relative larger receptive field.

Females pass through several age-related morphological changes that may influence thermal perception; however, tactile perception is also a critical contributor to behavioural and clothing-related comfort. Because tactile input shapes both physical comfort and the perception of clothing–skin interactions, it is necessary to consider tactile sensitivity alongside thermal sensitivity. The following section therefore outlines the underlying receptors and functional relevance of tactile detection.

2.3.3 Tactile sensitivity

Tactile receptors fall under the umbrella of mechanoreceptors which detect touch, pressure and vibration stimuli (McGlone & Reilly, 2010). The sensation of touch can take many forms; texture, shape, force, friction, pain, and other related physical properties (Dargahi & Najarian, 2004). Non-noxious cutaneous touch sensations are mediated by a variety of primary afferent nerve fibres that transduce, encode and transmit tactile information to the central nervous system (Serino & Haggard, 2010) Tactile receptors comprise of corpuscular (specialised cells) and non-corpuscular (free nerve endings) nerve endings which are centrally integrated to drive a central nervous system response. The root hair plexus is made up of free nerve endings which are stimulated by hair displacement and respond to distortion and movement across the body surface. Meissner corpuscles are sensitive to fine touch and pressure stimuli and low-frequency vibrations. The Merkel's disks are also fine touch and pressure receptors but mainly located in the deepest epidermal layer of the hairless skin. Pacinian corpuscles are large receptors sensitive to deep pressure, pulsing and high-frequency vibrations. Finally, Ruffini corpuscles are sensitive to pressure and distortion of the skin and are found in the deepest layer of the dermis.

As with thermal sensation, skin surface area plays a role in tactile sensation. Previous research investigating breast sensitivity to tactile stimuli has indicated that larger breasts tend to have lower sensitivity (as evidenced by higher tactile detection thresholds) (Cornelissen et al., 2018; DelVecchyo et al., 2004; Tairych et al., 1998), as well as lower spatial acuity (Long et al., 2022), than smaller breasts.

Tactile sensations are a fundamental cutaneous sensory attribute that is necessary for sensing the external physical world, including one's interaction with clothing, e.g. the bra (Havenith, 2002; Song, 2011). Mechanoreceptors innervating the skin convey sensory inputs associated with feelings of pressure, itchiness and clinginess which are key drivers in the perception of clothing comfort (Song, 2011), thus have value when considering application to clothing design. Furthermore, tactile sensation is also integral to the perception of wetness, which arises from the integration of both mechanical and thermal cues. Given that wetness perception strongly influences thermal comfort, behavioural responses, and clothing acceptability during activity, it warrants separate examination. The subsequent section explores the sensory basis and regional variation of wetness perception.

2.3.4 Wetness perception

Thermosensitivity is not the only cutaneous sensory factor that contributes to autonomic and behavioural thermoregulation. The perception of wetness on the skin is also a key driver for behavioural and autonomic adaptations. Physical skin wetness is defined as the proportion of the skin that is wet (e.g. due to sweat, saturated clothing or water immersion) at a given time (Gagge, 1937). However, it is the perception of changes in skin wetness and ambient humidity that play a role in thermal comfort (Fukazawa & Havenith, 2009; Gagge et al., 1967) and clothing discomfort (Hollies et al., 1979), which in turn has shown to impact thermoregulatory behaviours (Schlader et al., 2010; Vargas et al., 2018).

From an autonomic standpoint, sweat gland function can be supressed in the presence of physically wetted skin due to hidromeiosis (Brown & Sargent Ii, 1965) which limits the body's ability to lose heat to the environment via evaporation. However, despite this impact of physical wetness on thermoregulation, no evidence exists that humans have cutaneous moisture receptors, i.e. hygroreceptors (Clark & Edholm, 1985).

The perception of wetness has therefore been described as a synthetic response due to the integration of thermal and tactile inputs and as a result of perceptual learning (Filingeri, Fournet, et al., 2014b; Tiest et al., 2012). From a thermal perspective, perceptions of wetness are associated with the thermal conductivity of water and from the cooling provided from the evaporation of water from the skin. Water has a higher thermal conductivity than air such that when the skin is wet, heat is conducted away from the skin faster than when dry. Therefore water provides a cooling sensation (Tiest et al., 2012). This link between temperature sensation and the perception of wetness was further highlighted when Filingeri, Redortier, et al. (2014) demonstrated that with the application of a cold-dry stimulus (cooling rate of 1.4 to 4.1°C), one could invoke a perception of wetness, even in the absence of water.

The mechanical pressure of liquid and other tactile-related sensations, i.e. stickiness sensations, are also involved in the perception of wetness. For example, wet fabrics tend to cling to the skin which results in feelings of stickiness, thus contributes to the perception of wetness (Connor et al., 1990). Also, the presence of water in textiles in contact with the skin increases skin friction (Zimmerer et al., 1986).

If we accept the hypothesis that wetness is driven by cooling and tactile sensations, one could reasonably hypothesise that region- and size-dependent variations exist across the body for wetness perception also. In a study where local skin wetness was manipulated in a cohort of males, the torso was found to have lower wetness sensitivity than the limbs (Fukazawa & Havenith, 2009). Similar findings were also reported by Gerrett et al. (2013) in a non-manipulated condition (natural sweat across the torso during exercise). Furthermore, Ackerley et al. (2012) also demonstrated that the back tended to be amongst the most sensitive body regions in females to discriminate between stimuli of different water contents (range: 0.8 - 6.6 $\mu l.cm^{-2}$). With further investigation into the torso region in males, Filingeri, Fournet, et al. (2014a) demonstrated the lateral and lower back to have a greater frequency of perceived skin wetness than the medial chest. Despite investigations into regional variations across the torso region, most of these studies have been performed in males, and those investigating females make no mention of how wetness sensitivity may differ across the breast.

Collectively, thermal, tactile and wetness perception form the sensory foundation that informs thermal comfort and drives behavioural thermoregulation. These modalities are not only essential for maintaining thermal homeostasis but also directly influence how individuals experience and interact with clothing, particularly during exercise. Understanding these sensory processes is therefore critical for designing sports apparel that accommodates the unique thermophysiological and sensory needs of the female body.

2.4 Sex differences in human thermoregulation

As discussed, human thermoregulation is a powerful and necessary regulatory process for homeotherms, yet is restricted by physiological and biophysical factors such as sweat gland density, sweat output, number of capillaries, age, gender, fitness status and other factors (Kenney & Munce, 2003; Lei et al., 2019; Martini et al., 2012; Schlader et al., 2010). The differences in thermoregulatory control due to biological sex has generally been investigated under the lens of body morphology and anatomical differences, i.e. BSA, and its biophysical and perceptual impact (Cramer & Jay, 2014; Gagnon et al., 2013; Greenfield et al., 2023), or through a hormonal lens, i.e. the impact of hormonal fluctuations in females compared to the more steady hormonal status of males (Greenfield et al., 2023; Lei et al., 2019) (Table 2-3).

Table 2-3. Autonomic thermoregulation sex differences and their consequences.

Thermoregulatory variable	Gender difference	Consequence
Set point for sweat onset (T_{core} at which sweating is stimulated)	↑ Females Hormonal fluctuations in females also modify onset thresholds across the menstrual cycle / menopause	Less efficient cooling mechanism as allows for greater increase in T_{core}.
Sweat gland density and output	↓ Females	Reduced sweat output so less efficient cooling
Surface area – mass ratio	↓ Females	Heat loss is proportional to the gradient between the skin, environment, and surface area available for heat exchange so heat loss to the environment is limited.

Heat dissipation during exercise is largely dependent on biophysical modulators of sweat production and its evaporation (discussed more in section 2.2.3). Morphologically, relative to the average male, the average female tends to have a smaller surface area, lower mass, lower fitness, higher body fat and a greater BSA:mass ratio (Corbett et al., 2023). Body mass acts as an internal 'heat sink', thus for any change in core temperature, a given heat storage is inversely related to body mass (Cramer & Jay, 2016), thus females tend to see greater increases in body temperature than males for a given work rate. Furthermore, the smaller BSA and greater BSA:mass ratio that is more characteristic of females also results in a smaller surface area for heat exchange as BSA determines the area available for heat exchange through evaporation of sweat, conduction, and radiation in conditions where the ambient temperature is less than skin temperature.

Furthermore, from a thermal sensation angle, empirical evidence suggests that innate differences may exist between men and women in their skin thermal and wetness sensitivity (Greenfield et al., 2023). Females have shown to often report greater thermal sensation for the same absolute temperature (Gerrett et al., 2014; Inoue et al., 2016; Li et al., 2008) and present greater wetness perception than males (Valenza et al., 2019). It is hypothesised that a considerable proportion of the sex differences demonstrated in local thermal and wetness perceptions may be due to differences in morphology, specifically BSA. The same absolute BSA exposed to a thermal stimulus generally corresponds to a greater proportion of a females' total BSA, thus due to the concept of spatial summation, females tend to sense a greater intensity of thermal sensation. However, when BSA, or the proportion of BSA, stimulated is matched, these differences become minimised (Filingeri et al., 2018; Luo et al., 2020). Therefore, we can conclude that morphology plays a considerable role in the sensitivity differences seen between sexes.

Thermoregulatory differences between males and females have been well researched from hormonal and morphological standpoints. However, within female comparisons remain lacking. Females develop hormonally (e.g. puberty, menstrual cycle, pregnancy, post-partum, menopause) across the life course, which can also translate to morphological changes across the body. Following similar mechanisms to the between sex differences, it's possible to hypothesise that these within female developmental adaptations, that occur over the life span, may also impact thermoregulation.

It is appreciated that the realm of within-female factors that may impact thermoregulation is vast, spanning the impact of menstrual cycle, contraception, puberty, pregnancy, ageing and menopause. To maintain the scope of this Thesis within a reasonable experimental framework, it was therefore decided to investigate the mechanisms underlying local sweat production in females and their variation across the breast and during pubertal development - two characteristic, yet understudied, female-specific scenarios - to directly inform sports apparel design that reflects the needs of the female body, moving beyond traditional male-derived design standards.

On this basis, the sections below focus on critically appraising literature relevant to these two aspects of female physiology.

2.5 Female-specific factors and their impact on autonomic and behavioural thermoregulation

2.5.1 Female body morphology variations

Female body morphology is transient across the life span, primarily as a result of hormonal changes during development. Female puberty involves an intense period of full body development and morphological changes. A relevant example is breast development, which mostly occurs between the ages of 8½ and 13½ (Russo & Russo, 2004) and may vary greatly due to genetic factors, body mass index (BMI) and energy intake early in life (Trichopoulos & Lipman, 1992; Wade et al., 2010). Furthermore, breast size can continue to change during life due to body weight changes, the possibility of pregnancy and breast feeding, or aging. Pregnancy also provides a relevant example, whereby further body morphological change occurs during foetal development, resulting in an increasing bump size, thus considerable changes in female BSA. Variation in body morphology, BSA and BSA:mass ratios are key drivers in our thermoregulatory response across the lifespan and between individuals of different sizes, this is explained in Section 2.2.3.

From an applied apparel standpoint, sports clothing can have large psycho-social and physiological impacts during puberty. Up to 65% of girls drop out of sport as they reach puberty, with 46% of girls avoiding exercise due to their breasts and 73% of girls feeling uncomfortable in their body shape and image, leading to a fear of being judged (Women In Sport, 2022). Along with changes in body image and body shape, an increase in sweating and the fear of judgement due to looking red-faced and sweaty can be a significant deterrent for girls remaining engaged in sport. Yet little is known about the stages of sweating development during puberty, thus to better support pubertal females remaining active during this challenging life phase, there is a need to better understand the thermoregulatory changes that occur to better inform children's sports apparel design (Section 1.2.1).

Female puberty also encompasses the initiation of breast development, which is the principal morphological difference between females and males, for which the most important piece of equipment to support the breast is the sports bra. It has been shown that 86% of females consider sports bras essential during exercise to support and protect the breast and reduce discomfort (Brown et al., 2014; Norris et al., 2020), as this can act as a barrier to exercise participation (Gehlsen & Albohm, 1980; Lorentzen & Lawson, 1987; Scurr et al., 2010). To offer sufficient support, sports bras are often tight fitting, but this can act as a barrier to heat dissipation, thus can negatively affect thermoregulation and thermal comfort (Brotherhood, 2008; Havenith, 1999; Havenith et al., 2002). Therefore, the evidence above highlights the need to better understand thermoregulatory patterns at the breast, breast sensation and breast mechanics to better inform sports bra design (Section 1.2.2). An added consideration in the investigation of the breast is the problem of widely varying breast sizes which can change across the lifespan, even following puberty (i.e. body weight changes, pregnancy, mastectomy).

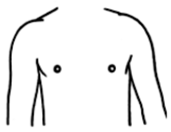
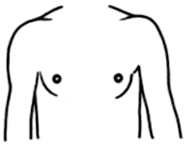
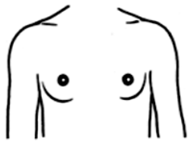
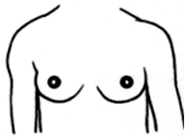
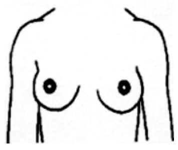
2.5.2 Female hormonal development during puberty

Puberty refers to the physical maturation process during adolescence where an individual reaches sexual maturity (Breehl & Caban, 2024). In females, puberty typically begins between 8 and 13 years of age and encompasses emotional and hormonal changes, as well as physical changes, such as breast development in females (thelarche), pubic hair development (pubarche), an increase in height, and the onset of menstruation (menarche).

Gonadotropin-releasing hormone (GnRH) neurons of the hypothalamus control the initiation of female puberty. Around one year before the onset of puberty, the central nervous system inhibition of GnRH subsides, causing the hypothalamus to release GnRH in a pulsatile manner, which stimulates the release of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) from the gonadotropic cells of the anterior pituitary gland (Whitlock et al., 2006). In turn, FSH and LH affect the theca and granulosa cells of the ovary to stimulate the synthesis and release of sex steroid hormones (i.e. oestrogen and progesterone) and support the formation and development of oocytes (gametogenesis). These hormonal changes, due to rises in FSH and LH, allow for the physical changes of puberty to begin.

Concentrations of oestrogens show wide variation across healthy females throughout life and tend to correspond with distinct stages of development from infancy to menopause. Tanner staging is a classification system used to assess stages of puberty. Tanner staging segments pubertal stages into 5 steps based on defining changes in thelarche, pubarche and menarche. This is visible in Table 2-4. This physical staging system corresponds directly to variation in oestrogen levels seen in females from infancy to adulthood (Frederiksen et al., 2019). Using liquid chromatography tandem mass spectrometry methods, which are validated, sensitive steroid hormone measurements, Frederiksen et al. (2019) found that almost all girls in Tanner stage 2 or above had oestradiol concentrations above 10 pmol/L, and all girls in Tanner stages 4 – 5 had oestradiol concentrations above 100 pmol/L. Furthermore, post-menarcheal girls had higher serum oestradiol concentrations than pre-menarcheal girls in Tanner stages 4 – 5. This progressive increase in oestradiol and oestrone levels can be seen in Figure 2-6.

Table 2-4. Tanner stages of development

	Stage 1	**Stage 2**	**Stage 3**	**Stage 4**	**Stage 5**
Breast development					
					
	The nipple is raised a little. The rest of the breast is still flat.	The breast is in the bud stage; the nipple is more raised than stage 1 and the breast is a small mound.	The breast and areola are both larger than stage 2. The areola does not stick out away from the breast	The areola and nipple make up a mound that sticks out above the shape of the breast.	Mature adult stage; the breasts are fully developed. Only the nipple sticks out now as the areola has moved back to the general breast shape.
Pubic hair development					
	No pubic hair at all.	There is a little soft, long, lightly coloured hair. This may be straight or curly.	The hair is now darker, coarser and more curled. It has spread out and thinly covers a wider area.	Hair is as dark, curly and coarse as in adulthood. Hair has not spread out to the legs yet.	Hair is like that of an adult female. Covers the same area as that of a female with some spread onto the legs.
Growth	2 - 2.4 inches per year	2.8 - 3.2 inches per year	3.2 inches per year	2.8 inches per year	Cessation of linear growth
Other	Adrenarche and ovarian growth	Clitoral enlargement Labia pigmentation Growth of uterus	Axillary hair, acne	Menarche and development of menses	Adult genitalia

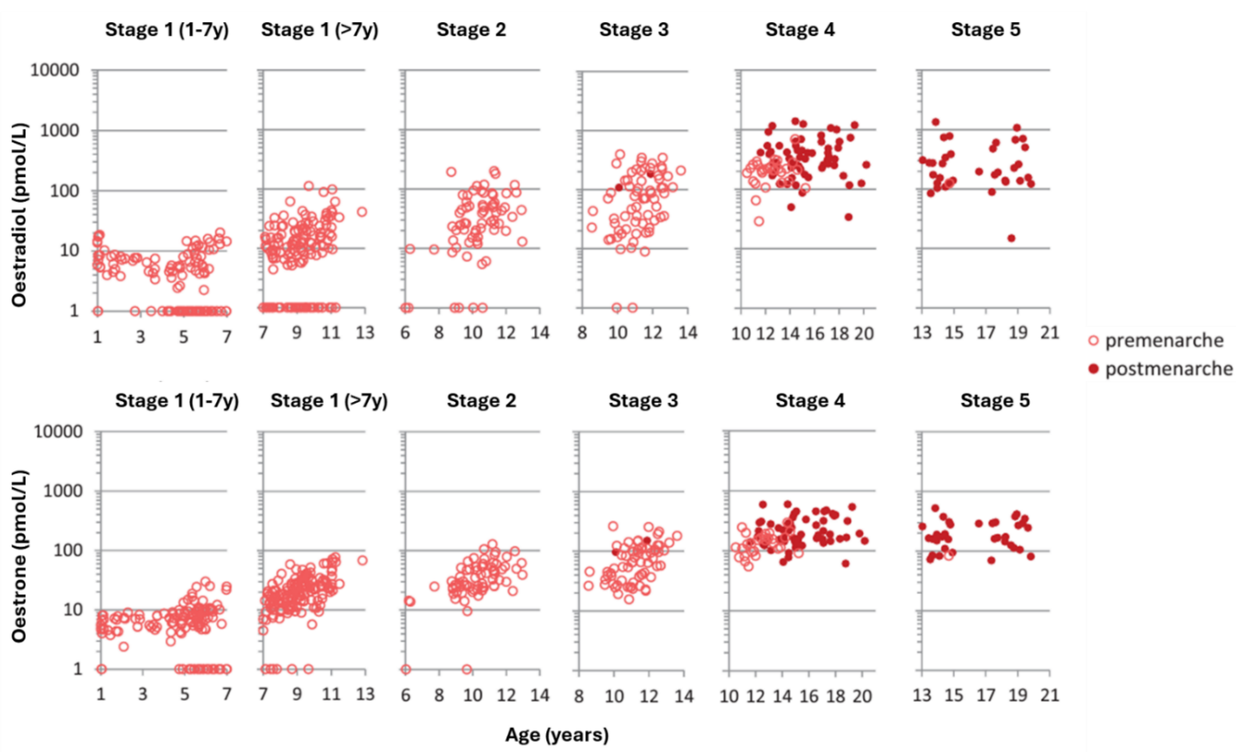


Figure 2-6. Female serum concentrations (n = 456) of oestradiol (E2) and oestrone (E1) by age, stratified by Tanner stages T1–T5: T1, n = 178; T2, n = 71; T3, n = 69; T4, n = 95; and T5, n = 43. Number of adolescents post-menarche (filled circles), n = 112. Reprinted with permission from Frederiksen et al. (2019).

Gaps in the Literature: The specific role of oestrogen in thermoregulation is not fully understood, yet oestrogen receptors have been found in several hypothalamic structures which are involved in thermoregulation (Rance et al., 2013). Increased circulating oestrogens in humans appears to increase heat dissipation responses, such as cutaneous vasodilation and sweating (Stephenson & Kolka, 1999). This aligns with core temperature fluctuations we see during the menstrual cycle, whereby in periods of elevated oestrogen, unopposed by progesterone, we find small decreases in female body temperature (De Mouzon et al., 1984; Marshall, 1963). However, understanding the impact of this on local sweating responses has not been investigated in the context of puberty and the systemic increase in oestrogen during this life stage.

Furthermore, an interesting point to note is that in rat models, a specific sub-population of neurons within the arcuate nucleus (a homolog of the infundibular nucleus in humans) has shown involvement in the thermoregulatory effects of oestrogen (Mittelman-Smith et al., 2012; Rance et al., 2013). These neurons, called KNDy, express ER-alpha. Withdrawal of oestrogen has shown to cause changes in the morphology of these neurons, and in their interaction with nuclei involved in thermoregulation, including the median preoptic nucleus (Mittelman-Smith et al., 2012). It has been proposed that during perimenopausal and menopausal years, the change in this neural morphology is involved in driving the altered thermoregulation (e.g., hot flushes) associated with changing oestrogen levels (Rance et al., 2013). This neural morphological change has not however been investigated in the context of increasing oestrogen levels during female pubertal development, nor has this been investigated in humans.

Despite the limited research directly investigating the impact of hormonal changes on thermoregulation throughout all of puberty, research has investigated the impact of physical growth and development occurring during puberty from a biophysical standpoint which is discussed in further detail below.

Previously it was thought that children were at a thermoregulatory disadvantage due to (i) physiological differences impacting active heat exchange and the control of cutaneous vasodilatation and sweating; (ii) morphological differences, which modify passive heat exchange between the body and surrounding environment; and (iii) differences in the ratio of external work accomplished to the rate of energy expenditure (mechanical efficiency) (Bar-Or, 1998; Drinkwater et al., 1977; Inoue et al., 2004; Meyer et al., 1992).

As discussed in Section 2.2, humans depend heavily on active heat exchange through the autonomic thermoeffector responses of cutaneous vasodilatation and sweating to actively facilitate heat exchange during exercise heat stress. Previous evidence has suggested children are disadvantaged due to having lower sweat rates during exercise (Bar-Or, 1998; Drinkwater et al., 1977; Inoue et al., 2004; Meyer et al., 1992).. However, these proposed age-dependent differences are seemingly biased by prescribing exercise at fixed percentages of $VO_{2max,}$ rather than a fixed rates of H_{prod} or E_{req} (Davies, 1981; Drinkwater et al., 1977; Meyer et al., 1992; Rivera-Brown et al., 2006; Wilk et al., 2013), thus eliciting a lower thermal drive in the children than adults (Cramer & Jay, 2014). The current evidence on sweating development during female puberty is outlined below in Section 2.5.3.

The most prominent morphological characteristic of children that differs to adults is their greater BSA:Mass ratio, allowing them to have greater capacity for passive dry heat exchange

(Rowland, 2008). Therefore, when a thermal gradient exists for heat loss (i.e., ambient temperature cooler than skin temperature), children would be expected to dissipate more heat per unit mass than adults. In contrast, in hotter environments (i.e., ambient temperature warmer than skin temperature), children would gain more heat per unit mass than adults. The gradient between skin temperature and ambient temperature is the driver for dry heat exchange. Evidence for changing skin temperatures during pubertal morphological development is discussed in Section 2.5.4.

2.5.3 Sweating during puberty

As to date, only one study has been found to directly compare thermoregulatory responses between children and adults, including females, using exercise prescriptions that allowed for unbiased age-related comparisons of responses to exercise heat stress through the consideration biophysical differences (Section 2.2.3). Smallcombe et al. (2025) demonstrated that children aged 10-16 are at no greater risk than adults of hyperthermia and dehydration during exercise up to 40°C. This comprehensive study tackled the limitations of previous research that has aimed to compare whole body sweating responses between young girls (8-12yr) and adult women (i.e. (Drinkwater et al., 1977; Meyer et al., 1992; Rivera-Brown et al., 2006) by prescribing exercise at intensities scaled to (1) fitness (60% VO_{2peak}), (2) body mass (7.5 METS) and (3) surface area (300W/m^2) to account for these inherent differences between adults and children. During 45 minutes of treadmill walking and running in warm (30°C, 40% relative humidity [RH]) and hot (40°C, 30% RH) conditions, children had an equal rise in core temperature to adults when exercise was prescribed through H_{prod} relative to body mass (METS) and an equal total body water fluid deficit relative to body mass (%) which provides a measure of dehydration. Despite no difference in the risk of dehydration between children and adults, as this is measured as water loss relative to body weight, WBSR was still significantly lower in children than adults, but exercise was not prescribed in absolute H_{prod} (W) to investigate this.

Only 3 other studies have been found to directly compare whole body sweating responses between young girls (8-12yr) and adult women (i.e. (Drinkwater et al., 1977; Meyer et al., 1992; Rivera-Brown et al., 2006)). During a submaximal bout of exercise on a cycle ergometer, both Meyer et al. (1992) and Rivera-Brown et al. (2006) found that whole body sweat rates (WBSR) were lower in girls compared to women (by ~2.6 to 2.9 g/m^2/min) when exercising in 42 °C and 18% RH and 34 °C and 55% RH respectively. In contrast, Drinkwater et al. (1977) only found a difference in WBSR between girls and women (by ~2.4 g/m^2/min) when exercising in 48 °C and 10% RH conditions, but not at 28 °C and 45% RH or 35 °C and 65% RH. These studies indicate that girls tend to exhibit lower WBSR than women. However, all 3 studies prescribed exercise intensity as a fixed % of $VO_{2max.}$ As a result of prescribing exercise at a fixed % of VO_{2max}, absolute metabolic heat production during exercise (i.e. H_{prod} in W) was consistently lower in girls than in women by ~120 to 160W. Hence, it is likely that the WBSR differences observed in these studies are likely due to biophysical rather than developmental factors.

If we consider the literature more broadly, with the inclusion of males, still only one further study was found to have directly compared sweating responses between boys and men using an exercise prescription that allows for unbiased age-related comparisons of thermoregulatory responses (Leites et al., 2016). In this study, exercise was prescribed at a fixed H_{prod} in W/kg for boys and men, as well as the adult males repeating the exercise protocol at the same fixed absolute H_{prod} (in W) as the boys. When exercising at fixed H_{prod} in W/kg, boys had an absolute H_{prod} that was ~160W lower than that of men due to their lower body mass. Therefore, the lower absolute H_{prod} was associated with a lower WBSR in boys compared to men (i.e. difference ~600ml). However, when exercising at the same absolute H_{prod}, boys still had a lower WBSR than men, but the difference was significantly reduced (i.e. difference ~200ml). It has also been shown that in children, no sex-related differences in WBSR exist when exercise is prescribed at the same H_{prod} in W (Topham et al., 2024). This evidence would support the hypothesis that, had the 3 studies discussed above (Drinkwater et al., 1977; Meyer et al., 1992; Rivera-Brown et al., 2006) investigating girls vs. women prescribed an exercise intensity to match absolute H_{prod} in W, then the WBSR difference between girls and women may have greatly reduced.

When considering local sweating responses, there is limited evidence regarding the difference in LSR between children and adults in response to exercise heat stress. Most recently, a study by Amano et al. (2025) used a local cholinergic agonist at the forearm to induce sweating locally in both males and females from age 6 to young adulthood. The findings of this study showed a significant relationship between age and local cholinergic-agonist-induced sweating and sweat output per gland during development (Amano et al., 2025). Thus, suggesting that an increase in sweat rate with age may be due to an increased output capacity per gland. This is also supported by Landing et al. (1968) who found that sweat gland size (secretory tubular diameters) increases with maturation. Whilst Amano et al. (2025) provide valuable, novel insights on local sweating, using cholinergic stimulation only provides information on the capacity of the post-synaptic sweating apparatus. It does not provide insight into how sweating responses may vary with age in response to environmental or exercise heat stress, during which a centrally-controlled sympathetic response is required to drive sweating (Saltin & Gagge, 1971; Saltin et al., 1970; Shibasaki & Crandall, 2010).

When we consider the impact of development through adolescence on LSR, again one must consider the implications of exercise prescription (Section 2.2.3). Evidence from Arlegui et al. (2021) indicates that the regional distribution of LSRs in pre-pubertal girls (~8 years old) does not resemble the regional patterns seen in women (Smith & Havenith, 2012), however exercise was prescribed at a fixed percentage of maximal heart rate and VO_{2max} in these studies. Girls presented higher LSRs at the extremities (forehead, hands, feet) than at the torso, with the LSR at the hand and feet resembling that of adults across the same regions (i.e. hands and feet) (Arlegui et al., 2021) (Figure 2-7). However, girls presented much lower LSRs across the rest of the body compared with women, who presented their highest LSR across the back and bra triangle (Blount et al., 2024b; Smith & Havenith, 2012) (Figure 2-8). Via an indirect comparison between these studies, it can be inferred that the LSR normalised over metabolic rate is slightly lower in girls than in women. The evidence above would therefore indicate that maturation of the sweating system must occur in girls to a greater extent centrally across the body compared the periphery, and that the development of adultlike regional LSR patterns must occur at some stage during puberty. However, there are no studies that have directly compared regional patterns of LSRs between girls and women exercising at the same E_{req} in W/m^2 (i.e. the correct approach for a reduced bias comparison of LSR; section 2.2.3). Furthermore, there are no studies that have directly determined how and when regional patterns of LSRs in girls start to resemble those of women throughout development.

Gaps in the Literature: It remains unclear whether differences in LSR capacity and regional patterns would be observed when girls and women are directly compared when using an exercise intensity eliciting the same E_{req} in W/m^2. Furthermore, should regional patterns of LSR be different between girls and women when using an unbiased exercise prescription, it is unknown at what age or stage of development that these patterns mature.

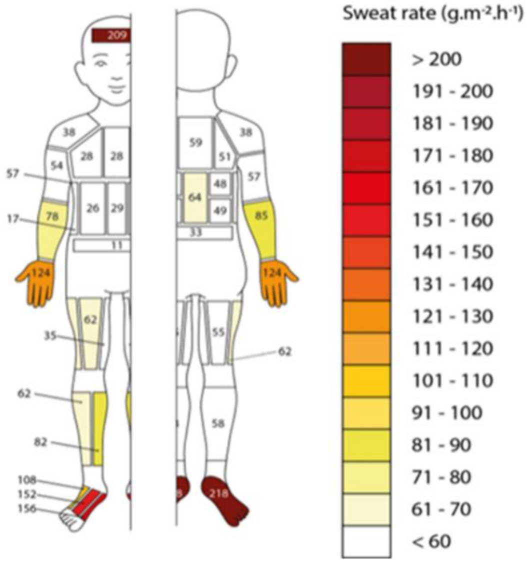


Figure 2-7. Median regional sweat rates (g.m^{-2}.h^{-1}) of girls after moderate intensity (60% HR_{max}) treadmill exercise in the heat (30°C, 40% RH). Reprinted with permission from Arlegui et al. (2021).

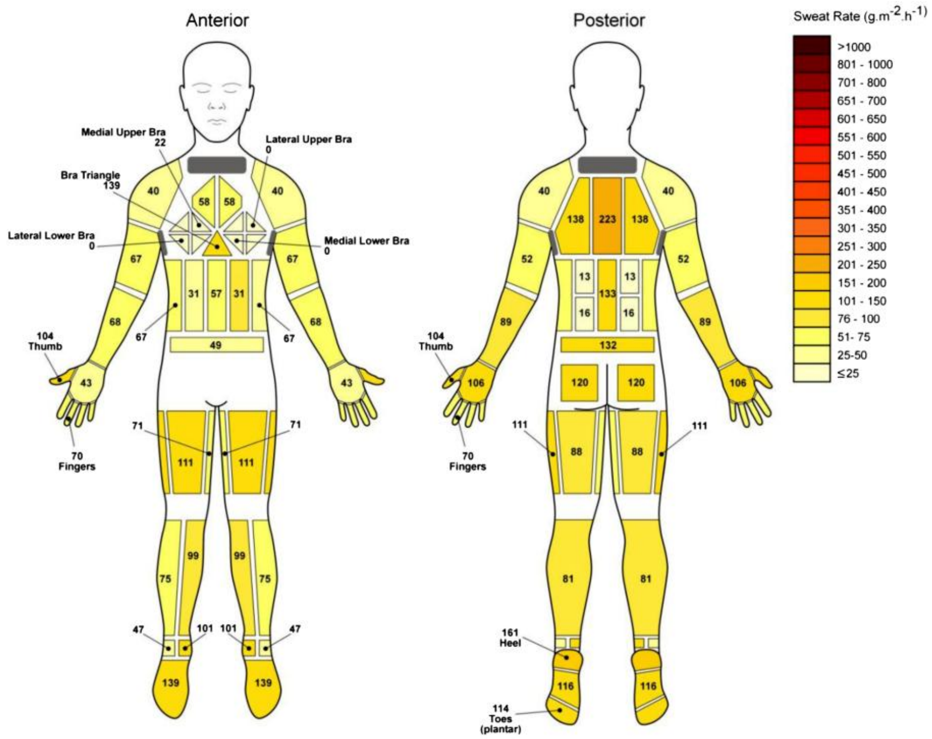


Figure 2-8. Median regional sweat rates (g.m^{-2}.h^{-1}) of adult females after moderate intensity (60% VO_{2max}) treadmill exercise in the heat (26°C, 45% RH). Reprinted with permission from Smith and Havenith (2012).

2.5.4 Skin temperature during puberty

As discussed in Section 2.3.1, the skin plays an important role in body temperature regulation as it acts as a barrier between the core and external environment. As a thermoregulatory tool, it functions as a route for heat exchange and temperature detection via thermoreceptors. The skin can dissipate heat from the body through channels of convection and radiation when the blood vessels near the surface dilate (section 2.2.1) or from the evaporation of sweat (section 2.2.2) (Parsons, 2007). It has also been proposed that skin temperature can act as a modulator of exercise intensity and work performance due to its impact on thermal sensation and perceived exertion (Schlader et al., 2011). Elevations in skin temperature in hot conditions can cause a rise in heart rate and blood perfusion to the skin, which can increase thermal discomfort (discussed further in 2.5.5) and perceived exertion even if core temperatures stay the same. In turn, this can alter an individual's behaviour, such as altering their pacing (and hence their metabolic heat production) to lower skin temperatures and perceived exertion and restore thermal comfort (Foster et al., 2021).

Skin temperature can be impacted by internal and external (i.e. environment and clothing) factors. Internal factors affecting skin temperature include several individual physiological characteristics such as body surface area-to-mass ratio, body composition, fat insulation, blood flow efficiency, metabolic heat production and sweat production. Furthermore, it is known that sex, ethnicity, geographical location, acclimatisation status, and age also affect skin temperature (Fournet et al., 2013). Research has demonstrated that there is a distinction between prepubertal, pubertal and adult thermoregulation in that prepubertal children have been found to depend more heavily on dry heat loss mechanisms compared to pubertal children and adults (Davies, 1981; Drinkwater et al., 1977). This is likely due to their rapid vasodilatory response which enables efficient peripheral blood flow as well as their larger BSA-to-mass ratio, allowing for a faster rate of cooling. During puberty, children's thermoregulation begins to reflect that of an adult, however it is unknown if this occurs in line with specific developmental Tanner stages or simply progresses with age.

Previous research has investigated skin temperature differences between children and adults using direct skin contact and non-contact measurement techniques. Drinkwater et al. (1977) used thermocouples to measure skin temperatures of 5 prepubertal girls (age 12 ± 0 years) and 5 adult women (age 20.6 ± 0.7 years) at 7 sites. Results showed that the girls had warmer mean skin temperatures compared adult women exercising at 30% VO_{2max} walking on a treadmill in three environmental conditions (28℃ & 45%, 35℃ & 65%, and 48℃ & 10%). Similarly, Davies (1981) found that boys (age 12.9 ± 0.8 years) and girls (age 13.8 ± 0.7 years) had higher mean skin temperatures than adult men (age 36.1± 6.7 years) during a 1 hour run at 68% individual VO_{2max} in a thermoneutral environment (30.9℃, 31.8℃ and 29.1℃, respectively). Furthermore, in males, Leites et al. (2016) also found higher skin temperatures at the chest, upper back and thighs in boys (age 11.5 ± 1.3 years) compared to men (age 22.9 ± 2.3 years) when performing four 20-min bouts of cycling at 35℃ and 35% RH. Arlegui (2022) investigated skin temperature responses in prepubertal (age 9 ± 0.6 years), pubertal (age 12.6 ± 0.5 years) and adult (age 22.3 ± 0.7 years) females using non-contact thermal imaging techniques pre, during and post a sub-maximal treadmill protocol. Results of this study showed prepubertal girls had the warmest skin temperatures despite them having the lowest metabolic rates, yet the adults had the lowest skin temperatures yet a higher metabolic rate. These results can be visualised in a temperature map in Figure 2-9.

Gaps in the literature: The general outcome from these research studies suggest that children tend to display higher skin temperatures. However, there is still little granularity as to when these changes from pre-pubertal to adult thermoregulatory mechanisms occur. It is also unknown as to whether these changes in skin temperature align to changes in local sweating patterns as discussed in section 2.5.3.

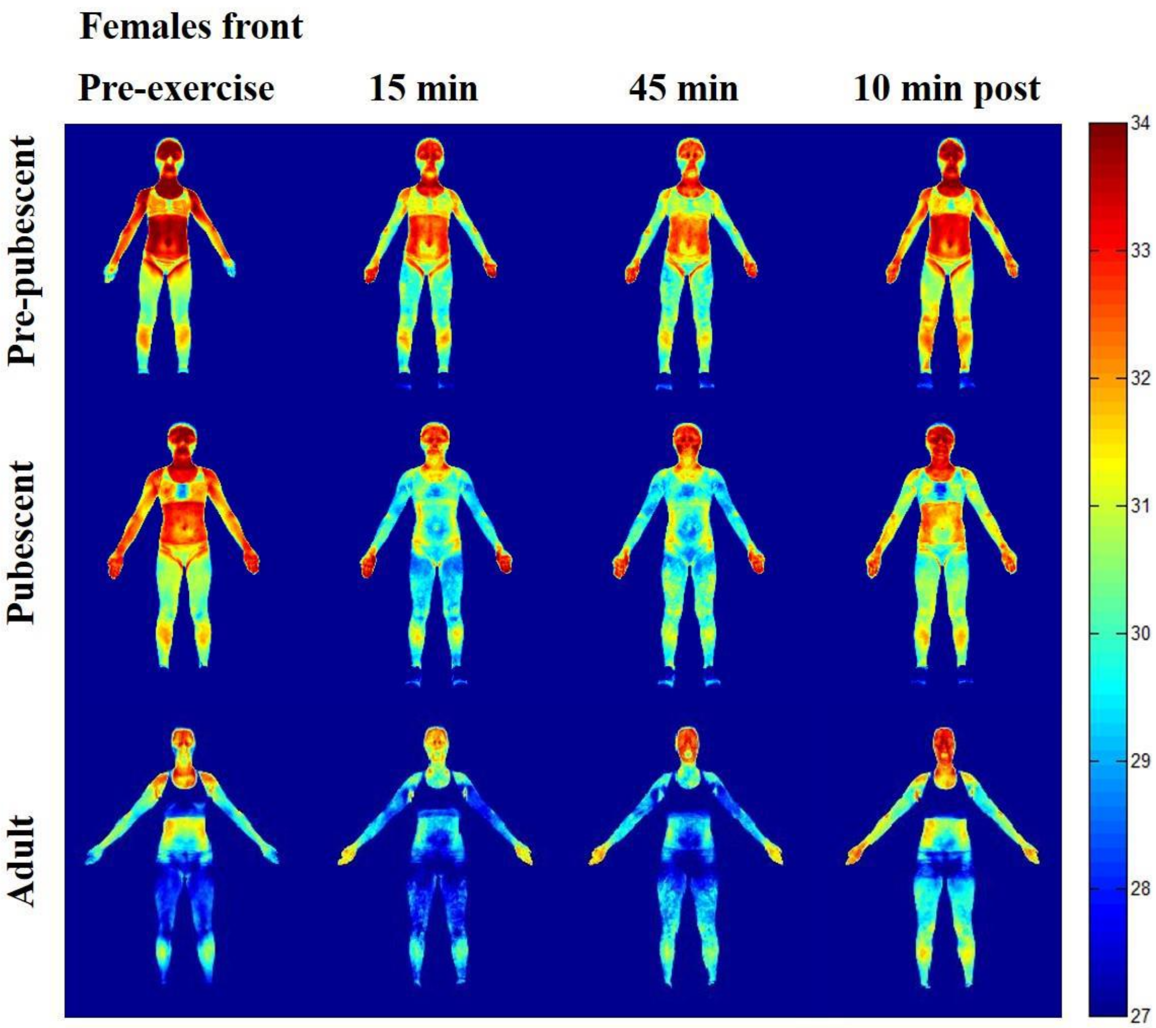


Figure 2-9. Female front skin temperature maps showing median skin temperatures for each age group at different timepoints of the experimental protocol. Reprinted with permission from Arlegui (2022).

2.5.5 Perceptual sensitivity during puberty

From section 2.3, we know that the skin plays a substantial role in our sensation and perception as it contains several specialised nerve endings which respond to changes in the surrounding environment. Changes in skin temperature and wetness, through sweating, can be large drivers in the perception of thermal comfort. The notion of thermal comfort depends on the interaction of physiological and psychological factors (Gagge et al., 1967). As children pass through puberty, they undergo a series of physiological, hormonal and morphological changes, as discussed above, but also psychological changes and life experiences which can alter ones perception or preference of a thermal environment, given comfort is based on past recall of exposures (Fabbri, 2015; Montazami et al., 2017; Parsons, 2007).

From a thermal sensation and comfort perspective, little research has been done to investigate changes in thermal perceptions with aging from childhood to adulthood, especially in an exercise heat stress setting. Inoue et al. (2009) performed 60-minute passive heat exposure ramps from 28°C to 40°C in pre-pubertal boys (9-11 years) and young men, during which they used thermography and perceptual measures throughout. This study found that the boys felt statistically significantly hotter than the adult males in the final 25 minutes of exposure, when air temperature was higher than T_{skin}, which also coincided with the time point at which mean T_{skin} was significantly greater in boys than men (Δ>0.5°C). In contrast, a study that investigated behaviour, thermal perception, thirst, and heat management strategies of children and adults during extreme heat alerts through survey responses found no statistically significant effects of age on thermal sensation or thermal comfort (Ravanelli et al., 2023). However, the ambient temperature and humidity conditions for such 'extreme heat alerts' are unknown. Only one study has been found to directly compare thermal sensitivity and comfort during exercise heat stress, however this was only performed in males (Leites et al., 2016). During 4 consecutive 20-minute bouts of cycling in 35°C and 35% RH, boys (10-12 years) felt statistically significantly hotter and thermally uncomfortable than the men (19-25 years) from as early as 10minutes into the exercise. What is interesting about this study however is that exercise was prescribed for the men through 2 modalities: equal H_{prod} in W/kg and equal absolute H_{prod} in W to the boys. Thermal sensation and comfort were statistically significantly different between boys and men exercising at the same absolute H_{prod} in W from minute 10 and 20 respectively with the boys feeling hotter and more uncomfortable. However, differences in thermal sensation and comfort did not reach statistical significance between boys and men exercising at the same H_{prod} in W/kg until minute 80. This is likely due to the fact that exercising at the same H_{prod} in W/kg led to more similar increases in mean T_{skin} and T_{core} in the men and boys (Section 2.2.3). As discussed previously (section 2.3.2), it is known that T_{skin} plays a large role in the perception of temperature.

The perception of wetness arises from higher-order neural structures optimally integrating multisensory thermal (e.g. cold) and tactile (e.g. stickiness) inputs arising from the skin's contact with moisture (Filingeri, Fournet, et al., 2014b). Little evidence exists indicating how and when in development that children learn to integrate the sensory cues used to infer wetness on the skin. A recent study by Valenza et al. (2025) investigated the multisensory integratory mechanisms underlying the perception of wetness in a cohort of young children from age 7 to 16 years of age. Results indicated that children (boys and girls) aged ~12 years presented similar multisensory integratory mechanisms for wetness perception as those observed in adults. Furthermore, the younger children perceived cold-wet stimuli to a greater extent (around ~20%) than older adults (45-65yo) but not the younger adults (20-34yo). This study has great value in highlighting the age-dependent variations in wetness perception and the integrated multi-sensory approach applied by children, as well as younger and older adults. However, this single external application of a wet stimulus does not inform us as to how whole-body wetness perceptions may differ across puberty during exercise under heat-stress, in which the perception of wetness arises from one's own sweat.

Gaps in the Literature: The development of thermal and wetness perception in pubertal children, especially females, has been minimally investigated thus it is unknown whether perceptual tolerance to heat stress differs with age. Therefore, there is a need to explore whether thermal sensations in females during exercise heat stress differ in relation to age.

As discussed in Section 2.5.1, the initiation of thelarche represents a key morphological milestone of female puberty. Because breast development and growth vary markedly among females, this anatomical change presents a critical challenge for sportswear manufacturers, necessitating the design of sports bras that provide appropriate comfort and support.

2.5.6 Anatomy of the female breast

The breast lies on the anterior chest wall, over the pectoralis major muscle, between the 2nd and 6th ribs (Gefen & Dilmoney, 2007). The breast tissue is predominantly formed of adipose and glandular tissue, the ratio of which can vary largely across females and across the lifespan (Hassiotou & Geddes, 2013). Female breast size and shape can vary over time due to body mass, menstrual phases, pregnancy, breast feeding and menopause (Azar et al., 2001; Wade et al., 2010). However, the predominant changes in breast morphology occur during puberty, normally between the ages of 8½ and 13½ (Russo & Russo, 2004). During this development, there is large variation across females in the extent of breast growth, thus final breast size. This is thought to be in part due to genetic factors, BMI and energy intake early in life (Trichopoulos & Lipman, 1992; Wade et al., 2010). Variation in breast size will of course cause variation in the skin surface area across the breast. This may have impacts on biophysical parameters across the breast, such as sweat gland density or local sweat rates due to their relationship with skin expansion. Variations in breast size may also influence skin mechanical parameters (e.g. skin thickness, skin stiffness) and perception across the breast (thermal, wetness, tactile) as previously highlighted in section 2.3. Each of these parameters in relation to breast development will be discussed below.

2.5.7 Thermophysiology of the female breast

The number of sweat glands is set from age 2 (Kuno, 1956), but breast size is not. This raises the question as to how heat-activated sweat gland density (HASGD) may differ across the breast of females with different breast sizes and how differences in breast surface area for heat exchange will impact local sweat rates for a given evaporative requirement. Improving our understanding of how breast size impacts the evaporative requirements and sweating patterns of the breast will have implications for sports bra design in terms of improving breathability and insulation across a range of sizes.

Historically regional HASGD has been investigated across large surface areas (Kawahata, 1939; Kuno, 1956; Szabo, 1958). However, to date, no investigations have been made across the breast or in females of different breast size. For example, early work by Kawahata (1939) investigated regional HASGD over large body areas in people of varying ages. They grouped body areas by the head, neck, trunk, upper extremities, and lower extremities, giving an average number of sweat glands per square cm (Table 2-5**).** This gives a broad scope of regional HASGD differences but with no mention of gender differences, the impact of body size or more localised differences.

Table 2-5. The number of sweat glands per sq. cm of the skin (Kawahata, 1939).

		Age (years)			
		20	**26**	**29**	**35**
Sweat gland density (glands/cm2)	**Head**	260	268	281	143
	Neck	222	132	209	177
	Trunk	114	145	199	131
	Upper Extremities	114	196	241	183
	Lower Extremities	100	119	156	127

Regional sweat rates have been measured to a greater extent more recently than HASGD, in multiple body regions, yet large numbers of these studies were conducted only on males or reported mixed sex data (Machado-Moreira, Smith, et al., 2008; Machado-Moreira, Wilmink, et al., 2008; Smith & Havenith, 2011; Taylor et al., 2006). However, Smith and Havenith (2012) produced full body sweat maps (

Figure 2-8 2-8) across the female body which found the central upper back, heels, dorsal foot and between the breasts (bra triangle) to produce the highest sweat rates on the female body. On the other hand, the breasts and middle and lower back produced the lowest, yet breast size was not taken into consideration in this study. In this study, LSR was measured using a modified absorbent technique which involved cutting 78 absorbent pads scaled to the individual body size. This allowed for segmentation of the body to investigate regional differences, but this requires secure affixation of the pads to prevent evaporation and sweat run-off/transfer between sites. This ensures sweat measured at the bra triangle for example was produced in that location and is not a product of sweat trapping between the breasts. Despite the practicality of the absorbent patch technique, it does have some limitations. The patch under an occlusive dressing creates a microenvironment (Smith & Havenith, 2011) which can alter the regional sweating rate compared to uncovered skin as it will reduce the ability for evaporative cooling. To avoid this effect, Morris et al. (2013) suggested limiting patch adhesion time to 5 minutes.

Gaps in the Literature: It remains unknown how HASGD and sweat gland output vary across different sized breasts, and whether there is a relationship between these two variables. It is also unknown how sweat accumulation in a bra will affect thermal and tactile comfort, therefore it is necessary to investigate how this may differ across the breast.

2.5.8 Perceptual sensitivity of the female breast

Thermal and tactile sensation are fundamental cutaneous sensory attributes that are necessary for sensing our surrounding environment, including the interaction with clothing, in this case the bra (Havenith et al., 2002; Song, 2011). Wetness perception also impacts the subjective experience of the clothing-skin interface (Gwosdow et al., 1986). Wetness perception is a synthetic response developed from the integration of thermal and tactile inputs and as a result of perceptual learning. To date, there is a paucity of research investigating thermal, tactile and wetness sensitivity over the breast region in females. This is surprising as thermoreceptors in this area play an important role in female thermal comfort at rest (Ayres et al., 2013) and mechanoreceptors across the breast provide valuable information of feelings of pressure, itchiness, clinginess, and comfort in an area that is almost always covered by a bra or t-shirt (Song, 2011).

Regarding tactile sensitivity, the breast is significantly more sensitive in post-pubescent females than males with distinct regional differences in response to light touch (Cornelissen et al., 2018; Robinson & Short, 1977). Previous research investigating tactile sensitivity at the breast has demonstrated that smaller breasts tend to have lower tactile detection thresholds (Cornelissen et al., 2018; DelVecchyo et al., 2004; Tairych et al., 1998) and greater spatial acuity (Long et al., 2022) than larger breasts. Long et al. (2022) investigated tactile spatial acuity at the breast, hand and back and found the breast to have much lower acuity compared to the hand and back with acuity decreasing as breast size increased. However, in this study breast size was only estimated from bust and under-bust circumference measures with no reference to breast skin surface area. Further support for inter-individual variation in breast tactile sensitivity comes from recent clinical sensory profiling work. Bubberman et al. (2025) quantified tactile sensibility across 572 breasts in a large breast-cancer cohort and established normative values for healthy breast tissue, demonstrating that even in non-operated breasts, tactile thresholds vary meaningfully across individuals.

Previous investigations into the effect of body size on sensory innervation have shown that people with larger hands have lower acuity (Peters et al., 2009; Wong et al., 2013)(Figure 2-10) and higher tactile detection thresholds (Li & Gerling, 2023; Vega-Bermudez & Johnson, 2004) than people with smaller hands. This has led to the hypothesis that the number of nerve fibres does not scale proportionally with surface area. As the breasts grow later in life - after the nervous system has reached near-full maturity (Javed & Lteif, 2013) - a similar inverse relationship between size and tactile acuity may apply at the breast. The normative sensory variability reported by Bubberman et al. (2025) strengthens this hypothesis by illustrating that breast cutaneous sensitivity is inherently heterogeneous and plausibly influenced by underlying differences in sensory innervation density.

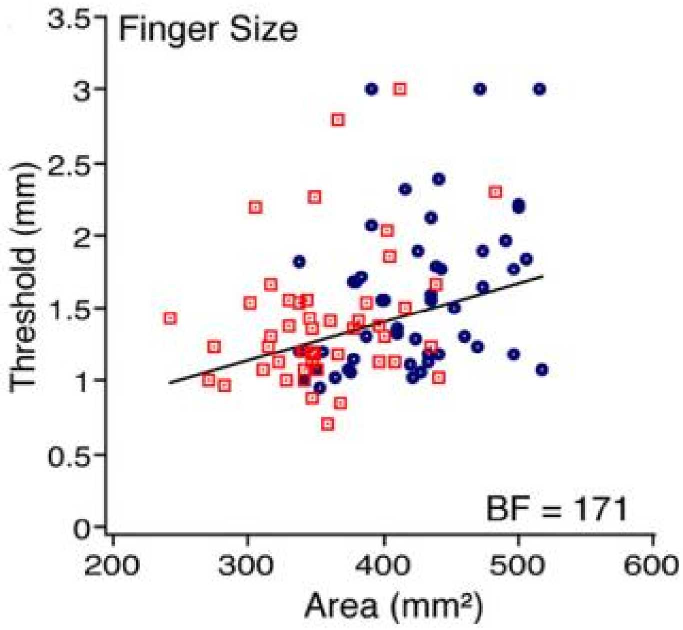


Figure 2-10. Increasing finger surface area increased tactile thresholds, i.e. reduced tactile sensitivity in males (blue) and females (red). Reprinted with permission from Peters et al. (2009) - Copyright © 2009 Society for Neuroscience 0270-6474/09/2915756-06.

To date, only a few studies have investigated breast thermal sensitivity. Luo et al. (2020) found homogenous thermal sensitivity distribution across the breast (Figure 2-11 A). However, other studies have reported uneven thermal sensitivity (Terzis et al., 1987; Valenza et al., 2023) thus the current findings are inconclusive (Figure 2-11 B). The variation in results to date appear to be temperature modality sensitive and affected by the stimulus probe size which would impact spatial summation of a signal, thus change perception. Spatial summation refers to the process where a larger relative area of the body receives a stimuli which can result in a cumulative effect upon membrane potentials and is then sensed as a more intense stimulus (Moini et al., 2021). As mentioned above, breast size varies greatly among females and can vary over time (Azar et al., 2001; Wade et al., 2010). As the nervous system reaches maturity prior to breast development, thermal sensation at the breast has potential to be impacted by breast size. It could be hypothesised that greater skin surface area leads to reduced density of thermal receptors, thus reduced spatial summation of stimuli, therefore reduced sensation. Moreover, neither of these studies investigating breast thermal sensitivity measured menstrual phase. Hormonal fluctuations across the female menstrual cycle have shown to cause changes in sensory perception (Bajaj et al., 2001; Uchida & Izumizaki, 2021). Transient receptor potential channels (TRP) are sensory nerve channels that are thermoreceptive and open and close in response to temperature, thus provide feelings of thermal sensation. TRPM2 and TRPM8 are found on the breast (Uchida & Izumizaki, 2021). There is evidence that TRPM8 expression may be decreased by oestrogen which is elevated in the luteal phase of the menstrual cycle, thus may alter thermal perception at the breast (Uchida & Izumizaki, 2021).

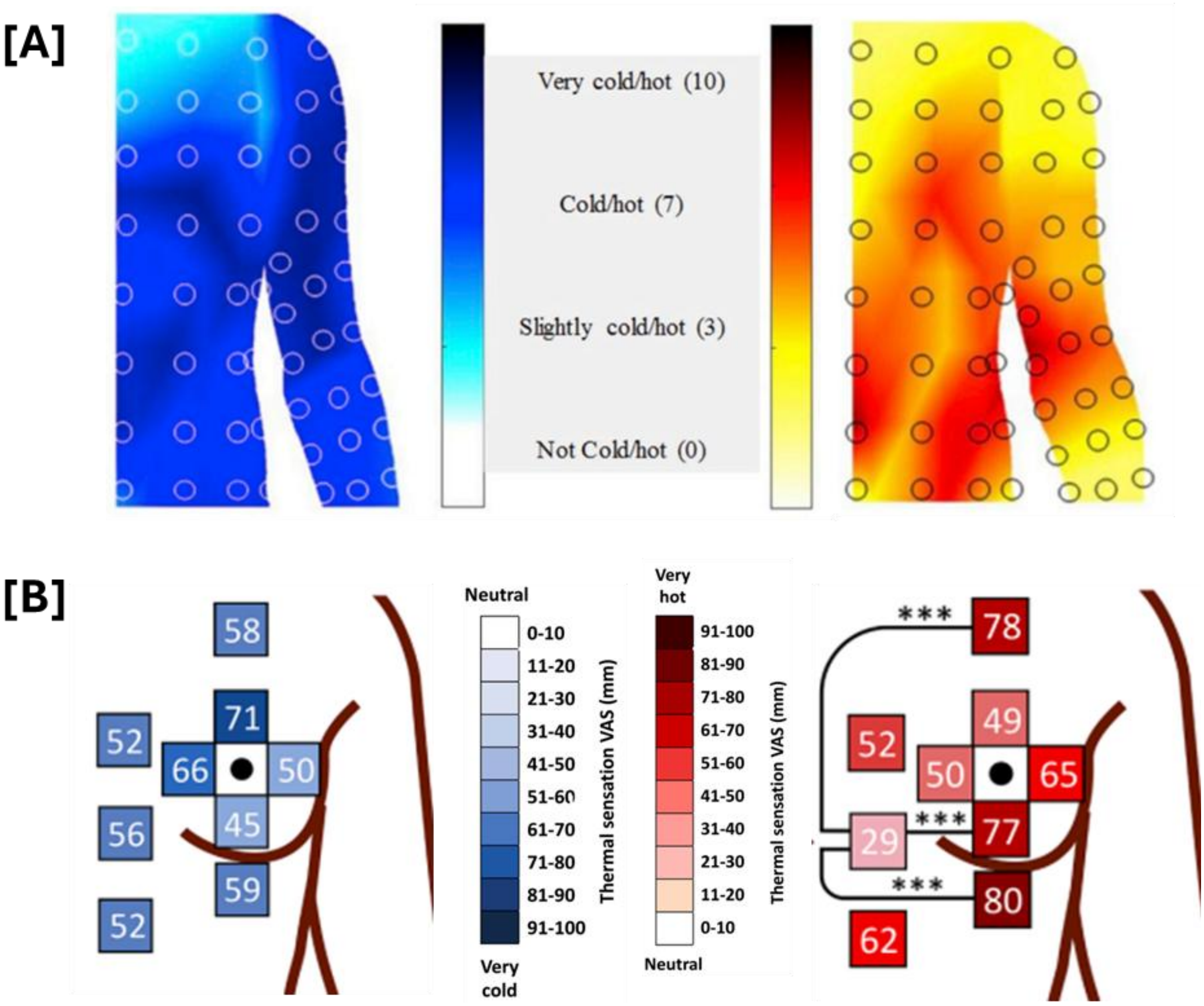


Figure 2-11. Thermal sensitivity maps across the breast from [A] Luo et al. (2020) (Luo et al., 2020) demonstrating more homgenous distribution and [B] Valenza et al. (2023) showing more heterogenous distribution. Reprinted with permission from both authors.

Gaps in the Literature: The need to understand breast sensitivity and means to manage this through effective sports bra design are becoming more important. Breast displacement during exercise has shown to significantly correlate with exercise-induced breast discomfort and pain (Gehlsen & Albohm, 1980; Lorentzen & Lawson, 1987; Scurr et al., 2010) as well as hotter chest temperatures inducing greater thermal discomfort (Ayres et al., 2013) which limits females' ability and desire to participate in physical activity (McGhee et al., 2013; White et al., 2015). To ensure discomfort around the bra and breast are not a barrier to exercise participation, greater understanding of cutaneous sensitivity in this region is required. An important consideration point when discussing cutaneous sensitivity is also the mechanical properties of skin which can influence sensation.

2.5.9 Mechanical properties of female breast

Human skin mechanical properties are non-linear, viscoelastic, highly variable with age, hydration, disease and anatomical site (Gefen & Dilmoney, 2007). For example, it is well known that aging causes changes to skin mechanical properties, reducing skin stiffness and elasticity (Escoffier et al., 1989), which at the breast has been thought to result in breast ptosis ("dropping") in females (Groyecka et al., 2017; Rinker et al., 2010). The skin is highly adaptable and able to remodel and modify mechanical properties such as stiffness, elasticity and thickness based on the strains or mechanical loading applied (Joodaki & Panzer, 2018). Norris et al. (2020) investigated strain rates across the breast during static and dynamic activities and found the greatest strains in the upper, lateral breast regions. Yet, no investigation was done to see how that translated to skin mechanical differences across the breast. However, it has been shown in other body regions that increased vertical strain rates, partly due to gravity, induce skin stiffness changes (Choo et al., 2010). This is because the collagen fibres in the skin are increasingly under tension so the fibres become straightened and begin to carry most of the load which increases the stiffness of the tissue (Benítez & Montáns, 2017; Joodaki & Panzer, 2018). As the skin is one of the major intrinsic breast support systems, along with the Coopers ligaments (Gefen & Dilmoney, 2007; Hindle, 1991), understanding the skin mechanical changes when put under greater strains (e.g. due to greater breast mass or movement) is of value. But also understanding how these mechanical properties may change with temperature at the breast has not been investigated. Increases in soft tissue and skin temperature have been shown to reduce tissue stiffness due to collagen denaturation (Wall et al., 1999; Wright & Humphrey, 2002). In animal soft tissue, significant reductions in the shear modulus occur when heated from 25 to 43°C (Sapin-de Brosses et al., 2010), which encompasses the normal range of skin temperatures from 30.7 to 35.6°C (Mehnert et al., 2000). However, dynamic variations in tissue stiffness differ from one organ to the other (Sapin-de Brosses et al., 2010) and it is unknown how the effect of changing skin and tissue temperature at the breast will affect it's supporting structure, the skin.

Furthermore, it has been demonstrated larger breasted females also appear to have reduced skin thickness at the breast (Wilson et al., 1983). Skin thickness plays an important role in cutaneous sensitivity. The thermal perception originates from the temperature difference between the skin and contact surface and the rate of change at thermoreceptors, which relates to physical and thermal properties, initial temperature difference, thermal contact resistance, and other factors (Park et al., 2018). Thinner skin, or a smaller barrier for heat conductance would allow for a greater rate of change of stimulation at the thermoreceptor which will therefore impact thermal sensitivity (Chen & Ding, 2019)

Gaps in the Literature: The relationships between skin mechanical properties, sensation and temperature have not been elucidated at the breast. Changes in the breast intrinsic support system or knock on effects on thermal and tactile sensitivity may provide valuable insight into bra requirements to best manage these dynamic interactions.

2.6 Summary of the literature review and conclusions

The sequence of studies presented in this thesis does not mirror the biological progression of female development as outlined in the preceding literature review – for instance, the transition from pubertal onset to subsequent variation in breast development and size. Instead, the chapter order reflects industry-driven timelines, including the need to generate essential foundational insights for work later conducted during a research placement at the Nike Sports Research Lab in Portland, USA (Chapter 9), as well as methodological and ethical considerations. Accordingly, the initial studies focused on adult participants with varying breast sizes (Chapter 5, Chapter 6, Chapter 7), a comparatively less vulnerable population. These studies enabled refinement and validation of some of the experimental methods subsequently applied to the paediatric cohort in the final study (Chapter 8).

In alignment with the industry motivations described above, and after reviewing the current literature addressing female specific thermoregulatory responses to heat stress, the following conclusions can be drawn:

1) Human thermoregulation maintains core temperature near 37 °C to preserve physiological function, with clothing acting as a key modulator of heat exchange and thermal comfort during exercise. Despite this, females are markedly underrepresented in thermoregulatory research, even though they undergo significant hormonal and morphological changes across the lifespan, such as during puberty and breast development, that may alter heat balance and interactions with clothing.
2) Breast displacement during exercise can cause exercise-induced breast discomfort and pain as well as hotter chest temperatures inducing greater thermal discomfort which may limit females' ability and desire to participate in physical activity.
3) To ensure discomfort around the bra and breast are not a barrier to exercise participation, greater understanding of sweating patterns, cutaneous sensitivity and breast mechanics in this region is required.
4) There is a lack of data within the literature exploring whether anatomical differences at the breast drive differences in biophysical properties, such as sweat gland density or local sweat rates.
5) It is not known whether anatomical differences at the breast drive differences in perception at the breast (thermal, wetness and tactile).
6) The effect of breast size on skin mechanical properties (e.g. skin stiffness, epidermal thickness) at the breast remains unclear.
7) Development from childlike to adultlike regional sweating patterns must occur at some point during puberty. However, no studies have directly assessed how and when regional patterns of LSR in girls start to resemble those of women throughout pubertal development, nor have these studies prescribed exercise at an intensity to allow unbiased comparisons of sweating responses.
8) Some evidence suggests children have a greater reliance on dry heat exchange for heat loss than adults, yet little evidence exists to validate this point using exercise prescription techniques to allow unbiased comparisons of thermoregulatory responses.
9) The development of thermal and wetness perception in pubertal children, especially females, has been minimally investigated thus it is unknown whether perceptual tolerance to heat stress differs with age.

Chapter 3 Aims and Objectives

The overarching aim of this thesis is to broaden our fundamental understanding of how females regulate their body temperature during exercise in the heat and of how the complex hormonal and developmental stages of a female's life impacting their morphology (e.g. breast development and puberty) alter these thermophysiological responses (Figure 3-1). The applied implications of this research are to inform sports apparel design to accommodate the unique needs of females, with support from Nike Inc., a global sport apparel manufacturer and co-funder of this PhD.

Based on the knowledge gaps highlighted in Section 2.3, the following aims and objectives were developed:

1. To quantify the influence of breast size on sweat gland density and output in healthy individuals with varying breast sizes (Chapter 5).
    a. Recruit females of varying breast sizes who can run for 45minutes under heat stress.
    b. Develop a means to measure breast surface area using a 3D scanner.
    c. Examine the relationship between breast surface area and local sweat rate and heat-activated sweat gland density following a bout of exercise in the heat.
    d. Explore the impact of size-dependent differences in sweat rate on breast movement during running (Chapter 9).

2. To assess the impact of breast size on skin stiffness and tactile sensitivity across different breast regions in healthy females, both at rest and following exercise (Chapter 6).
    a. Examine the relationship between breast surface area and breast skin stiffness using a myotonometer, at rest and following exercise in the heat.
    b. Analyse the relationship between breast surface area and tactile sensitivity thresholds, using Von Frey monofilaments across the lower breast, at rest and following exercise in the heat.
    c. Explore the relationship between skin stiffness and tactile sensitivity on the female breast.

3. To evaluate the influence of breast size on thermal and wetness perception, and on epidermal properties, in healthy females of varying breast sizes at rest (Chapter 7).

a. Examine the relationship between breast surface area and breast thermal and wetness perception using quantitative sensory testing, across different areas of the breast.
b. Investigate the relationship between breast surface area and epidermal thickness and skin surface roughness using optical coherence tomography, across different areas of the breast.

4. To characterise how regional sweating patterns change during childhood and adolescence in young females to resemble those observed in adult females (Chapter 8).
    a. Recruit females from age 8 to young adulthood to study the relationship between age and local sweat rates and heat-activated sweat gland density.
    b. Evaluate the physiological development of the female participants via Tanner Staging and investigate this relationship with local sweat rates.
    c. Explore at what stage of maturation (chronological or physiological) the sweating patterns of girls resemble those of adult females.

5. To identify age-related differences in whole-body thermal and wetness perception during exercise heat stress in females (Chapter 8).
    a. Evaluate the relationship between age and thermal sensation, thermal comfort and wetness perception, using Likert scales during exercise in the heat.

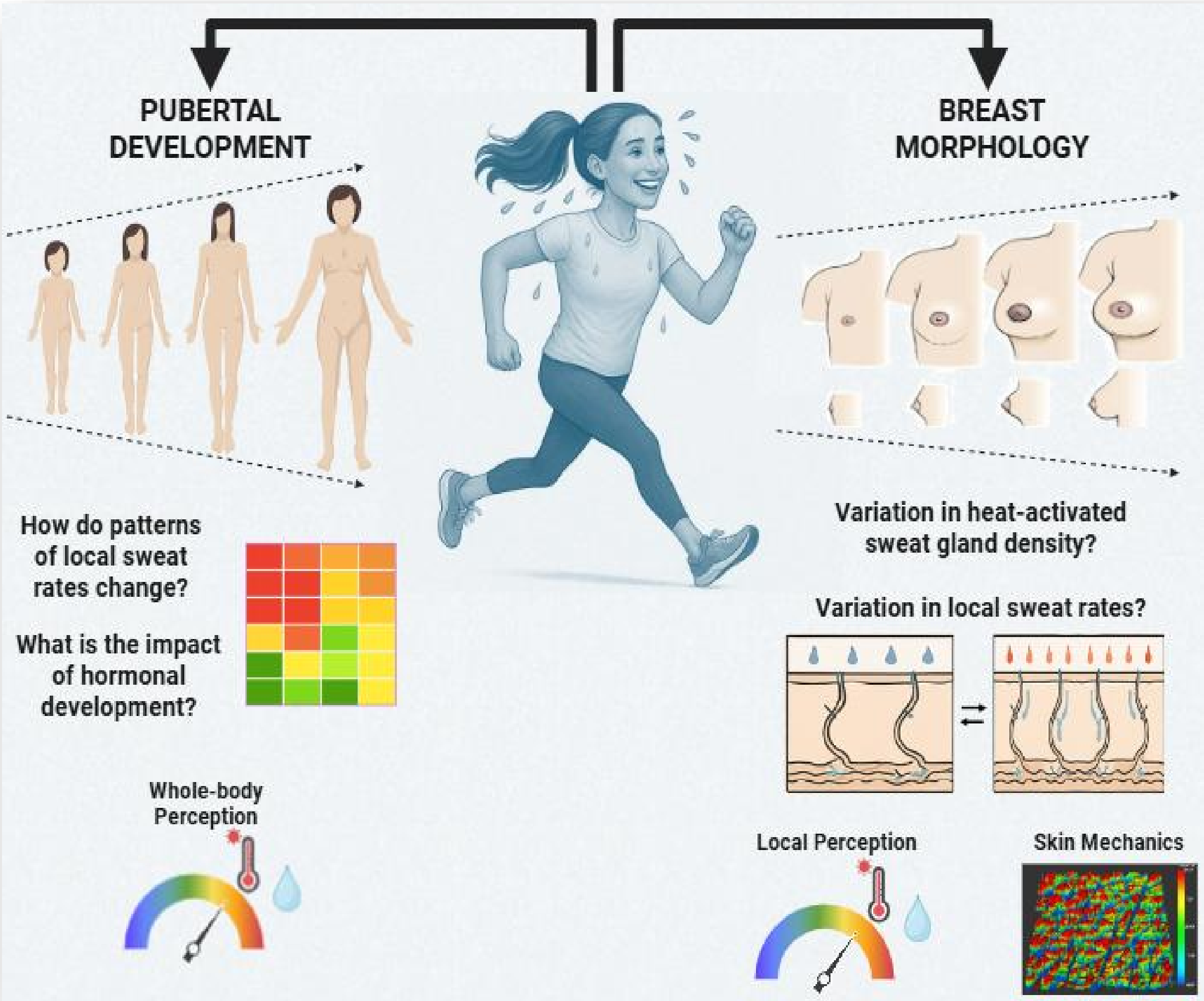


Figure 3-1. A summary of the PhD project research aims.

Chapter 4 Experimental Methodology

In order to achieve Aims 1-3, a large experimental campaign, comprising of 3 studies (Chapter 5, Chapter 6, Chapter 7) was performed in a singular cohort of adult females to investigate the effect of female breast morphological differences at rest and during exercise. This experimental campaign allowed for an in-depth investigation of the impact of breast size variation on:

1) local sweating responses across the breast (thermoregulation),
2) skin stiffness and epidermal properties such as epidermal thickness (biomechanical), and
3) local thermal and wetness perceptions across the breast (perceptual).

A second large experimental campaign was undertaken to explore the impact of pubertal development (Chapter 8), from age 8 to young adulthood, on the spatial and temporal changes in local sweating responses across the body during exercise heat stress, as well as whole-body thermal perceptual assessments.

These comprehensive investigations into the thermophysiological, biomechanical and perceptual properties across women of varying breast size, and during puberty, has valuable application in informing the design of sports clothing and bras that better meet the support and comfort needs of females.

To address the aims and objectives outlined above, several methodological approaches were required. This chapter provides an overview and appraisal of the methods employed in the upcoming results chapters as outlined in the table below (Table 4-1). The experimental chapters contained within the Thesis were conducted and led by the candidate (HB). Due to the industry co-funded nature of this PhD, further studies were conducted during two 3-month secondments to the Nike Sports Research Lab, Portland, USA, which involved a range of in-house testing and product evaluation and are outlined in Chapter 9.

Table 4-1. Summary of the methods and parameters employed within the experimental chapters.

Study Chapter	Methods	Outcome measures
Chapter 5	Modified iodine technique. Technical absorbents. Partitional calorimetry. 3D breast scan. Core temperature.	Sweat gland density. Local sweat rate. Evaporative requirement for heat balance. Breast surface area.
Chapter 6	Myoton pro. Von Frey monofilaments. 3D breast scan. Core temperature.	Skin stiffness. Tactile threshold estimation. Breast surface area.
Chapter 7	Infra-red camera. Quantitative sensory test (thermal and wetness). OCT scan. 3D breast scan.	Thermal sensation. Wetness perception. Epidermal thickness. Surface roughness. Breast surface area.
Chapter 8	Technical absorbents. Modified iodine technique. Partitional calorimetry. iButtons. Perceptual scales. Tympanic temperature.	Local sweat rate. Sweat gland density. Evaporative requirement for heat balance. Skin temperature. Thermal sensation / Wetness perception.

- **Ethics**

The laboratory methods undertaken are described in the experimental protocols within the experimental chapters and were approved by The University of Southampton's Ethical Committee:

- ERGO 79007: Impact of breast size on sweat gland density, sweat gland output and breast sensation during exercise heat stress
- ERGO 99072: The influence of pubertal stage on whole body and local sweating patterns in girls exercising in the heat.

Following familiarization with a participant information sheet and the testing procedures and laboratory equipment, participants signed an informed consent form. For participants under the age of 18, parents / guardians were also required to complete an informed consent form. A health screen questionnaire was completed by every participant to ensure suitability for each specific study. An example participant information sheet can be found in Appendix A.

○ Thermometry, calorimetry and hygrometry

▪ Core temperature

Performing exercise or heat stress studies carries a safety concern due to excessive elevations in core temperatures, accordingly participants must be monitored for safety. Core temperature was measured using the e-Celsius system, consisting of a gastrointestinal telemetric pill and a receiver (BodyCAP, Caen, France). These pills are non-invasive and are easy to use, with a range of 25-45°C and accuracy of 0.2 °C. The e-Celsius system is factory calibrated. Also, unique to this device is that the pill is equipped with a memory chip which allows data to be stored in case of loss of connection with the receiver.

The ease of use and comfort makes gastrointestinal pills more appealing and tolerated than other core temperature measures, such as the rectal or oesophageal probe. However, the pills are quite large so can be difficult to ingest for some and carry a greater economic cost (£50/pill).

Despite their benefits, gastrointestinal pills require the participant to have a minimum weight of 40kg, therefore could not be used in the puberty study (Chapter 8) as many of the youngest participants were below this threshold. As such, tympanic temperature was measured as a proxy.

Figure 4-1. Core temperature reader device collecting data whilst the participant runs on a treadmill in the climate chamber.

- **Tympanic temperature**

In contexts when core temperature data could not be measured using gastrointestinal pills, tympanic temperature was measured using an aural thermometer (Braun ThermoScan® 7, Kronberg, Germany). This gives an indirect measurement of core temperature thus is less physiologically meaningful and tends to underestimate core temperature but provides a simple and rapid means to assess participant body temperature increases, thus safety (Huggins et al., 2012).

- **Skin temperature**

Numerous techniques exist to measure skin temperature, including thermocouples, thermistors, iButtons, and infrared thermography. Each method has inherent strengths and limitations, and therefore no single "gold standard" currently exists (MacRae et al., 2018). The choice of measurement technique in this Thesis was guided by the specific demands of each experimental task (i.e. dynamic exercise versus resting perceptual testing) where different trade-offs related to accuracy, invasiveness, stability, and practicality were required.

Rationale for Using iButtons During Exercise

A key limitation of many wired temperature sensors, such as thermocouples and thermistors, is their sensitivity to movement artefacts. During dynamic activities such as running, these devices can produce substantial noise due to cable motion and challenges in maintaining secure bonding to the skin. Their use also introduces practical issues: wires can obstruct movement, cause discomfort, and require a receiver unit that must remain close to the transmitter.

To mitigate these limitations, iButton wireless temperature and humidity loggers were used during the exercise trials. Their small size, light weight, and wireless operation minimise interference with natural movement and reduce participant discomfort. The absence of cables also removes the risk of crosstalk between devices, allowing multiple sensors to be used simultaneously without interference. These properties make iButtons particularly well-suited for measuring skin temperature in dynamic, free-moving conditions. A limitation of iButtons, however, is that they do not provide real-time temperature readouts.

Local skin temperature during exercise was therefore measured using iButtons (Hygrochron, Maxim, San Jose, USA), which operate between –20 and 80 °C with a resolution of 0.125 °C. To estimate mean skin temperature, four iButtons were taped to the left side of the body (chest, shoulder, thigh, calf) and combined using Ramanathan's (1964) equation:

$$Mean\ T_{skin} = (0.3 * T_{chest}) + (0.3 * T_{shoulder}) + (0.2 * T_{thigh}) + (0.2 * T_{calf})$$

Rationale for Using Infrared Thermography During Sensory Testing

In contrast to the exercise trials, sensory testing required precise measurement of relative changes in local skin temperature at rest, before and after applying an external thermal or wetness stimulus. In this context, the strengths of infrared thermography outweighed its limitations.

Infrared thermography provides a non-contact, non-invasive method for rapidly capturing skin temperature via detection of thermal radiation from the surface. This is advantageous during perceptual testing (discussed below), where contact-based sensors such as thermocouples or thermistors can interfere with the sensation being assessed. These devices also remain highly sensitive to subtle movements and depend heavily on secure attachment, both problematic in protocols where a large probe is placed on the skin surface to apply the thermal stimulus. Although infrared devices may be less accurate when measuring absolute skin temperature, they are sufficiently accurate when assessing relative changes in temperature under resting conditions (James et al., 2014; van den Heuvel et al., 2003). This aligns directly with the aims of the quantitative sensory testing, where the focus was on stimulus-induced temperature change rather than absolute temperature values.

Local skin temperature was therefore measured using a FLIR ER53 infrared thermal camera (Flir Systems, Boston, MA, USA), offering a resolution of 240 × 180 pixels and a temperature range of –20 to 650 °C (accuracy ± 2%). Prior to use, the camera was calibrated against a matt black screen monitored by a thermistor (Grant Instruments, Cambridge, UK).

Figure 4-2. Thermal image using the infra-red camera.

- **Partitional calorimetry**

'Calorimetry', i.e. the measurement of heat transfer, is a valuable tool for the assessment of heat balance. Direct calorimetry is the gold standard however this method is largely inaccessible due to high economic and maintenance costs. Partitional calorimetry however is much more accessible and provides an estimation of calorimetry by relying on the calculation of each avenue for heat exchange based on fundamental physical laws governing dry and latent heat transfer. By partitioning internal heat production and elements of human-environmental heat transfer, one introduces several potential sources of error through various pieces of measurement equipment (e.g. temperature/humidity or oxygen/carbon dioxide sensors) and assumptions (e.g. clothing insulation values), which can subsequently be compounded (Cramer & Jay, 2019). However, due to its accessibility and versatility, partitional calorimetry has been used regularly over the last 80 years to address various topics in thermal research (Cramer & Jay, 2019).

Partitional calorimetry is based around the fundamental heat balance equation outlined in Section 2.1:

$$M - Wk = E + R + C + K + S$$

Where:

M = rate of metabolic energy production (W)

Wk = rate of mechanical work (W)

E = rate of evaporative heat loss (W)

R = rate of radiative heat loss (W)

C = rate of convective heat loss (W)

K = rate of conductive heat loss (W)

S = rate of heat storage (W)

Metabolic energy expenditure

For every 1 litre of oxygen that is consumed to catabolize carbohydrates, 21.13kJ of energy is released, yet to catabolize fats,19.62 kJ of energy is released (Cramer & Jay, 2019). Therefore, the ratio of each fuel source used influences M for a given VO_2. If solely carbohydrates are utilized, CO_2 is generated in equal amounts to the volume of O_2 consumed [i.e., a respiratory exchange ratio (RER) of 1.00], whereas a fat-only fuel source returns a RER of 0.70. Thus, M can be calculated as:

$$M = VO_2 \cdot \frac{\left(\left(\left(\frac{RER - 0.7}{0.3}\right) \cdot 21.13\right) + \left(\left(\frac{1.0 - RER}{0.3}\right) \cdot 19.62\right)\right)}{60} \cdot 1000 \text{ (W)}$$

Where VO_2 is the oxygen consumption in L/min (STPD), and RER is the respiratory exchange ratio (VCO_2/VO_2). Estimates of M via this method rely on the assumption that metabolic energy is derived from aerobic rather than anaerobic energy sources.

To calculate metabolic energy expenditure, a gas analysis system performed breath-by-breath analysis of O_2 and CO_2 fractions in expired air from flow through a turbine to calculate oxygen uptake (VO_2). Participants wore a facemask with the turbine and connected to the COSMED metabolic cart (Quark CPET, COSMED, Rome, Italy; see Figure 4-3) which was calibrated prior to use following the manufacturer's instructions. For gas fraction calibration, a two-point calibration using ambient air and a gas of known concentrations of O_2 (16%), and CO_2 (5%) was used. Gas volumes were calibrated using a 3L syringe.

Figure 4-3. Participant performing exercise in the climate chamber with breath-by-breath analysis to calculate metabolic energy expenditure.

Estimating heat production

The rate of metabolic heat production (H_{prod}) is calculated from the rate of metabolic energy production (M) minus the rate of any external work performed (Wk) in Watts (W):

$$H_{prod} = M - Wk \text{ (W)}$$

The rate of evaporation required for heat balance (E_{req}) can be calculated using the following formula (Parsons, 2007):

$$E_{req} = H_{prod} - H_{dry} - H_{resp} \ (W)$$

Where H_{prod} is the rate metabolic heat production, H_{dry} is the rate of dry heat exchange and H_{resp} is respiratory heat exchange.

The rate of dry heat exchange (H_{dry}) from the skin is calculated as the sum of convective (C) and radiative (R) heat transfer from the skin using the equation:

$$H_{dry} = C_{sk} + R_{sk} = \frac{T_{sk} - T_o}{R_{cl} + (\frac{1}{f_{cl} \cdot h})}$$

T_{skin} is skin temperature and T_o is operative temperature:

$$T_o = \frac{h_r T_r + h_c T_a}{h_r + h_c}$$

R_{cl} is the dry heat transfer resistance of clothing and was calculated as:

$$R_{cl} = 0.155 \cdot I_{cl} \, [m^2 \cdot {}^oC \cdot W^{-1}]$$

where I_{cl} is 0.3 (Tang et al., 2022).

h is the combined heat transfer coefficient ($h_c + h_r$) where h_r is the radiative heat transfer coefficient estimated using:

$$h_r = 4\epsilon\sigma \frac{A_r}{A_D} [273.2 + \frac{T_{sk} + T_r}{2}]^3 \; [W/m^2/K]$$

ε is the emissivity of the body surface (0.95). σ is the Stefan- Boltzmann constant (5.67×10^{-8} $Wm^{-2} K^{-1}$). A_r/A_D is the effective radiative area of the body (0.7 m^2) for a sitting person. T_r is the mean radiant temperature (°C) which was equivalent to the dry- bulb temperature as tests were conducted indoors.

$C_{res} + E_{res}$ is respiratory heat exchange and was calculated as the sum of convective (C) and radiative (R) heat transfer from respiration using the equation:

$$C_{res} + E_{res} = (0.001516 \cdot M \cdot (28.56 + 0.641 \cdot P_a - 0.885 \cdot T_a) + (0.00127 \cdot M \cdot (59.34 + 0.53 \cdot T_a - 11.63 \cdot P_a)) \; [W/m^2]$$

where P_a is the ambient water vapor pressure (kPa).

- **Local sweat rates**

Local sweat rates were measured using technical absorbents, replicating the technique from Smith and Havenith (2012) which is a well-accepted technique for body sweat mapping that gives comprehensive measurements of local sweat rates (Figure 4-4). The absorbent patch is beneficial during dynamic exercise because the collection unit (absorbent pad) is covered with an occlusive adhesive dressing (prevents contamination and does not fall off easily), does not interfere with athlete's movement, and can be placed almost anywhere on the body (i.e. allows options for placement depending on accessibility and the clothing/equipment worn) (Baker, 2016).

Prior to each trial, a set of absorbent material patches (maximum absorption = 4655 ± 220 g.m-2) were cut to size (9 cm^2), individually sealed in Ziplock bags, marked and weighed to the nearest 0.1 mg using a precision scale (PCB 350-3, KERN, Balingen, Germany). For each sample, the test site was wiped dry by the researcher then patches were affixed to a plastic insulating border then to the skin using a waterproof film dressing (Tegaderm, 3M, Minnesota, United States) to prevent the evaporation of sweat during the test periods. After a fixed period of time, the patches were removed, quickly sealed in Ziplock bags, and re-weighed. Local sweat rate ($g.m^{-2}.h^{-1}$) was calculated using the difference in pre- to post- patch weight, divided by the patch surface area and duration of application.

The use of 3x3 cm patches was selected as this permitted detection of regional differences while maintaining good inter-day reliability in the measurement of heat activated sweat gland density, as discussed below (Peel et al., 2022). To allow the investigation of estimated sweat output per gland, which required the normalisation of the LSR to the heat activated sweat gland density, we opted to use the same size patches for both measurements, such that they could be applied to the same test area.

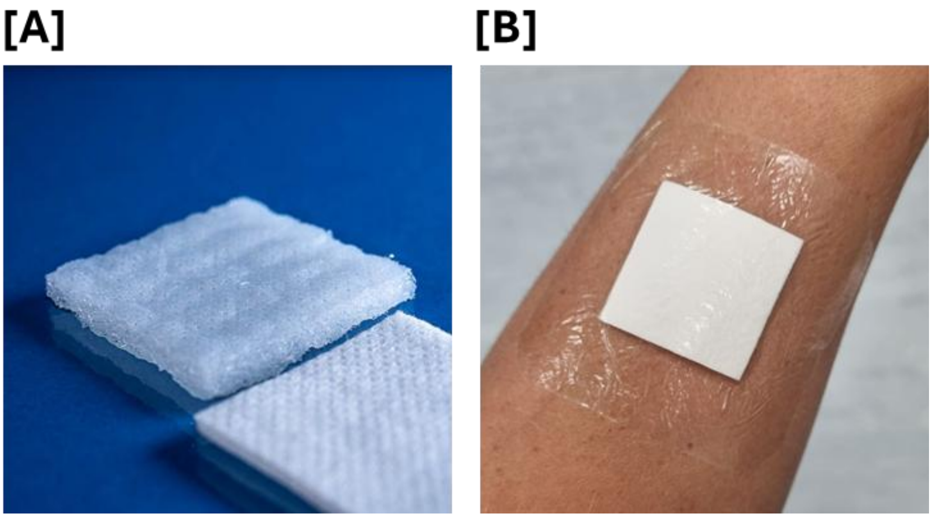


Figure 4-4. Technical absorbent patch [A] in saturated and unsaturated states, [B] affixed to the skin using a waterproof film dressing.

- **Sweat gland density**

Heat activated sweat gland density was measured non-invasively using the modified iodine technique (Gagnon et al., 2012) (Figure 4-5). Cotton paper patches were cut to 3x3cm squares and impregnated with iodine for 24 hours then sealed in air-tight bags. Following an exercise bout, when at a steady state of sweating, the skin was blotted dry to move excess water, then the iodine paper firmly pressed to the skin for ~5 seconds. Sweat from active sweat glands appeared as small blue dots on the iodine infused paper. The paper was sealed in air-tight bags and scanned immediately after testing at a high resolution (600 dots/inch) using a commercially available scanner, then analysed using ImageJ (http://rsbweb.nih.gov/ij/index.html). This process is explained in detail by Gagnon et al. (2012), but to review briefly, ImageJ software can easily identify the number of individual particles in a scanned image. The number of glands counted by the software is then divided by the surface area of the paper to give a value of active sweat glands per square centimetre. The use of 3x3 cm patches permitted detection of regional differences while maintaining good inter-day reliability (Peel et al., 2022).

A necessary point to bear in mind when using the modified iodine technique is that it becomes less reliable at lower sweat rates (Peel et al., 2022), i.e. at rest, the coefficient of variation (CV) is 54.1% (± 32.0% [95% CI]), working at 200W/m^2 the CV is 22.9% (± 11.0%), and working at 300W/m^2 the CV is 19.0% (± 11.4%). As such, when used in the puberty study, when the exercise intensity was limited by the leg strength of our youngest participants, a reliability assessment was performed to improve the rigor of this assessment. To this end, a sub-set of images was assessed by two raters to ensure rigor in the analysis. When raters agreed (<10% variation), the primary investigator's measurement was taken, where disagreement between raters was >10%, an average from the two raters was used.

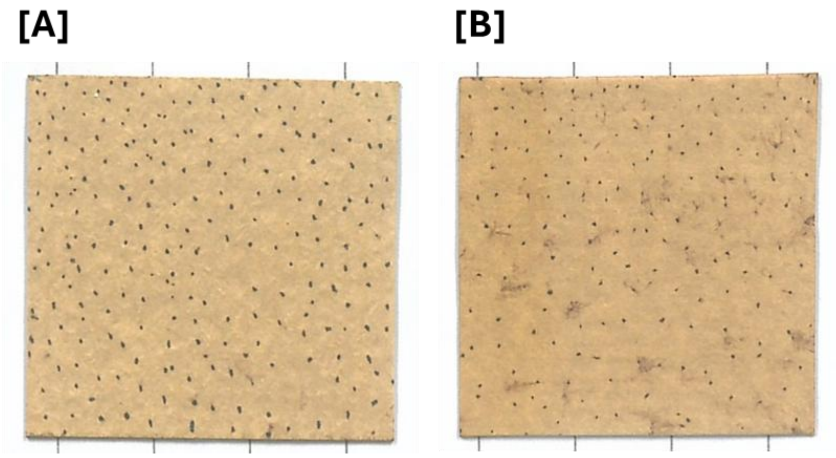


Figure 4-5. Scanned iodine patches demonstrating differences in sweat gland density. [A] 254 glands (28 glands/cm^2), [B] 226 glands (25 glands/cm^2).

○ Skin mechanics

▪ Skin properties

• MyotonPRO

Skin biomechanics across the breast was measured using the MyotonPRO device (Myoton SA, Tallin, Estonia) (Figure 4-6). The MyotonPRO uses a triaxial accelerometer (3200Hz sampling frequency) and applies a small mechanical displacement parallel to the skin surface with a J-shaped probe, specifically designed to provide a tangential perturbation. To ensure fixed contact between the probe and skin, thin (0.1 mm) double-sided stickers (10 mm diameter sticker attached to the disc) were used. For each probe, an initial force was exerted on the skin surface (0.18 N), and an additional mechanical force (0.4 N) for 15 ms, with a quick release, was applied on the skin surface to induce local deformation. The resultant damped natural oscillations caused by the viscoelastic properties of the tissue were captured with an inbuilt accelerometer. Skin stiffness and elasticity were estimated based on the oscillatory tissue response. This device has shown high reliability (intra-class correlation coefficients > 0.70) for muscle and skin stiffness assessment (John et al., 2023; Rosicka et al., 2021).

Figure 4-6. MyotonPRO device with J-shaped probe.

• Optical coherence tomography (OCT)

Skin morphology was measured using optical coherence tomography (VivoSight OCT, Michelson Diagnostics Ltd, Kent, UK). The VivoSight is a Fourier domain OCT system which captures image data at 20Hz. The OCT image volume obtained from each skin site was 6 x 6 x 2 mm^3 (width x length x depth). Epidermal properties such as skin surface roughness and epidermal thickness were estimated using the proprietary software associated with the imaging system (VivoTools, Michelson Diagnostics Ltd, Kent, UK).

Epidermal thickness

Epidermal thickness is defined by the difference in depth values of the two peaks in the Averaged A-scan plot (Welzel et al., 2004) (Figure 4-7A). The first peak relates to the surface of the skin and the second peak corresponds the dermal-epidermal junction, such that the layer between these peaks corresponds to the epidermis (Mogensen et al., 2008). Skin thickness can be influenced by gender, age, and anatomic site (Gambichler et al., 2006).

Surface roughness

The roughness of the skin surface can be estimated from 2D-OCT scans by calculating the root mean square of the deviation of the peaks and troughs from the mean line of the skin surface (Maiti et al., 2016)(Figure 4-7B). Mechanical forces interacting with the skin (e.g. breast mass) influence roughness; thus this could be a parameter of interest in this research.

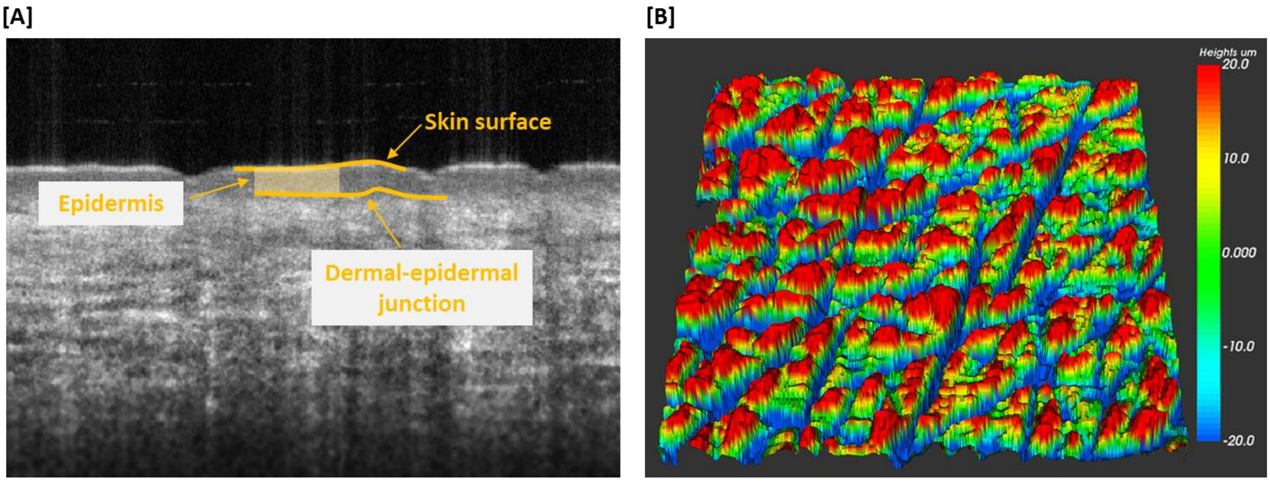


Figure 4-7. [A] Annotated 2D-OCT scan of the breast skin. [B] 3D surface roughness scan with scale.

- **3D Scanner**

Three-dimensional (3D) scanning is a well-established method of measuring breast volume and breast surface area. Göpper et al. (2020) developed a reliable marker placement set to estimate breast volume which was replicated in this study to define the breast borders. To review briefly, the area of the scan is based on defined anatomical landmarks: the midsternal line forms the medial border, the caudal border is one centimetre below the sub-mammary fold, laterally it incorporates the anterior axillary fold, and cranially the border is a straight line connecting the anterior axillary fold to the medial border.

Piloting of marker placement demonstrated the need to apply markers when in a 4-point prone position, allowing the breasts to hang down such that all the breast borders were visible. Scanning was performed with a white-light scanner (EinScan H, Shining 3D Tech. Co. Ltd., Hangzhou, China; resolution = 0.25mm, accuracy = 0.05mm), generating a 3D mesh from which surface area could be extracted using MeshLab (Visual Computing Lab, CNR-ISTI, Pisa, Italy).

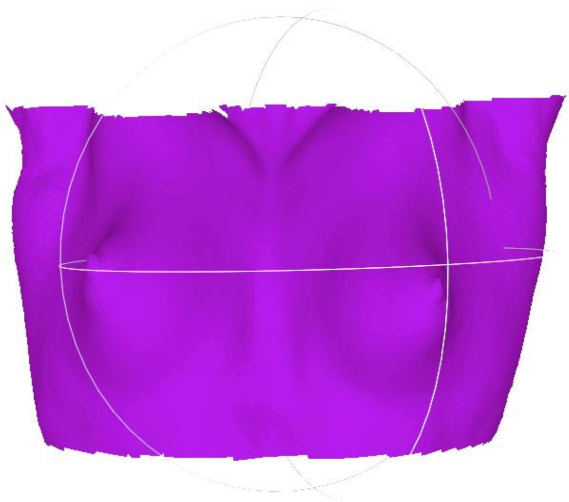


Figure 4-8. Breast scan from which breast surface area could be measured.

Perceptual assessment

Psychometric scales

Two main psychometric scales were used in this Thesis to assess thermal sensation, thermal comfort, and wetness perception: Likert scales and Visual Analogue Scales (VAS). The choice of scale was determined by their suitability to the experimental context and participant group.

Likert scales were selected for use during exercise, particularly in children, because the presence of verbal anchors helps participants interpret and express sensations despite external noise or distraction (Lee et al., 2010). Their reduced granularity also makes them easier for paediatric participants to understand and apply consistently (Teli et al., 2013). However, their simplicity is also a limitation: the discrete categories restrict sensitivity and may mask subtle changes in perception, particularly during rapidly changing thermal states. Additionally, participants may gravitate toward central categories or interpret descriptors differently, hence the need for well explained descriptors – especially for paediatric participants.

In contrast, Visual Analogue Scales (VAS) offer greater sensitivity by allowing participants to express perceptual changes along a continuous line, without being constrained by verbal labels (Lee et al., 2010). This finer discrimination is advantageous during quantitative sensory testing at rest, where controlled stimuli and ample time enable participants to use the scale accurately. Nonetheless, VAS also carry limitations. They require higher cognitive demand and familiarity, making them less suitable for use during exercise or with younger participants. They can also introduce greater variability if participants differ in how they conceptualise and anchor their sensations along the continuum. Figure 4-9 shows an overview of the psychometric scales used for the assessment of all the perceptual measures at rest and during exercise.

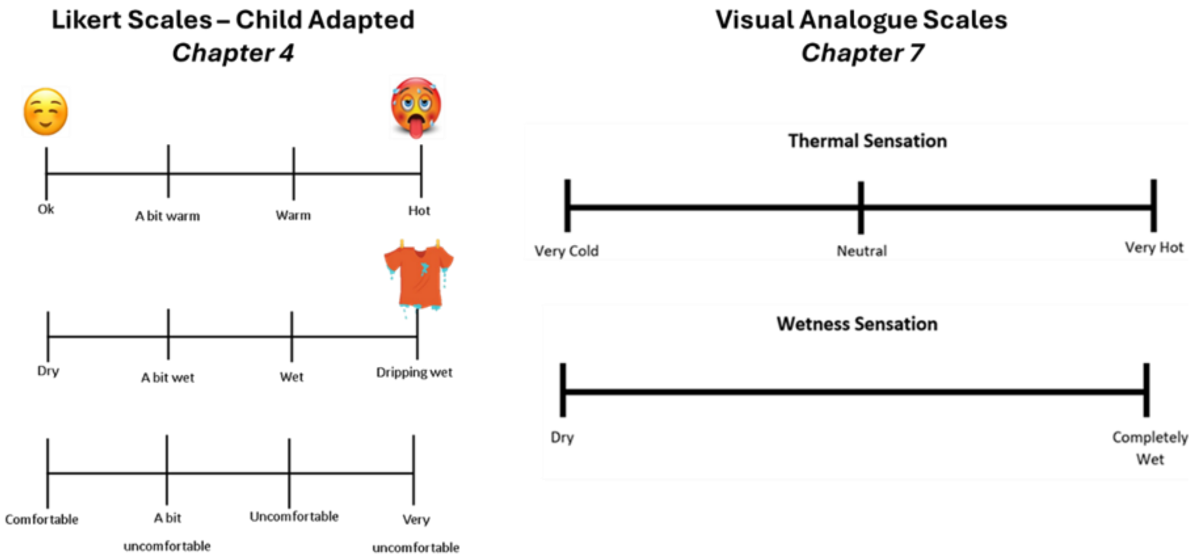


Figure 4-9. Overview of the Likert and Visual Analogue scales used for thermal sensation and wetness perception assessments. The length of the lines for the Visual Analogue scales were 100mm.

Perceptual stimulator

Quantitative sensory testing requires the use of a controlled stimulator capable of delivering precise thermal and wetness stimuli to the skin. In this Thesis, a Physitemp thermal stimulator (Physitemp Instruments Inc., USA) was used for this purpose. The device consists of a temperature controller and a water tank connected to a 25 cm^2 metallic thermal probe weighing

269 g, which is driven by a thermoelectric (Peltier) module. The thermal probe provides a controlled temperature range of 15–45 °C with a resolution of 0.1 °C, enabling accurate and repeatable delivery of thermal stimuli during perceptual testing.

To use the probe to assess wetness perception, a 100% cotton fabric patch was attached to the probe interface and wetted with a fixed volume of ambient temperature water which would equate to the probe surface temperature before application to the skin.

- **Sensory threshold estimation**

Tactile sensation at the breast was assessed using Von Frey monofilaments (Figure 4-10) due to their ease of use and low cost. Measurements can also be easily repeated with small standard deviations, and it is the most used instrument in previous literature assessing sensation of the breast (Yap et al., 2005). However, it is necessary to bear in mind that there is an inverse linear relationship between relative humidity and the bending force for each monofilament with a 1% increase in relative humidity corresponding to a 1–4% relative decrease in numerical bending force (Werner et al., 2011). Therefore, use of the monofilaments was avoided in the climate chamber when the water vapour pressures was set above ambient.

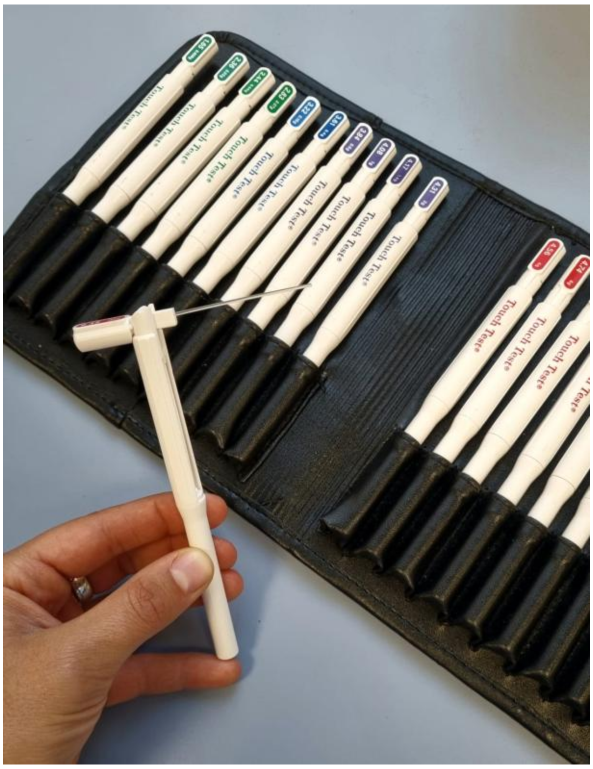


Figure 4-10. Von Frey monofilaments used to measure tactile thresholds

Chapter 5 Experimental Study 1: The effect of female breast surface area on heat-activated sweat gland density and output

Manuscript published in Experimental Physiology

Blount, H., Valenza, A., Ward, J., Caggiari, S., Worsley, P. R., & Filingeri, D. (2024). The effect of female breast surface area on heat-activated sweat gland density and output. Experimental Physiology, 109, 1330–1340. https://doi.org/10.1113/EP091850

○ Abstract

Female development includes significant morphological changes across the breast. Yet, whether differences in breast surface area (BrSA) modify sweat gland density and output remains unclear. The present study investigated the relationship between BrSA and sweat gland density and output in 22 young to middle-aged females (28 ± 10yr) of varying breast sizes (BrSA range: 147 - 561cm^2) during a submaximal run in a warm environment (32 ± 0.6℃; 53 ± 1.7% RH). Local sweat gland density and sweat rate (LSR) above and below the nipple and at the bra triangle were measured. Expired gases were monitored for the calculation of E_{req} (in W/m^2). Associations between BrSA and i) sweat gland density; ii) LSR; iii) sweat output per gland for the breast sites were determined via correlation and regression analyses. Our results indicated that breast sweat gland density decreased linearly as BrSA increased (r = -0.76, p<0.001), whereas sweat output per gland remained constant irrespective of BrSA (r = 0.29, p = 0.28). This resulted in LSR decreasing linearly as BrSA increased (r = -0.62, p = 0.01). Compared to the bra triangle, the breast had a 64% lower sweat gland density (p<0.001), 83% lower LSR (p<0.001) and 53% lower output per gland (p<0.001). BrSA (R^2 = 0.33, p = 0.015) explained a greater proportion of variance in LSR than E_{req} (in W/m^2) (R^2 = 0.07, p = 0.538). These novel findings extend the known relationship between body morphology and sweat gland density and LSR, to the female breast. This knowledge could innovate user-centred design of sports bras by accommodating breast size-specific needs for sweat management, skin wetness perception, and comfort.

Introduction

As stated in section 2.2, following behavioural thermoregulation, the production and evaporation of sweat from the skin surface is the human body's principal and most powerful method of heat loss during exercise and heat stress (Havenith, 1999; Havenith et al., 2008). By 2 years of age, our skin contains 2-5 million sweat glands, which are the main end organs supporting sweat production and secretion onto the skin (Kuno, 1956). The number of sweat glands does not appear to change beyond this age, hence sweat gland density decreases with skin expansion during physical growth and musculoskeletal maturation (Kuno, 1956; Szabo, 1958).

In contrast to males, female development includes significant morphological changes across specific body parts, such as the breast, as discussed in section 2.5.1. Female breast development, and the resulting BrSA, can vary greatly due to genetic factors, body-mass-index, and energy intake early in life (Trichopoulos & Lipman, 1992; Wade et al., 2010). However, as highlighted in section 2.5.7, it is unknown whether regional sweat gland density further decreases as breasts grow.

Understanding the relationship between BrSA and sweat gland density over this body part is important, as sweat gland density and output per gland may impact LSR (Kondo et al., 2001), and consequently the distribution of sweat across the breast during exercise. LSRs across the breast have been previously measured by Smith and Havenith (2012), who found most regional differences between the bra triangle (i.e. higher LSR) and the breast (i.e. lower LSR). However, the work of Smith and Havenith (2012) did not address the impact of breast size as a variable in modulating LSR. The majority of females use sports bras as an essential item of clothing during exercise to support the breast and reduce the amount of breast movement (Gehlsen & Albohm, 1980; Lorentzen & Lawson, 1987; Scurr et al., 2010) and breast discomfort (Brown et al., 2014). Differences in the distribution of sweat across breasts of different surface areas could modify the pattern of sweat accumulation in sport bras, which could in turn impact breast's heat balance and comfort during exercise heat stress in females (Ayres et al., 2013; Gorea et al., 2020).

The number of females taking part in sport has increased considerably over the last 50 years with data indicating almost 50% of females worldwide are now interested in sport (Eime et al., 2021; Ose et al., 2025); yet, kit and equipment can be a barrier to exercise participation for many females (Brown et al., 2014; McGhee & Steele, 2020; Norris et al., 2020). Furthermore, females continue to be largely unrepresented in heat stress research, with a recent review highlighting that only 12-18% of participants in thermoregulation research were female over the last decade (Hutchins et al., 2021). Hence, increasing our fundamental understanding of sweat gland distribution and function at the breast may support innovation in female's sportswear design to remove barriers to an active lifestyle across the lifespan, with related health benefits for the global female population.

The primary aim of this study was to investigate the relationship between BrSA and sweat gland density across the female breast in a cohort of healthy females of varying breast sizes. This was assessed during a submaximal run in a warm environment. Our primary hypothesis was that sweat gland density over the breast would decrease with increasing BrSA. The secondary aim of this study was to investigate the relationship between BrSA and sweat output per gland and associated LSR across the female breast in the same cohort of females. Our secondary hypothesis was that sweat output per gland would not vary with BrSA, thereby leading to decreasing LSR(s) at the breast with increasing BrSA.

○ Materials and methods

Ethical approval

This study was approved by the University of Southampton Ethics Committee (approval no.79007). All participants provided written informed consent prior to testing. The study conformed to the ethical standards set by the Declaration of Helsinki, except for registration in a database.

Participants

The study involved a convenience sampling approach of females varying in BrSA. Due to the non-linear association between BrSA and bra size (i.e. the latter being the most intuitive way of determining one's breast size for eligibility purposes) we opted for the recruitment of 4 to 6 women for each bra-size category, namely small (corresponding size guide measurements of the bra: 32C-32E / 34A-34C), medium (34D-34E / 36A-36C), large (36D-36E / 38A-38C), and extra-large (38D-38E / 40A-40C). This purposeful recruitment was used to achieve a wide range of BrSA. Females are indeed typically familiar with such a classification of bra size, and this would have aided participant recruitment. As a result, we expected to recruit a total sample size of 20 to 24 healthy young and middle-aged females, which is in line with most studies in human thermoregulation (Buono & Connolly, 1992; Havenith et al., 2008; Kondo et al., 2001).

Participants' recruitment resulted in 22 females partaking in the study (age: 27.7 $\pm$ 9.6 years; weight: 72.2 $\pm$ 12.7 kg; height: 170.4 $\pm$ 4.8 cm) (Table 5-1). Inclusion criteria included physically active females (i.e. performing 30 minutes regular exercise of moderate intensity at least 3 days each week), free from musculoskeletal or neurological disease, not under any pharmacological treatment, with standard breast tissue type (i.e. no implants, reductions or mastectomy) and who fit size small, medium, large or extra-large sports bras. They were also instructed to refrain from: 1) performing strenuous exercise in the 48 hours preceding testing; 2) consuming caffeine or alcohol in the 24 hours preceding testing; 3) consuming food in the 3 hours prior to testing; and 4) applying creams or gels to the chest region. Nineteen participants were well spread across a typical 28-day menstrual cycle (mean day of cycle: 13.6 ± 8.2) and three participants presented irregular periods at the time of the study.

Table 5-1. Participant demographics (n=22). BMI = body mass index; BSA= body surface area; BrSA= breast surface area.

	Age (years)		**BMI (kg/m²)**		**BSA (m²)**		**BrSA (cm²)**	
Bra Size	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
Small (n=6)	23.3	18-30	21.8	19.5-25.5	1.68	1.60-1.75	168	147-230
Medium (n=5)	22.8	19-27	23.7	21.6-26.5	1.77	1.66-1.87	246	204-288
Large (n=6)	30.2	20-42	24.4	21.5-29.1	1.85	1.70-1.94	316	174-402
X-Large (n=5)	34.8	21-55	29.9	25.9-35.1	2.05	1.88-2.21	459	300-562

Experimental design

To establish breast size dependent differences in sweat gland density and output, we designed an experiment that aimed to achieve a steady state of sweating through a submaximal exercise protocol performed in the heat (Figure 5-1). At the start of each trial, breast geometry was captured using white-light scanning techniques; participants then performed a 50-minute run in a climatic chamber set to 32±0.6 °C and 53±1.7 % relative humidity, during which thermophysiological (e.g. T_{core} and respiratory gases) and perceptual parameters (e.g. rating of perceived exertion) were recorded. During the final 5 minutes of the run, sweat gland density and LSR(s) were measured at three locations across the breast (Figure 5-2). This data was then used to establish the associations amongst BrSA, sweat gland density and output, and LSR.

The running pace of the submaximal exercise protocol was kept constant throughout the trial and was self-selected by each participant in the initial 5 minutes to elicit an average rating of perceived exertion (RPE) of 13, i.e. 'somewhat hard' using the Borg Scale (Borg, 1982) over the course of the run. A fixed-RPE model was selected to resemble a real-life scenario whereby individuals run to a self-regulated steady-state pace based on perceived exertion. Pilot data also indicated that the resulting exercise intensity, combined with the warm environmental conditions, provided a sufficient thermal stimulus to elicit steady state sweating for the evaluation of sweat gland density and output (i.e. the former being our primary outcome for this study). This experimental model resulted in varying individual levels of H_{prod} and related E_{req}, which are well-known factors that contribute to individual variability in LSR (Cramer & Jay, 2015). On this basis, the protocol incorporated an assessment of expired respiratory gases for the calculation of E_{req}, which was subsequently used in the evaluation of its relative contribution to individual changes in LSR(s), alongside that of BrSA (see *Statistical Analysis* section for details). We acknowledge that a potential limitation of this approach is that a self-selected exercise intensity could have resulted in a decreasing level of E_{req} for participants with larger BrSA. As such, our data analysis incorporated an evaluation of the relationship between individuals E_{req} values and BrSA (see *Statistical Analysis* section for details).

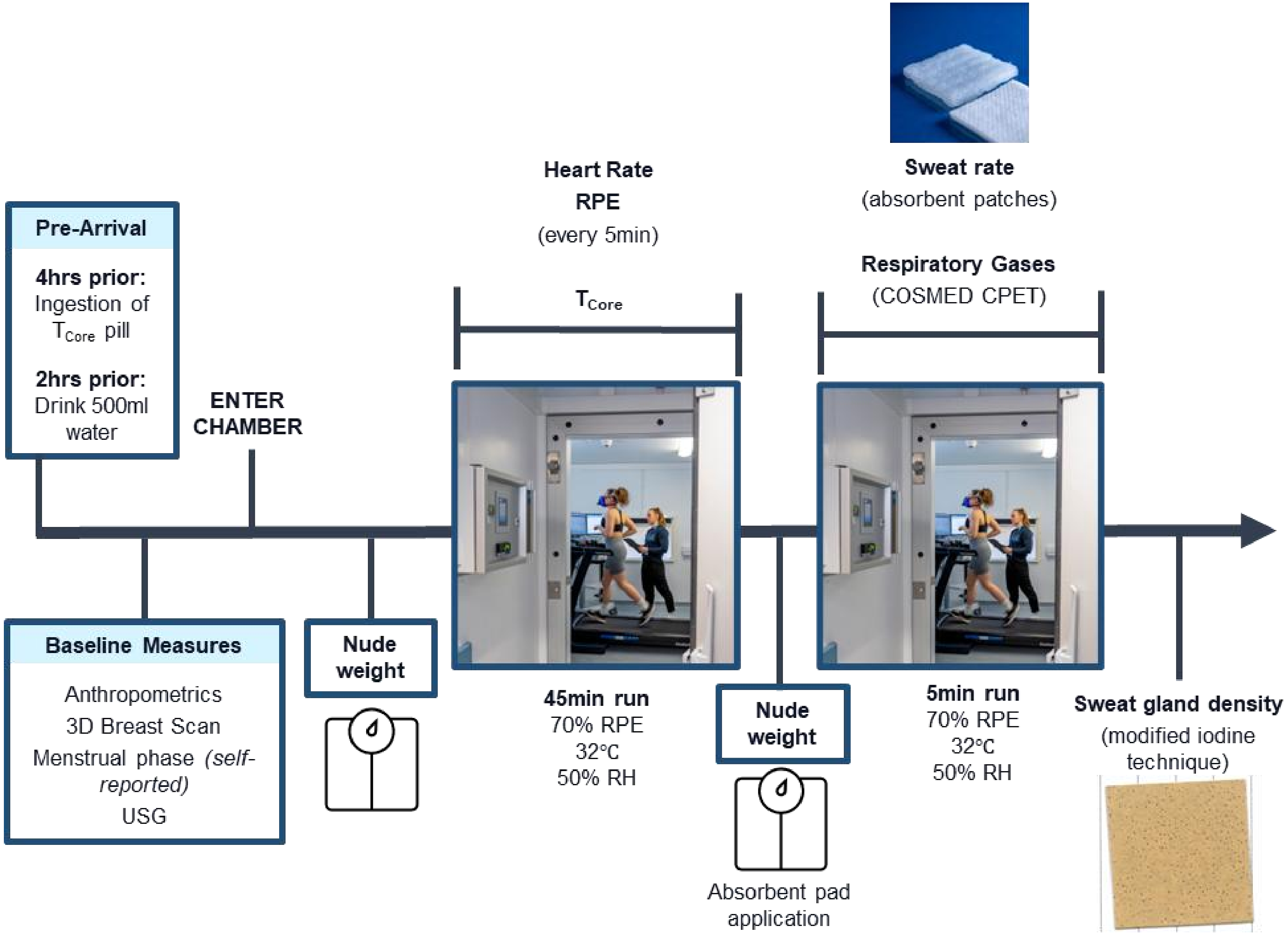


Figure 5-1. Schematic of experimental design.

Experimental procedures

Four hours prior to arrival at the laboratory, participants were instructed to ingest a telemetric pill (e-Celsius Performance pill, BodyCAP, France) to measure T_{core}. Pills were ingested 4hrs prior to the experimental session to allow sufficient transit time to the intestine. Participants were instructed to wear a wristband for the following 72 hours to identify that they had swallowed an MRI incompatible device. During the experimental session, data from the pill were sampled every 15 seconds to the receiver (EQ-eViewer Performance monitor, BodyCAP, France). Furthermore, participants were also instructed to drink 500 ml of water 2 hours prior to testing to ensure hydration.

Upon arrival to the laboratory participants provided a urine sample to measure urine specific gravity (Digital refractometer, KERN, Balingen, Germany). If urine specific gravity was >1.025 g/mL participants were provided with 500 ml of water and tested again after 30 minutes before proceeding with the protocol (Casa et al., 2005). Anthropometric measures of height and BrSA were taken at rest in a thermoneutral laboratory (~23 ℃ and ~50 % RH). Height was measured on a wall stadiometer and BrSA was estimated using a white-light scanner (EinScan H, Shining 3D Tech. Co. Ltd., Hangzhou, China). Firstly, reflective markers were placed around the breast border based on a validated breast volume model (Göpper et al., 2020). Participants were then asked to adopt a 4-point prone position such that the breasts could freely hang away from the torso, thus allowing a scan of the entire breast skin surface, from which surface area could be extracted using MeshLab (Visual Computing Lab, CNR-ISTI, Pisa, Italy).

Upon entry to the climate chamber, participants were instructed to fully undress behind a privacy curtain and dry nude body mass was measured on a precision scale (KERN 150K2DL, Balingen, Germany; accurate to 0.005 kg). Following the body weight measurement, participants were instructed not to drink throughout the trial until being weighed post run. Whole body sweat loss (WBSL) was calculated as the difference between pre- and post-exercise body mass. Post-exercise mass was measured as participants stepped off the treadmill following the initial 45 minutes of running.

Once weighed, participants were equipped with a heart rate (HR) monitor (1 Hz; Garmin 935, Garmin Ltd., Kansas, United States) at the forearm and provided with standardised running shorts and a sports bra and, whilst wearing their own personal trainers and socks. Next the participants were instructed to self-select a running pace to elicit an average rating of perceived exertion (RPE) of 13, or ‘somewhat hard’ using the Borg Scale over the course of the run, which was recorded every 5 minutes. This treadmill speed was kept constant throughout the trial. The treadmill gradient was maintained at 0 % throughout the run.

At minute 45 of the run, or once volitional cessation occurred, participants briefly stepped off the treadmill and were asked to step behind the privacy curtain and fully undress to take another nude measurement. Following this, the set-up of LSR and metabolic data collection for the final 5 minutes of the run occurred. LSR was measured using a modified absorbent technique developed by Smith and Havenith (2011). Before each trial, a set of absorbent material patches (maximum absorption = 4655 ± 220 $g.m^{-2}$) were cut to size (9 cm^2), individually sealed in Ziplock bags, marked and weighed to the nearest 0.1 mg using a precision scale (PCB 350-3, KERN, Balingen, Germany). Three sites across the chest were assessed including 3cm above areola top, 3 cm below areola bottom, and the xyphoid process (“bra triangle”) (Figure 5-2). Patches were affixed to a plastic insulating border then to the skin using a waterproof film dressing (Tegaderm, 3M, Minnesota, United States) to prevent the evaporation of sweat during the test periods. For each sample, the test site was wiped dry by the researcher, the patch was affixed to the skin and subsequently held in place with a dry bra. Following patch application, the participant donned the dry bra and was equipped with the gas exchange mask prior to completing the final 5 minutes run. Following this, the participant stepped off the treadmill, the mask was removed, and the absorbent patch removed and sealed. To ensure a standardised patch application time for all participants but also allow sufficient time for the mask set up and donning and doffing of clothing, the absorbent patch was affixed for 10 minutes for all participants. After exactly 10 minutes, the patches were removed, quickly sealed in Ziplock bags, and re-weighed. Local sweat rate ($g.m^{-2}.h^{-1}$) was calculated using the difference in pre- to post- patch weight, divided by the patch surface area and duration of application.

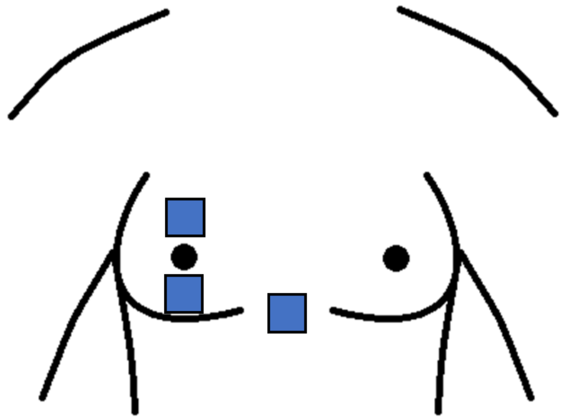


Figure 5-2. Absorbent patch and iodine paper contact locations; above nipple, below nipple, bra triangle. 3x3cm patches.

Oxygen consumption (VO_2) and carbon dioxide (VCO_2) production were measured by indirect calorimetry using a calibrated gas exchange analyser (Quark CPET, Cosmed, Rome, Italy) with a breathing mask. The mask was carefully placed over the mouth and nose to avoid air leakage and worn during the last 5 minutes of the running protocol. We opted for this sampling approach to eliminate the impact that wearing a mask throughout the whole trial could have had on running style and efficiency, the latter being a potential modulator of thermoregulatory responses (Smoljanić et al., 2014). In further support of the reliability of the measurements, we performed pilot studies with mask wearing throughout the 50-minute run to compare respiratory gas exchange levels between the initial 45 minutes and the final 5 minutes post mask wearing and confirmed that these levels were equivalent.

Partitional calorimetry was used to calculate E_{req} (in W/m^2) over the last 5 minutes of running using the formulas outlined in the Experimental Methodology chapter (Chapter 4: Partitional calorimetry) (Parsons, 2007).

Following cessation of the run and immediately after removal of the absorbent pads, heat activated sweat gland density was measured non-invasively using the modified iodine technique (Gagnon et al., 2012). Cotton paper patches were cut to 3x3cm squares and impregnated with iodine. The skin was blotted dry to move excess water, then the iodine paper firmly pressed to the skin for ~5 seconds. Sweat from active sweat glands appeared as small blue dots on the iodine infused paper. The paper was sealed in air-tight bags and scanned immediately after testing at a high resolution (600 dots/inch) then analysed using ImageJ (http://rsbweb.nih.gov/ij/index.html). This process is explained in detail by Gagnon et al. (2012). The use of 3x3 cm patches permitted detection of regional differences while maintaining good inter-day reliability (Peel et al., 2022). Sweat output per gland was subsequently calculated as the ratio between LSR and sweat gland density at each tested site (Buono & Connolly, 1992). It should be noted that this technique does not measure sweat output per gland directly, but rather it estimates mean glandular output in a local area from the LSR and density of active glands.

All data collection was performed by female researchers (although participants were always given the option of a male or female chaperone throughout testing).

Statistical analysis

Normality testing using the Shapiro–Wilk test was performed for all datasets and homoscedasticity was assessed using the Levene test for regression analysis. Data for E_{req}, WBSL, ΔT_{core}, HR, running speed, and running time are presented descriptively. Statistical analyses were carried out using SPSS (version 28.1; Chicago, USA). Data are reported as the means and SD and significance was set at $p < 0.05$.

It is important to note that not all our participants were able to complete the full 50-min trial duration, as some participants required an earlier termination of the run due to volitional fatigue. Thus, we divided the study cohort into 'finishers' (n = 16) and 'non-finishers' (n = 6) for the purpose of data analysis. Specifically, all participants in the XL bra category (n = 5) and one participant in the large bra category were unable to complete the full 45-minute run trial. Previous evidence indicated that full recruitment of sweat glands occurs after an average exercise duration of 8 minutes at a similar exercise intensity as the one utilised in this study (Kondo et al., 2001). As all participants ran for a minimum of 20 minutes (mean ± standard deviation [SD]; 44.6 ± 9.6mins), all data were included (N = 22) for the analysis of sweat gland density. In contrast, previous evidence indicated that LSR increases linearly with exercise duration (Kondo et al., 2001). Therefore, due to the exercise duration effect, only "finishers" (n = 16) were included in the LSR and sweat output per gland analysis. Furthermore, we conducted correlation analyses between individual E_{req} values (in W/m^2) and BrSA in all participants, as well as in the “finisher” cohort, to identify any potential association between varying E_{req} levels resulting from self-selected exercise intensities and BrSA.

Skin site dependent differences in sweat gland density amongst the above and below nipple sites and the bra triangle were analysed using a one-way repeated measures ANOVA. The Greenhouse–Geisser correction was applied if the assumption of sphericity had been violated. In the event of statistically significant main effects, post hoc analyses were conducted using Bonferroni tests. In the absence of differences between above and below nipple sites (effectively the breast sites), sweat gland density data for the above and below nipple sites were averaged to determine a cumulative “breast site”. At this point, and to address our primary outcome, Pearson correlation analyses between BrSA and sweat gland density was used, separately for the breast site and bra triangle.

Second, and to address the secondary outcome, the same site-related analyses (i.e. via a one-way repeated measures ANOVA), and Pearson correlation analyses (i.e. with BrSA), were performed using LSR and sweat output per gland data for both the (cumulative) breast site and bra triangle.

Finally, and in accordance with the previously cited biophysical role of E_{req} in contributing to individual variability in LSR(s) (Cramer & Jay, 2015), exploratory multivariable linear regression analysis was used to assess BrSA and E_{req} in W/m^2 (i.e. as the independent variables) and LSR(s) at the breast site (i.e. as the dependent variable). This analysis was designed to quantify the relative contribution of both BrSA and E_{req} in W/m^2 to individual variance in LSR(s), under conditions of self-selected exercise intensity that would have elicited natural variations in E_{req} in W/m^2 amongst participants. Assumptions of multi-collinearity between these variables were assessed and satisfied.

- ## Results

Descriptive exercise and physiological data

Exercise and physiological variables are presented in Table 5-2 for both finisher and non-finisher participant.

Table 5-2. Mean values, standard deviation (SD), minimum and maximum values of evaporative requirement for heat balance in W/m^2 (E_{req}), whole body sweat loss (WBSL), core temperature change (ΔT_{core}), heart rate, run speed and run time measured during the submaximal run in the heat. Split by bra size and finishers (n = 16) and non-finishers (n = 6).

	Finishers (n = 16)									Non-finishers (n = 6)				
	Small (n = 6)			Medium (n = 5)			Large (n = 5)			Large (n = 1)		X-Large (n = 5)		
	Mean	SD	Min-Max	Mean	SD	Min-Max	Mean	SD	Min-Max	Mean	Min-Max	Mean	SD	Min-Max
E_{req} (W/m^2)	356	36.1	289-380	337	15.9	316-358	318	43.5	275-386	307	307	364	44.2	318-416
WBSL (g)	605	196	298-605	793	169	670-1070	693	273	490-1155	465	465	400	123	245-545
Δ T_{core} (°C)	1.6	0.5	0.8-2.4	2.0	0.5	1.5-2.7	1.4	0.4	1.1-1.9	1.3	1.3	0.9	0.4	0.4-1.3
Heart rate (bpm)	151	5	142-155	165	9	154-176	160	11	143-171	160	160	151	24	122-152
Running speed (km/h)	7.5	1.2	6.4-9.7	7.2	0.8	6.4-8.0	6.8	0.8	6.1-8.0	7.2	7.2	7.6	1.2	6.1-8.9
Run time (min)	45	0	45	45	0	45	45	0	45	30	30	29	6.5	15-35

Test site dependent differences in sweat gland density, output and LSR

When considering data from all tested females (N = 22), sweat gland density ranged between 12.1 - 71.2 glands/cm^2 and 10.3 - 59.0 glands/cm^2 at the above and below nipple sites, respectively, and between 56.8 – 136.9 glands/cm^2 at the bra triangle. A significant effect of test site on sweat gland density was observed ($p < 0.001$) with sweat gland density at the bra triangle (92.8 ± 21.4 glands/cm^2) being ~3 times greater than above the nipple (35.8 ± 19.2 glands/cm^2, $p < 0.001$) and below the nipple (31.9 ± 16.0 glands/cm^2, $p < 0.001$). No differences were found between above and below nipple sites ($p = 0.155$).

When considering data from finisher females (N = 16), LSR ranged between 8.3 – 35.9 g/m^2/h and 6.4 – 44.4 g/m^2/h at the above and below nipple sites, respectively, and between 74.0 - 225.5 g/m^2/h at the bra triangle. A significant effect of test site on LSR was observed ($p < 0.001$) with LSR at the bra triangle (122.5 ± 43.4 g/m^2/h) being ~6 times greater than above the nipple (20.8 ± 7.6 g/m^2/h, $p < 0.001$) and below the nipple (21.2 ± 12.0 g/m^2/h, $p < 0.001$). No difference was found between above and below nipple sites ($p = 0.917$).

When considering data from finisher females (N = 16), output per gland ranged between 1.04 – 2.94 mg/h and 0.64 – 5.79 mg/h at the above and below nipple sites, respectively, and between 2.6 – 7.8 mg/h at the bra triangle. A significant effect of test site on output per gland was observed ($p < 0.001$) with output at the bra triangle (4.31 ± 1.45 mg/h) being ~2 times greater than above the nipple (1.80 ± 0.54 mg/h, $p < 0.001$) and below the nipple (2.24 ± 1.36 mg/h, $p = 0.007$). No difference was found between the above and below nipple sites ($p = 0.619$).

Correlation of BrSA with sweat gland density, output and LSR

First, we found no statistically significant correlation between BrSA and E_{req} neither when considering all participants ($r = 0.28$, $p = 0.201$; Figure 5-3A) nor the finisher participants ($r = -0.10$, $p = 0.726$; Figure 5-3B).

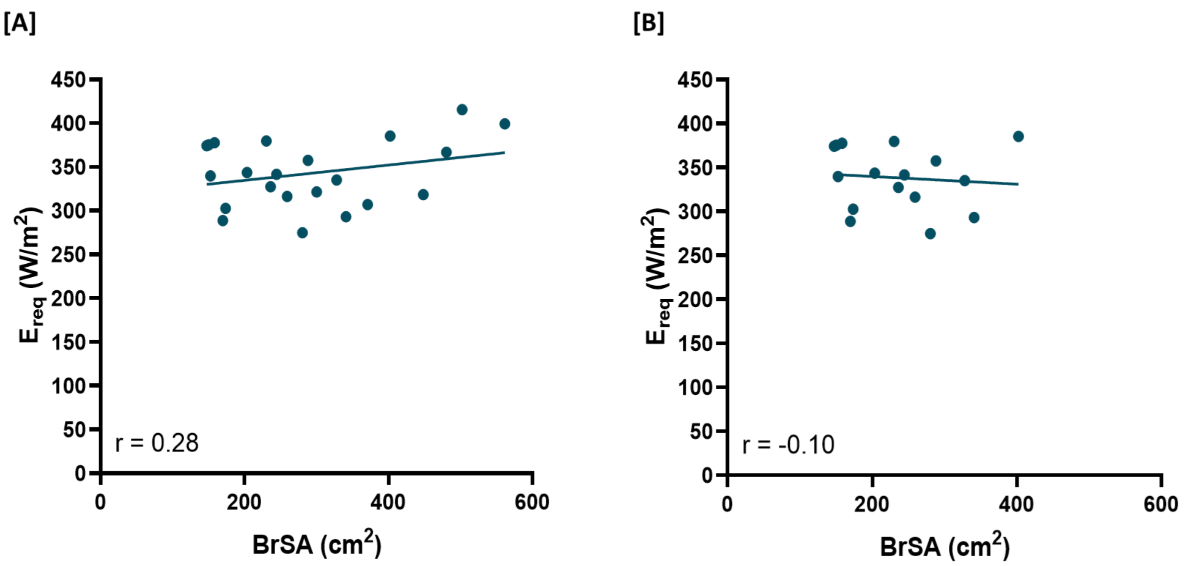


Figure 5-3. Relationship between breast surface area and evaporative requirement for heat balance (in W/m^2) for [A] all participants (n=22; used in sweat gland density analysis) and for [B] the full 45-minute trial finishers (n=16; used in LSR analysis).

Second, given the lack of differences for all assessed variables between the above and below nipple sites, the data between these test sites was averaged, and from herein we report breast [average] sweat gland density, LSR and output data.

When considering sweat gland density data (N = 22), a statistically significant negative correlation was found with BrSA across the breast (r = -0.76, p < 0.001; Figure 5-4A). A statistically significant, yet weaker correlation between BrSA and sweat gland density at the bra triangle was also observed (r = -0.48, p = 0.023; Figure 5-4B). Regarding LSR data (N = 16), a statistically significant negative correlation was found with BrSA across the breast site (r = -0.62, p = 0.011; Figure 5-4C). However, no significant relationship was found between BrSA and LSR at the bra triangle (r = 0.12, p = 0.654; Figure 5-4D).When considering sweat output per gland data (N = 16), no significant relationships were found between BrSA and output neither across the breast (r = 0.29, p = 0.279; Figure 5-4E) nor at the bra triangle (r = 0.05, p = 0.842; Figure 5-4F).

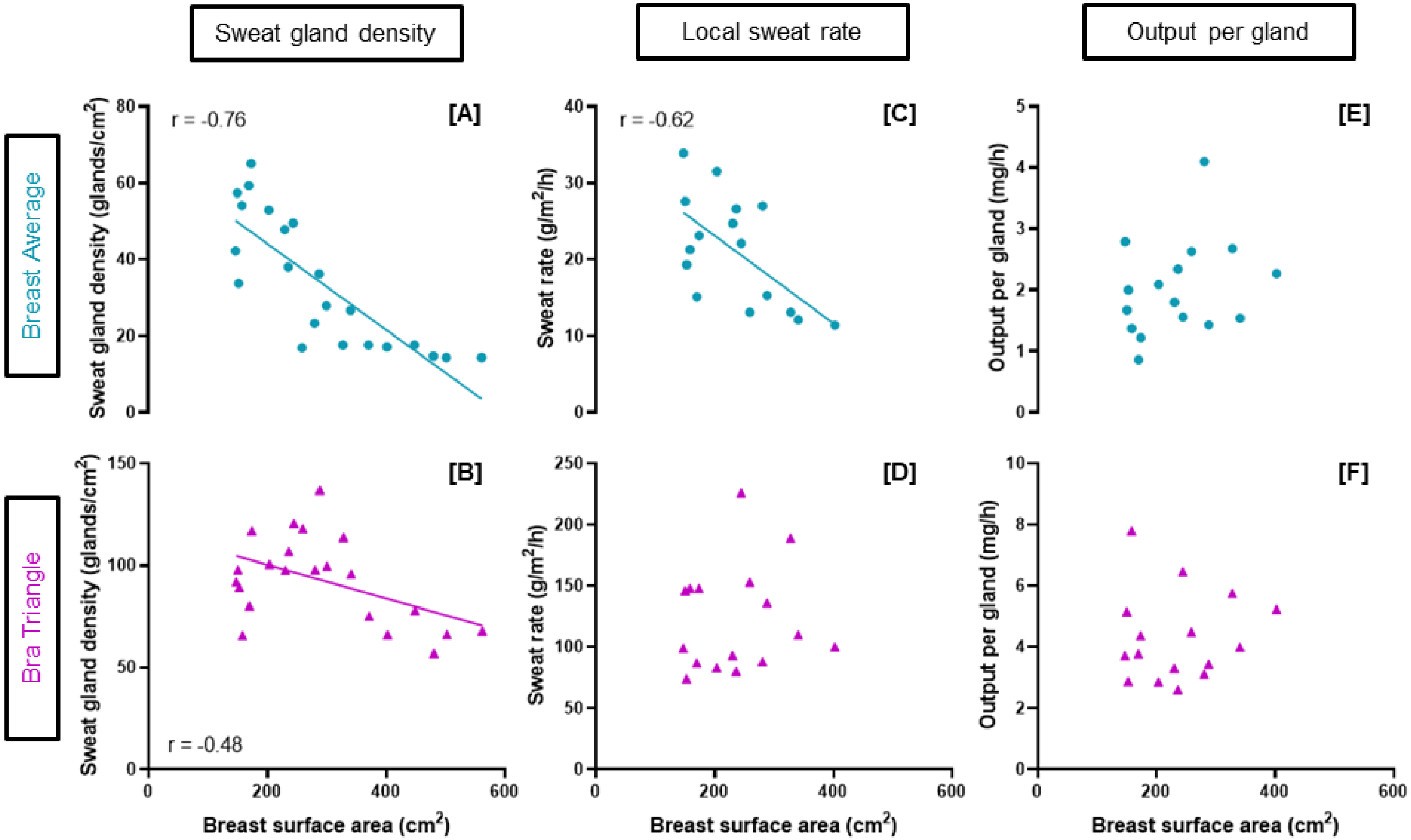


Figure 5-4. Relationship between sweat gland density (n = 22) [A, B], LSR (n = 16) [C, D] and output per gland (n = 16) [E, F] in 2 locations [breast average, bra triangle] relative to breast surface area.

Multiple regression model for LSR

The multiple regression model indicated that together BrSA and E_{req} (in W/m^2) explained 40 % of the total variance (*p* = 0.036) in LSR at the breast (Table 5-3). Out of the total variance explained, ~33% was determined by BrSA (*p* = 0.015) and 7% by E_{req} in W/m^2 (p=0.538).

Table 5-3. Multiple regression model for changes in local sweat rate at the breast (n = 16). *p < 0.05.

		b	SE	P Value	Tolerance	r^2 Value
Breast Average	**Constant**	24.955	15.959	0.142	1.564	
	BrSA (cm^2)	-0.056	0.020	**0.015***	-2.802	**32.6%**
	E_{req} (W/m^2)	0.028	0.044	0.538	0.632	7.4%

Discussion

In relation to our primary aim, the results of this study confirmed our hypothesis that sweat gland density over the breast decreased linearly with increasing BrSA in healthy young to middle-aged females. In relation to our secondary aim, our findings also confirmed our secondary hypothesis that sweat output per gland did not vary with BrSA, thereby leading to decreasing LSR(s) with increasing BrSA. Of note, individual differences in BrSA explained a greater proportion of variance (i.e. ~33 %) in breast LSR(s) than E_{req} in W/m^2(i.e. ~7 %), albeit this finding should be considered within the range of natural variation in E_{req} achieved in this study (i.e. min to max E_{req}: 275 to 386 W/m^2). In addition to our initial hypotheses, our results also indicated that, irrespective of BrSA, the breast had lower sweat gland density and output per gland than the bra triangle. Altogether, our findings confirm an established relationship between sweat gland density and local sweat rates and extends this finding to the female breast, highlighting the relationship between breast morphology and sweat gland density and output, which has valuable implications for our understanding of sweat management requirements for sport bras.

Historically, regional sweat gland density has been investigated across large body regions, (Kawahata, 1939; Kuno, 1956; Szabo, 1958). For example, early work by Kawahata (1939) investigated regional sweat gland density over the head (average sweat gland density: 260 glands/cm^2), neck (222 glands/cm^2), trunk (114 glands/cm^2), upper extremities (114 glands/cm^2) and lower extremities (100 glands/cm^2). These investigations provided reference values, and they highlighted regional differences in sweat gland density across the human body. However, these studies had limited consideration of sex-related differences and of the impact of body size/surface area across unique body parts such as the female breast. In this respect, the sweat gland densities that we observed for the female bra triangle (i.e. 92.8 ± 21.4 glands/cm^2), i.e. an area of the trunk presenting minimal breast development-dependent variation in surface area, mostly corroborate with those previously measured in the trunk region by Kawahata (1939) (i.e. 114 glands/cm^2). Yet, when considering the breast, we found that sweat gland densities decreased with increasing BrSA from a maximum of ~71 glands/cm^2 (i.e. in our smallest breasted females) to a minimum of ~10 glands/cm^2 (i.e. in our largest breasted females). This finding indicated that, while our smallest breasted females (i.e. BrSA = ~168 cm^2) presented sweat gland densities over the breast that were only slightly lower (i.e. maximum of 71 gland/cm^2) than those measured at the bra triangle (and at the trunk, by Kawahata (1939)), sweat gland density in our largest breasted females (i.e. BrSA= ~458 cm^2) approached some of the lowest sweat gland density values ever reported across the body (Taylor & Machado-Moreira, 2013). It has been previously reported that the maximum number of sweat glands that our skin contains is achieved by 2 years of age (Kuno, 1956). Hence, our findings provide compelling evidence that as the skin of the female breast stretches during the breast-growth period occurring during puberty, sweat glands become less densely populated locally and in proportion to the extent of the breast growth.

It should be noted that our data also indicated a (weak) relationship between sweat gland density and BrSA at the bra triangle. However, this relationship may be primarily dependent on the observed strong and positive correlation between BrSA and BSA. Put in context, our larger breasted females also tended to be individuals with larger BSA. Hence, the size-dependent mechanism associated with sweat gland density that we clearly observed at the breast, may have partly applied at the bra triangle of larger females (i.e. who exhibited reduced sweat gland density at the bra triangle likely due to greater skin stretch). This observation demonstrates a more general size-dependent mechanism associated with BSA and sweat gland density reported in humans, irrespective of sex (Bar-Or et al., 1968; Best et al., 2023).

In relation to the secondary aim of this study, we found that LSR(s) at the breast also decreased linearly with increasing BrSA. This response was primarily driven by the fact that, while sweat gland density over the breast decreased with increasing BrSA, sweat output per gland remained predominantly constant. It therefore appears that in the case of the breast, sweat output per gland is not upregulated to accommodate a size-dependent change in the density of sweat glands across the female breast. In the present study, the BrSA of participants within the small to extra-large bra categories accounted for between 1 % to 2.2 % of participants' BSA. This means that the 7-fold reduction in active sweat gland density that we observed between the smallest and largest breasts (see Fig. 3A) occurred across a very small portion of whole-body surface area. Differences in local evaporative capacity between larger and smaller breasted females did not translate to differences in core temperature changes. Therefore, it can be inferred that the observed reduction in active sweat gland density in larger breasts was not accompanied by a greater drive for sudomotor output, hence a consequent (and observed) lack of upregulation of LSR(s) at the breast. It should also be noted that sweat rates at the breast are generally low in comparison to other body parts, for example areas of the highest sweat rates on the female body (upper back, dorsal foot, bra triangle) produce 139 - 223 $g.m^{-2}.h^{-1}$ (Smith & Havenith, 2012) compared to 21 $g.m^{-2}.h^{-1}$ seen here at the breast. Hence, it appears that female breasts may, on the whole, play a relatively limited role in the regulation of whole-body heat balance. Nevertheless, future studies should consider experimental designs where the independent role of sweat gland density and output over the breast on increases in core temperature can be assessed more directly.

As previously noted, we recognise the LSR(s) findings presented in this study should be considered through the lens of an experimental protocol that was not designed with the primary purpose of isolating the independent effect of BrSA on LSR(s) (i.e. in that case the administration of an exercise intensity at a fixed E_{req} expressed in W/m^2 would have been more appropriate). Nevertheless, a relevant finding of this study is that individual differences in BrSA explained a greater proportion of variance (i.e. ~33 %) in breast LSR(s) than E_{req} in W/m^2(i.e. ~7 %). Drivers of variability in LSR(s) have previously been investigated and modelled by Cramer and Jay (2015), who concluded that E_{req} (in W/m^2) plays a prominent role in describing individual variations in LSR, as discussed in Section 2.2.3. This is in contrast with our findings over the breast, and it may highlight site-dependent differences in the biophysical drivers of LSR(s) (note: most data for the Cramer and Jay's model arise from measurements at the forearm). However, it is important to note that in our study, the range of E_{req} in W/m^2 achieved by our finisher participants (i.e. n = 16, E_{req} = 275 – 386 W/m^2) was the result of the natural variation associated with participants having to self-select a running speed at a fixed RPE. Our E_{req} range was half as large as that employed in the study by Cramer and Jay (2015) (i.e. E_{req} in the range of 137 - 350 W/m^2) and it also reached beyond their absolute maximum. These considerations may partly explain our observation of a less prominent role of E_{req} in driving LSR(s) at the breast. In support of this, we note that the linear relationship between E_{req} and LSR in the study by Cramer and Jay (2015) becomes much more variable at higher levels of E_{req} (i.e. >200 W/m^2). Hence, it cannot be excluded that a more complex interplay amongst biophysical, physiological, and morphological factors in driving variability in LSR(s) at the breast may occur when exercising at higher E_{req} (in W/m^2). It is of course important to note that 60% of the variance in LSR(s) at the breast remains unexplained in this study, and it is reasonable to hypothesise that variability in age (Larose et al., 2013), heat acclimation level (Lorenzo & Minson, 2010), training status (Armstrong & Maresh, 1998; Armstrong & Armstrong, 2000), amongst our cohort may contribute to such unexplained variance. Furthermore, and as opposed to the sweat gland density analysis, only 'finisher' participants were included in this the LSR analysis (which constituted a secondary aim). This may somewhat limit the generalizability of our LSR findings to larger-breasted females. Nevertheless, we believe that the role of body morphology and associated sweat gland density and output as important contributors to variations in LSR(s) should be emphasized, particularly across regions such as the female breast.

Finally, we note that irrespective of BrSA, the breast had lower LSR(s) than the bra triangle due to presenting both a lower sweat gland density and lower sweat output per gland. These regional differences in LSR are in line with those previously reported by Smith and Havenith (2012), who also observed lower LSR(s) at the breast than bra triangle (i.e. bra triangle LSR = 139 g.m^{-2}.h^{-1} vs. upper breast LSR = 11 g.m^{-2}.h^{-1}). Our findings build upon this previous work as we have now demonstrated that these regional differences are driven by the presence of both a lower sweat gland density and lower sweat output per gland over the breast. This observation highlights further the complex relationship amongst body morphology, body regional differences, and sweat gland density and output across the female body.

Beside their fundamental relevance to understanding female-specific body temperature regulation, our findings carry important applied implications to sport bra design and sex-specific clothing evaluations with thermal manikins. Models of human thermophysiology have been evolving from simple two-factor models (core and skin compartments (Gagge, 1971)) to multi-segmented models to reflect whole body shape from a heat transfer and sweat production approach (Fiala et al., 2012; Smith & Havenith, 2012). Thus, our findings could inform the development of female-specific models that incorporate a more evidence-based approach to the investigation of heat transfer and sweat production across the female breast. Better understanding of how breast size impacts local sweat gland density and output could support the design of sports bras that serve a wider range of consumers with tailored solutions based on individual needs regarding heat dissipation and skin wetness-dependent comfort (Filingeri et al., 2015).

- ## Conclusion

Individual differences in BrSA were observed to modulate both sweat gland density and local sweat rates in healthy young to middle-aged females. Our findings confirm the established relationship between sweat gland density and body morphology, and they further extend this observation to the female breast, highlighting a similar relationship between breast surface area and sweat gland density and LSR(s). This observation provides novel insights on individual differences in the anatomy and physiology of sweating at the female breast, which may impact the thermoregulatory responses (both autonomic and behavioural) of females of different breast sizes. Furthermore, our results have important applied implications to inform the design of sports bras that meet the thermal needs of females with a range of breast sizes. This may ultimately increase clothing comfort and performance, thus reducing barriers to maintaining an active lifestyle in females of all bra sizes. However, increased knowledge of breast size-dependent variations in sweating alone is not sufficient to provide valuable design insights. Heat and movement during exercise may also have distinct impacts on skin mechanics and sensations, thus bra comfort across the breast, which are investigated in the following chapters.

Chapter 6 Experimental Study 2: The effect of female breast surface area and exercise on breast skin stiffness and tactile sensation

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Blount, H., Valenza, A., Ward, J., Caggiari, S., Worsley, P. R., & Filingeri, D. (2024). The effect of female breast surface area on skin stiffness and tactile sensitivity at rest and following exercise in the heat. Experimental Physiology, 109, 1698–1709. https://doi.org/10.1113/EP091990

○ Abstract

Female development includes significant morphological changes across the breast. Yet, whether differences in BrSA modify breast skin stiffness and tactile sensitivity at rest and following exercise in the heat, remain unclear. We investigated the relationship between BrSA and skin stiffness and tactile sensitivity in 20 young to middle-aged women (27 ± 8yr) of varying breast sizes (BrSA range: 147 - 502cm^2) at rest and following a submaximal run in a warm climatic chamber (32 ± 0.6°C; 53 ± 1.7% RH). Skin stiffness above and below the nipple and tactile sensitivity from the nipple down were measured. Associations between BrSA and i) skin stiffness; ii) tactile sensitivity at rest were determined via correlation analyses. Effects of exercise and test site were assessed by a 2-way ANOVA.

Skin stiffness positively correlated with BrSA 3cm above the areola edge (r = 0.61, p = 0.005) and at the superior areola border (r = 0.54, p = 0.016), but not below the nipple (p > 0.05). The area 3cm below the areola was also significantly stiffer than all other test sites (p < 0.043). Tactile sensitivity did not vary with BrSA (p > 0.09), yet it varied across the breast (i.e. the area 3cm below the areola was more sensitive than the inferior areola edge; p = 0.018). Skin stiffness and tactile sensitivity across the breast decreased following exercise by ~37% (p < 0.001) and ~45% (p = 0.008), respectively.

These findings expand our fundamental understanding of the mechano-sensory properties of the female breast, and they could help inform sportswear innovation that better meets the support needs of women of different breast sizes at rest and following exercise.

○ Introduction

The breast is a complex part of the female anatomy that is highly deformable and when unsupported, moves independently during dynamic movements such as when running (Haake & Scurr, 2010; Nolte et al., 2016; Rajagopal et al., 2008). These dynamic breast movements can cause discomfort and represent a barrier to exercise for some women (Lawson & Lorentzen, 1990). As a result, more than 85 % of women deem sports bras an essential item of clothing to support the breast and reduce the amount of breast movement (Gehlsen & Albohm, 1980; Lorentzen & Lawson, 1987; Scurr et al., 2010) and discomfort (Brown et al., 2014) during exercise. Yet, intrinsic support systems in the breast do exist, a primary one of which being the skin (Gefen & Dilmoney, 2007; Hindle, 1991).

The mechanical properties of human skin, including skin stiffness, are non-linear, viscoelastic, highly variable with age, hydration, disease, and anatomical site (Soetens et al., 2018). Skin stiffness is defined as the resistance to an external force which deforms the tissue from its original shape. Less stiff (i.e. softer) skin deforms at higher rates at the point of contact than stiffer skin (Li & Gerling, 2023). It is well known that aging causes changes to skin mechanical properties, reducing skin stiffness and elasticity (Escoffier et al., 1989), which may result in breast ptosis ("dropping") in females (Groyecka et al., 2017; Rinker et al., 2010). However, it has also been hypothesised that damage to the breast structure due to repetitive stretch or strain experienced during exercise, or from lack of external support, could also lead to changes in the mechanical properties of local skin tissues (Page & Steele, 1999). Cyclical strain of ex vivo skin models has shown to drive reductions in mechanical stiffness (Remache et al., 2018). Furthermore, increased tissue temperature due to exercise has also been shown to reduce stiffness in a range of other soft tissues (Sapin-de Brosses et al., 2010; Wu et al., 2001; Xu et al., 2008; Zhou et al., 2010). Due to the differences in breast mass and corresponding strain, there may be a relationship between breast size, associated skin remodelling, and consequent changes in skin stiffness at rest and following exercise.

Breast size varies greatly among women and can diverge over time due to changes in body mass, menstrual phases, pregnancy, breast feeding and menopause (Azar et al., 2001; Wade et al., 2010). Variation in breast size can lead to differences in breast skin surface area (BrSA), and the corresponding breast skin stretch, as well as differences in breast volume and mass, which may in turn place further strains on the breast skin tissue. Norris et al. (2020) measured breast skin strain rates during static and dynamic activities and found most females had peak values in the upper, lateral breast region when tested with no bra support. In the presence of high strain, collagen fibres in the skin are increasingly under tension, becoming un-crimped which increases the stiffness of the tissue (Benítez & Montáns, 2017). Although this evidence indicates a relationship between the (breast region-dependent) extent of breast movement and the resulting skin stiffness, there have been limited investigations on the relationship between breast size and breast skin stiffness both at rest and following exercise, despite the observed patterns of greater movement in larger breasts (McGhee & Steele, 2020; White et al., 2015).

Besides its role as an intrinsic support system of the breast, the skin also acts as a sensory organ to convey tactile sensations upon contact with mechanical stimuli (e.g. light touch) (McGlone & Reilly, 2010). Tactile sensations are a fundamental cutaneous sensory attribute that is necessary for sensing the external physical world, including one's interaction with clothing, e.g., the bra (Havenith, 2002; Song, 2011). Mechanoreceptors innervating the breast skin convey sensory inputs associated with feelings of pressure, itchiness, clinginess and comfort in an area that is almost always covered by a garment (Song, 2011). Previous research investigating breast sensitivity to tactile stimuli has indicated that larger breasts tend to have lower sensitivity (as evidenced by higher tactile detection thresholds) (Cornelissen et al., 2018; DelVecchyo et al., 2004; Tairych et al., 1998), as well as lower spatial acuity (Long et al., 2022), than smaller breasts. However, the anatomical or physiological mechanisms underlying these breast size-dependent changes in tactile sensitivity are yet to be confirmed. Notably, changes in skin stiffness at the fingertip have been recently proposed to play a role in size-dependent changes in tactile sensitivity (Li & Gerling, 2023; Vega-Bermudez & Johnson, 2004); however, whether the same stiffness-dependent mechanisms apply at the breast and whether it contributes to modulate tactile sensitivity with increasing breast size, remain unknown. It is also necessary to consider the impact of exercise on tactile sensitivity, as this sensory input may contribute to sports bra comfort. Previous research investigating the effect of exercise on cutaneous sensitivity has proposed an analgesic effect of exercise (Janal et al., 1984; Koltyn, 2000; Paalasmaa et al., 1991; Post et al., 1994; Valenza et al., 2019). However, whether exercise may induce changes in tactile sensitivity at breast, in association with changes in skin mechanical properties, remains unknown.

Increasing our fundamental understanding of the role of breast size on skin mechanics and tactile sensitivity at rest and following exercise has valuable applications to inform the design of user-centred sports bras that help maintain skin health and improve the comfort of wearers of varying breast sizes. Hence, the first aim of this study was to characterise the relationship between breast size and skin stiffness over various breast regions, at rest and following exercise in the heat. We hypothesised that larger breasts would present greater skin stiffness than smaller breasts, because of experiencing greater skin strain from dynamic breast movements. The second aim of this study was to characterise the relationship between breast size and tactile sensitivity, at rest and following exercise. We hypothesised that increased breast size would result in decreased tactile sensitivity, secondary to size-dependent changes in skin stiffness. The third aim of this study was to determine the effects of exercise in the heat on changes in breast skin stiffness and tactile sensitivity. We hypothesised that exercise would result in decreased skin stiffness and tactile sensitivity, secondary to increased tissue temperatures and analgesic effects.

○ Materials and methods

Ethical approval

This study was approved by the University of Southampton Ethics Committee (approval no.79007). All participants provided written informed consent prior to testing. The study conformed to the ethical standards set by the Declaration of Helsinki.

Participants

The same cohort of females who participated in the study outlined in Chapter 5 participated in this study following the same sampling approach and inclusion and exclusion criteria. Two participants data were excluded from this section of the study due to discomfort with the tactile sensory assessment, resulting in a sample of 20 females of varying BrSA (age: 26.7 ± 7.7 years; weight: 72.2 ± 13.3 kg; height: 170.6 ± 4.8 cm) (Table 6-1). Menstrual phase was not “controlled for” based on preliminary evidence that thermal sensation in females may not be independently modified by menstruation (Matsuda-Nakamura et al., 2015). However, self-reports of menstrual phase were collated. The participants were spread across a typical 28-day menstrual cycle (mean day of cycle: 13.6 ± 8.5) and two participants presented irregular periods at the time of the study.

Table 6-1. Participant demographics (n=20); BrSA= breast surface area.

	Age (years)		Height (m)		Weight (kg)		BrSA (cm^2)	
Bra Size	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
Small (n=5)	24.0	18-30	1.68	1.63-1.72	59.0	56.4 – 66.7	170.0	147.2-230.1
Medium (n=5)	22.8	19-27	1.69	1.65-1.70	67.5	59.8 - 76.1	246.3	203.5-288.0
Large (n=6)	30.2	20-42	1.72	1.68-1.77	72.3	61.3 - 83.4	316.0	173.7-402.2
X-Large (n=4)	29.8	21-44	1.75	1.66-1.83	94.1	87.0 - 97.9	432.7	300.0-502.2

Experimental design

To establish breast size-dependent differences in skin stiffness and tactile sensitivity at rest and following exercise, participants visited the laboratory on one occasion in a quasi-experimental study design. First, BrSA geometry was captured, then skin stiffness and tactile sensitivity were assessed at rest, at multiple breast locations longitudinally down the breast, and in line with the nipple (Figure 6-1). Assessments over multiple breast regions were deemed necessary to capture potential regional differences in skin properties and sensitivity (Norris et al., 2020; Valenza et al., 2023). For skin stiffness assessments, two areas above and below the nipple-areola complex were selected, to correspond with higher (above nipple) and lower (below nipple) strain areas (Norris et al., 2020). Tactile sensitivity assessments were also performed on the nipple-areola complex, as well as at two sites in the lower breast. Indeed, the nipple-areola complex has been shown to be the anchor of breast sensitivity (Long et al., 2022), while the lower breast is an area more commonly associated with pressure discomfort when wearing a sport bra (Gho et al., 2010). This regional assessment also enabled skin stiffness and tactile sensitivity associations in the lower breast.

Following assessments at rest, participants wore standardised running shorts and a sports bra. They also used their own personal trainers and socks to perform a 50-minute run in a climatic chamber set to 32 ± 0.6 ℃ and 53 ± 1.7 % relative humidity. Following the termination of the exercise, skin stiffness and tactile sensitivity at the breast were measured again according to the same procedures (Figure 6-1). We selected an exercise paradigm performed in the heat as the stiffness and sensitivity data were collected as part of a larger project also investigating breast-size dependent changes in sweat gland function and output, and for which a combination of endogenous (i.e. exercise) and exogenous thermal loads (environmental heat) was required.

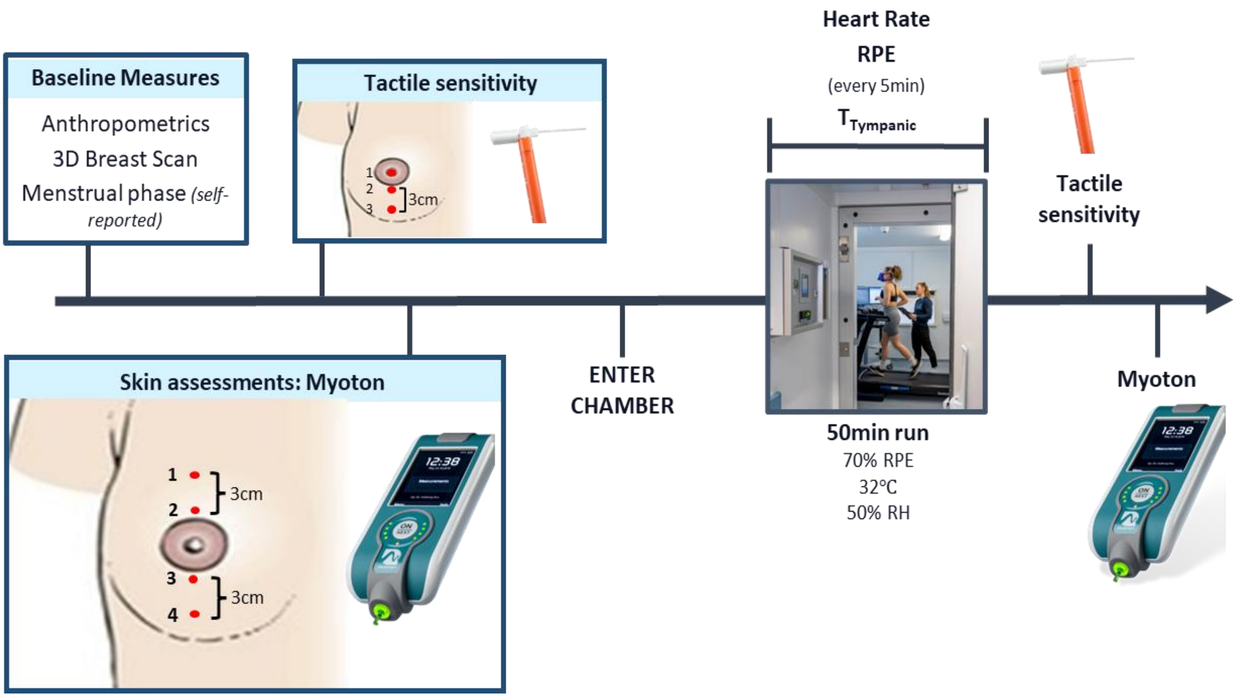

Figure 6-1. Schematic of experimental design.

Experimental procedures

Participants were instructed to drink 500 ml of water 2 hours prior to testing to ensure hydration during exercise. Upon arrival to the laboratory participants provided a urine sample to measure urine specific gravity (Digital refractometer, KERN, Balingen, Germany). If urine specific gravity was >1.025 g/mL participants were provided with 500 ml of water and tested again after 30 minutes before proceeding with the protocol, to avoid the risk of dehydration (Casa et al., 2005).

Firstly, participants completed a questionnaire to report estimated menstrual phase and contraceptive use. Anthropometric measures of height, weight and BrSA were taken in a thermoneutral laboratory (21 ± 1.5 °C and 37 ± 5.2 %). Height was measured on a wall stadiometer and weight on a precision scale (KERN 150K2DL, Balingen, Germany). Participants were then asked to adopt a 4-point prone position such that the breasts could freely hang away from the torso, thus allowing a scan of the entire breast skin surface, using a pre-calibrated three-dimensional (3D) white-light surface scanner (EinScan H, Shining 3D Tech. Co. Ltd., Hangzhou, China; surface height accuracy of 0.05 mm). Markers were placed around the breast border based on a validated breast volume model (Göpper et al., 2020), from which surface area could be estimated using MeshLab (Visual Computing Lab, CNR-ISTI, Pisa, Italy).

Following the 3D scan, participants were asked to lie in a supine position and tactile sensitivity assessments were performed. Whilst tactile sensitivity is the secondary outcome of this study, it was tested prior to the skin stiffness assessment to minimise perceptual sensitization due to mechanical stimulation from the skin stiffness assessments (Banik & Brennan, 2008). Tactile sensitivity assessments were performed on the nipple, at the base of the areola and 3 cm below, both in line with the nipple (Figure 6-1). Test sites were marked with a washable marker, and participants were familiarised with the procedure using the index finger as a practice body site. To evaluate sensitivity, we calculated tactile detection thresholds (i.e. the smallest amount of skin indentation that can be reliably reported by a participant as a tactile sensation) for each breast region, which were assessed using a set of 20 calibrated von Frey's monofilaments (North Coast Medical, Inc., Morgan Hill, LA, USA)**.** Tactile detection thresholds were determined using the up-down method (Chaplan et al., 1994; Dixon, 1965), whereby stimulation began using the smallest monofilament (0.008g) with progressive incrementation based on the participant's feedback. Inability to perceive indentation led to stimulation with the next greatest monofilament until a perception was reported. At this stage an up and down sequence between the just perceivable and the non-perceivable monofilament was conducted for a minimum of 3 reversals. Successful completion of the reversals led to test termination and the bending force (in g) of the just-perceivable monofilament was deemed as the tactile detection threshold. To minimise testing errors the same investigator and instruments were used for all measurements in a thermal neutral laboratory. The order of site was randomised following a simple random allocation to minimize order effects.

Upon completion of the tactile sensitivity testing, skin stiffness was evaluated non-invasively using a myotonometer (Myoton Pro, Myoton SA, Estonia). Skin stiffness and elasticity were estimated based on the oscillatory tissue response measured by the MyotonPro. Skin stiffness was assessed in four locations across the right breast (3 cm above the areola edge, the superior and inferior areola edge, 3 cm below the areola edge; all in line with the nipple) with mechanical impulses applied tangentially to the skin, 5 times, in a caudal direction. Test sites were marked with a washable marker, and participants were familiarised with the procedure. A verbal warning was given then skin stiffness was measured.

Upon completion of both tactile and skin stiffness assessments, participants entered the climate chamber set to 32 $\pm$ 0.6 ℃ and 53 $\pm$ 1.7 % relative humidity. They were required to perform a 50-minute run at a self-selected speed eliciting a rating of perceived exertion (RPE) of 13, or 'somewhat hard' using the Borg Scale (Borg, 1998). Following cessation of the run, participants towelled off any sweat and resumed a supine position. The tactile sensitivity and skin stiffness tests were then repeated according to the procedures described above, whilst in the climate chamber.

Statistical analysis

Data normality and homoscedasticity were assessed using the Shapiro–Wilk and Levene tests, respectively. Skin stiffness data were identified to be normally distributed, hence parametric tests were used for analysis. Tactile sensitivity data were identified to be non-normally distributed, hence non-parametric descriptors and tests were used. Statistical analysis was performed using SPSS statistical analysis software package (version 28.1, Chicago, USA). Data are reported as the means and SD and significance was set at $p < 0.05$.

Descriptive statistics for all parameters of interest, including exercise intensity and duration were collated. To establish breast size-dependent differences in skin stiffness and tactile sensitivity at rest, the relationship between BrSA and skin stiffness, and BrSA and tactile sensitivity, were assessed using Pearson's correlation and Spearman's rank correlation analyses, respectively. Correlation coefficients were calculated separately for each of the skin site tested. In the event of a statistically significant correlation, regression analyses were performed (parametric data) to determine the extent of a parameter change (e.g. skin stiffness) for a unit change in BrSA.

Not all our participants were able to complete the full 50-minute exercise trial duration, as some participants required an earlier termination of the run due to volitional fatigue. Thus, for the exercise-effect analysis we divided the study cohort into 'finishers' (n = 15) and 'non-finishers' (n = 5). Specifically, all participants in the XL bra category (n = 4) and one participant in the large bra category were unable to complete the full 50-minute run trial.

To quantify exercise-induced differences in skin stiffness across the breast at each site, a 2-way repeated measures ANOVA with pre- and post-exercise and skin site as the independent variables was used for the 'finishers'. In the event of statistically significant main effects or interactions, post-hoc analyses were conducted with Bonferroni correction. To investigate the effect of exercise and site on tactile sensitivity, a Friedman test (followed by post-hoc Wilcoxon signed-ranks tests with a Bonferroni correction) was applied.

○ Results

Descriptive statistics for rest and post exercise data

Descriptive statistics on the range of variation in skin stiffness and tactile sensitivity across breast sizes at rest and following exercise, are reported in Table 6-2. Average exercise intensity (RPE) and run speed for the 'finishers' were 12.3 ± 1.0 (corresponding to between "light" and "somewhat hard") and 7.2 ± 0. 9 km/h, respectively.

Table 6-2. Descriptive statistics of skin stiffness and tactile sensitivity parameters at all test sites, as a function of bra size group, pre- and post-exercise

Skin Stiffness (N/m)		Small		Medium		Large		X-Large	
		Pre-Exercise (n=5)	Post-Exercise (n=5)	Pre-Exercise (n=5)	Post-Exercise (n=5)	Pre-Exercise (n=6)	Post-Exercise (n=5)	Pre-Exercise (n=4)	Post-Exercise (n=0)
3cm Above Areola Edge	Mean	244	211	292	216	311	238	504	-
	SD	85	47	69	48	123	58	168	-
	Min-Max	157 - 373	166 - 269	243 - 411	148 - 281	205 - 521	193 - 332	258 - 626	-
Superior Areola Edge	Mean	248	216	268	193	305	225	406	-
	SD	72	46	61	30	101	40	121	-
	Min-Max	163 - 327	165 - 282	214 - 361	154 - 235	200 - 471	168 - 270	230 - 508	-
Inferior Areola Edge	Mean	280	202	236	177	285	200	316	-
	SD	77	46	39	37	59	42	107	-
	Min-Max	206 - 408	166 - 272	187 - 283	119 - 213	187 - 342	140 - 255	223 - 444	-
3cm Below Areola Edge	Mean	326	219	327	239	409	323	487	-
	SD	81	63	28	38	101	82	165	-
	Min-Max	272 - 467	144 - 307	304 - 372	197 - 280	240 - 508	213 - 418	289 - 680	-
Tactile sensitivity (g)		**Small**		**Medium**		**Large**		**X-Large**	
Nipple	Median	0.07	0.40	0.07	0.40	0.28	0.40	0.235	-
	IQR	0.33	0.09	0.03	0.00	0.24	0.20	0.34	-
	Min-Max	0.04 - 0.40	0.04 - 0.40	0.02 - 0.40	0.04 - 0.40	0.07 - 0.40	0.07 - 1.40	0.04 - 0.40	-
Inferior Areola Edge	Median	0.16	0.16	0.16	0.40	0.40	0.40	0.38	-
	IQR	0.33	0.14	0.12	0.24	0.70	1.00	0.68	-
	Min-Max	0.02 - 0.40	0.04 - 0.60	0.008 - 0.40	0.008 - 0.40	0.008 - 1.00	0.04 - 1.40	0.008 - 1.40	-
3cm Below Areola Edge	Median	0.008	0.045	0.07	0.07	0.24	0.07	0.28	-
	IQR	0.00	0.073	0.15	0.38	0.82	1.33	0.24	-
	Min-Max	0.008 - 0.40	0.02 - 0.16	0.008 - 0.16	0.008 - 0.40	0.008 - 1.00	0.008 - 1.40	0.16 - 0.40	-

Breast size-dependent differences at rest

Regarding skin stiffness at rest (Figure 6-2), there was a statistically significant positive correlation with BrSA for sites 3 cm above the areola edge (r = 0.61, *p* = 0.005) and at the superior areola border (r = 0.54, *p* = 0.016), but not at the inferior areola border (r = -0.05, *p* = 0.84) nor at the 3 cm below the areola edge (r = 0.33, *p* = 0.16). Regression analyses indicated that skin stiffness increased by ~111 N/m at 3 cm above the areola edge [Stiffness = 111.0 + 0.78(BrSA); R^2 = 0.38, *p* =0.005], and by ~163 N/m the superior areola border [Stiffness = 163.2 + 0.49(BrSA); R^2 = 0.30, *p* = 0.016], for every unit change in BrSA.

The tactile sensitivity at rest results revealed no correlation with BrSA, neither at the nipple (r = 0.34, *p* = 0.13), the areola edge (r = 0.34, *p* = 0.14) nor at 3 cm below the areola (r = 0.39, *p* = 0.09) (Figure 6-3).

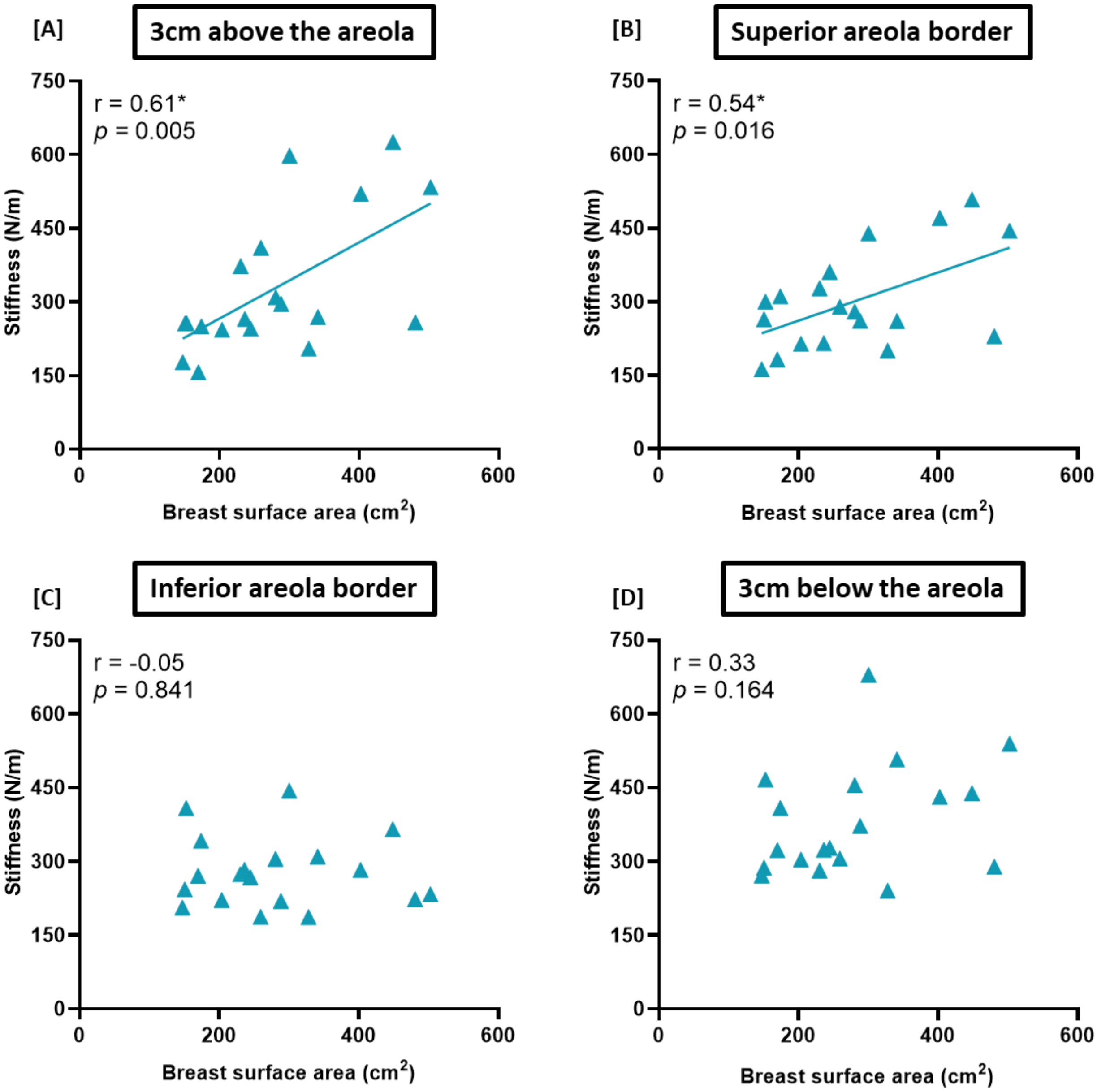

Figure 6-2. Relationship between breast surface area and skin stiffness at rest at [A] 3 cm above the areola, [B] the superior areola border, [C] the inferior areola border and [D] 3 cm below the areola. *Significant correlation ($p < 0.05$).

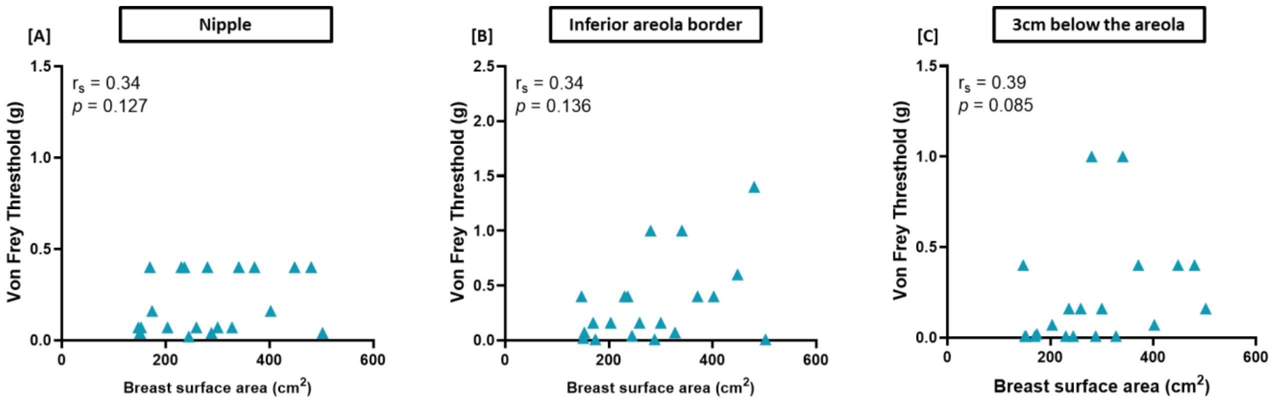

Figure 6-3. Relationship between breast surface area and tactile sensitivity thresholds at rest at [A] the nipple, [B] the areola edge and [C] 3 cm below the areola.

Effects of skin site and exercise

Results of the 2-Way ANOVA showed a significant effect of skin site (F(3,42) = 10.276, $p < 0.001$), and exercise (F(1,14) = 68.409, $p < 0.001$), but no significant interaction effect (F(3,42) = 1.066, $p = 0.374$) on skin stiffness in the 'finishers'. When considering the overall effect of skin site, the findings revealed that the site corresponding to 3 cm below the areola had statistically greater skin stiffness than the sites corresponding to 3 cm above the areola (mean difference = +55.0 N/m [95%CI = +1.2, +108.7]; $p = 0.043$), the superior areola site (+64.6 N/m [95% CI +12.4, +116.7]; $p = 0.012$), and the inferior areola site (+77.0N /m [95%CI +30.3, +123.7]; $p = 0.001$). No statistically significant differences were found between the sites 3 cm above the areola, or superior or inferior areola ($p = 1.00$). Regarding the main effect of exercise, this decreased skin stiffness by 72.6N/m (95%CI = +53.8, +91.4; $p < 0.001$), corresponding to a percentage reduction in skin stiffness of ~25% (Figure 6-4).

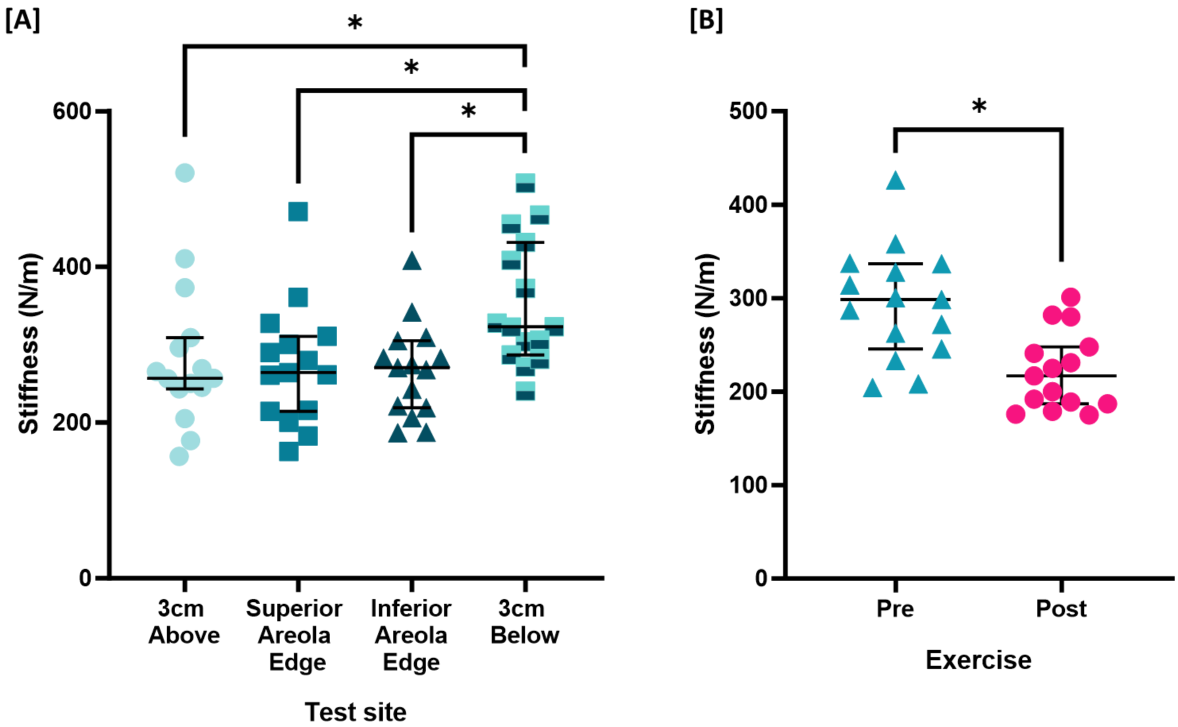

Figure 6-4. The main effect of [A] test site and [B] exercise on skin stiffness in the 'finishers' (n = 15). *Significant difference (p < 0.05).

Results of the Friedman's test indicated a main significant effect of test site and exercise on tactile sensitivity ($\chi^2(5) = 22.86$, $p < 0.001$). When considering the overall effect of skin site, the site corresponding to 3 cm below the areola had statistically lower tactile thresholds (-0.14g; p = 0.018) and therefore greater tactile sensitivity than the inferior areola site. No statistically significant differences were found between the nipple and inferior areola edge (p = 0.55) and 3 cm below the areola (p = 0.27). Regarding exercise, this increased tactile thresholds by an average of 0.21 g (p = 0.008), which corresponded to a percentage reduction in tactile sensitivity of ~45 % (Figure 6-5).

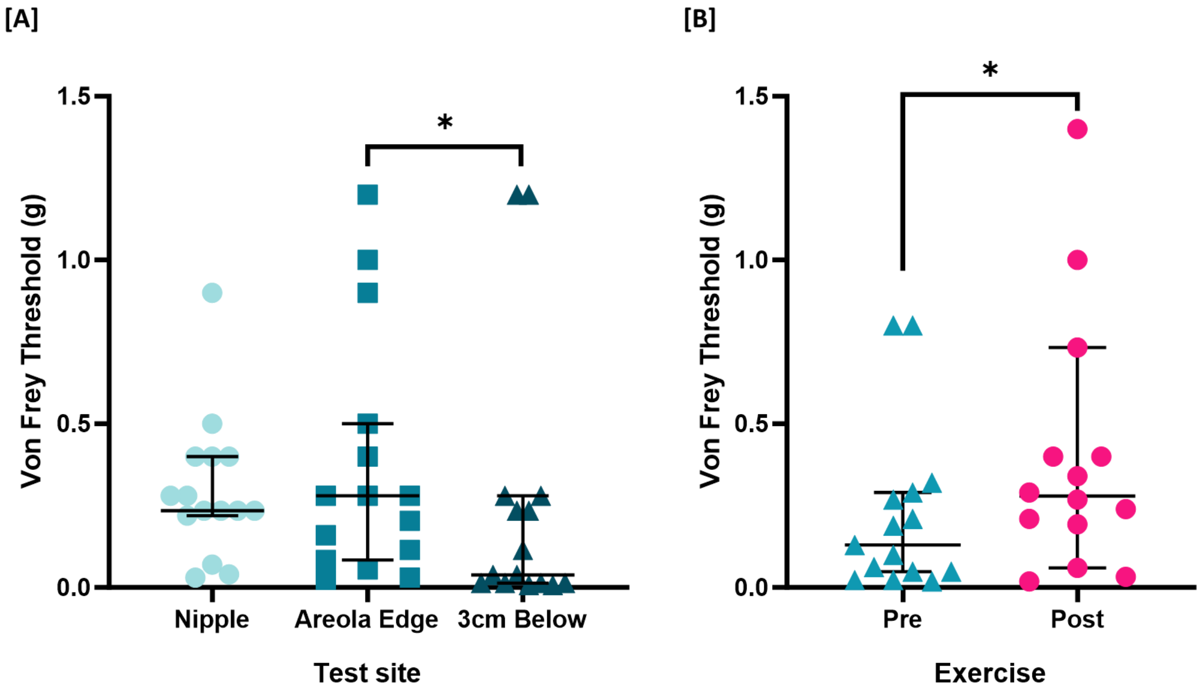

Figure 6-5. The effect of [A] test site and [B] exercise on tactile sensitivity thresholds in the 'finishers' (n = 15). Presented as median and 95% CI. *Significant difference ($p < 0.05$).

○ Discussion

The first aim of this study was to characterise the relationship between breast surface area and skin stiffness over various skin regions, at rest and following exercise. Furthermore, the second aim of this study was to characterise the relationship between breast size and tactile sensitivity, at rest and following exercise. Finally, the third aim of this study was to determine the effects of exercise in the heat on changes in breast skin stiffness and tactile sensitivity. Our findings partially supported our primary hypothesis that skin stiffness increased with greater breast size. However, this was only observed at above the nipple breast site. Regarding our secondary hypothesis, our findings did not evidence a relationship between breast size and skin tactile sensitivity. Finally, our findings supported our third hypothesis, as we recorded a post exercise decrease in skin stiffness and tactile sensitivity of ~37 and 45%, respectively. These findings highlight a novel, relationship between breast morphology and local skin stiffness, as well as the effects of exercise on skin properties and tactile sensitivity. These results provide novel fundamental and applied insights on breast mechanical and sensory properties, which could inform future research as well as apparel design considerations, as discussed below.

Breast surface area and skin stiffness

We had hypothesised that females with larger BrSA would demonstrate greater skin stiffness due to greater mechanical strain in these load bearing tissues (Norris et al., 2020). This was confirmed in the upper breast region, with around a third of the variance in skin stiffness being explained by BrSA. However, this was not consistent across breast sites, e.g. we did not observe this relationship at the sites below the nipple line. The observed site differences in skin stiffness in relation to BrSA are likely due to variability in breast skin strain (Norris et al., 2020). It has been previously shown that breast skin strain rates during static and dynamic activities are greatest in the upper, lateral breast region when tested with no bra support. Greater skin strain rates tend to occur in the vertical plane, due to gravitational pulling (Choo et al., 2010). It has also been previously identified that breast skin thickness decreases with increased breast size (Willson et al., 1982), and thinner skin may have reduced tensile strength than thicker skin (Hussain et al., 2013). The upper breast region may be more susceptible to this combined effect of thinner skin and greater strain rates as this region supports more of the breast mass. When collagen fibres in the skin are increasingly under tension and strain, fibres become un-crimped which increases the stiffness of the tissue (Benítez & Montáns, 2017). These considerations may provide an explanation for the stiffness-size relationship observed in the upper breast. It is important to note that our findings are in contrast with the skin mechanical changes observed due to prolonged skin stretch in obese populations (Choo et al., 2010; Ibuki et al., 2018; Smalls et al., 2006), where significant reductions in skin stiffness and elasticity have been revealed. A potential reason for these differences may be due to other factors such as dermal thickness, subdermal tissue composition (i.e., subcutaneous body fat vs breast tissue), and other comorbidities that may influence skin properties in obese people (Smalls et al., 2006).

Breast surface area and tactile sensitivity

In this study, no relationship was found between BrSA and tactile sensitivity in the lower breast region. By contrast, previous studies have demonstrated that smaller breasts tended to have higher tactile sensitivity (Cornelissen et al., 2018; DelVecchyo et al., 2004; Tairych et al., 1998) and greater spatial acuity (Long et al., 2022) than larger breasts. However, these differences may be due to variations in the breast areas tested across studies. For example, Tairych et al. (1998) found that the largest size-related differences (small vs. large breast) in tactile sensitivity occurred in the superior (small to large difference in Semmes-Weinstein value = 0.81), medial (0.86) and lateral (0.87) breast areas compared to e.g. the inferior (0.71) breast areas, the latter being the primary area tested in the present study. It is indeed a limitation of the current study that we did not collect tactile sensitivity data over the upper breast. Indeed, tactile sensitivity has been shown to decrease with increasing stiffness at the fingertip (Li & Gerling, 2023; Vega-Bermudez & Johnson, 2004). It is thought that if the skin fails to conform, or does so poorly, the mechanoreceptors responsible for detecting stimuli are not stimulated. Given our observation of increasing skin stiffness with BrSA at the upper breast, we could speculate that, had we assessed tactile sensitivity over this area, we may have also observed a similar reducing in tactile sensitivity as the one observed by Tairych et al. (1998). Clearly, further research is required to investigate the relationship between skin stiffness and tactile sensitivity across the whole breast.

Exercise effects on skin stiffness and tactile sensitivity

This study demonstrated that exercise under heat stress reduced breast skin stiffness and tactile sensitivity. This observation aligns with previous research into soft tissue biomechanics, which has identified that increases in tissue temperature, due to exercise and the external environment, reduces stiffness in a range of soft tissues (Sapin-de Brosses et al., 2010; Wu et al., 2001; Xu et al., 2008; Zhou et al., 2010). Increased temperature makes the skin more compliant, likely due to collagen denaturation, which reduces the tensile strength of the tissues (Wall et al., 1999; Wright & Humphrey, 2002). However, it is important to note that this study was not designed to delineate between temperature and exercise effects, due to the combined nature of the intervention. Cyclic strain from rhythmic breast displacement during the run (Remache et al., 2018) or changes in skin hydration status (Berkey et al., 2021) due to sweating may also drive changes in skin stiffness following a bout of running in the heat. For example, increased skin hydration causes the stratum corneum to swell and reduces the elastic modulus of skin from ~100-200 MPa values to as low as ~2 MPa (Berkey et al., 2021). Changes to the mechanical state of the upper stratum corneum layer subsequently change the mechanical environment of the deeper skin layers. This may lead to changes in the activation of afferent neurons innervating the skin and modify perceptions related to skin deformations (Bennett-Kennett et al., 2023). It would be therefore reasonable to expect that the exercise-induced reduction in stiffness, along with an increase in skin hydration due to sweating, would increase tactile sensitivity (André et al., 2010; André et al., 2011; Dione et al., 2023; Li & Gerling, 2023; Vega-Bermudez & Johnson, 2004). However, this is in contrast with our findings of a reduced tactile sensitivity post exercise. We therefore speculate that the observed post-exercise loss of sensitivity may be explained by the central, analgesic effects of exercise on tactile sensitivity (i.e. attenuation of neural responses) (Janal et al., 1984; Koltyn, 2000; Paalasmaa et al., 1991; Post et al., 1994) which may have been more prominent than the peripheral effect of reduced skin stiffness. Furthermore, it cannot be excluded that prolonged exercise may have also reduced cognitive performance, impacting participants' capacity to focus on a tactile discrimination task (Donnan et al., 2021; Gaoua et al., 2011). Future studies should therefore consider experimental design that more directly address the central vs. peripheral effects of exercise on local skin sensitivity.

Limitations and Future Directions

This study has some limitations. First, using the nipple and areola as a reference point with fixed distances for measurement meant that in smaller breasted women, 3cm from the areola edge could have been near the top of the breast or breast base, whereas in larger breasted women, these test sites fell mid-breast tissue. This method was selected as breast-specific acuity has previously been shown to be systematically biased to the nipple (Long et al., 2022). However, because of this approach, differences in the subdermal tissue (breast mass vs more bony structures) may have influenced the results. Future studies could consider outlining the breast border and measuring proportional distances from the nipple to the breast border instead of fixed distances. A further future point to consider in relation to our method of breast measurement would be to also investigate the effect of breast volume and density. Larger or more protruding breasts may be subject to higher strains and skin stiffness which we were unable to characterise using our measurement of breast surface area; therefore this may open further interesting investigations.

Second, the larger breasted females tended to be older than the smaller breasted participants. Overall, aging causes the epidermis to become stiffer (Diridollou et al., 2001; Hamasaki et al., 2018). It has been shown that females experience lesser age related changes in skin stiffness than men but the largest changes in skin stiffness at the face and cleavage have been shown to occur between the age of 20 and 40 years in females (Diridollou et al., 2001; Krueger et al., 2011). However, if the differences in skin stiffness across BrSA were an age-related effect, this relationship would likely have been present at all skin sites, not just the upper breast.

A final point to consider is that skin stiffness measurements in this study were taken in a supine posture, where the breasts were not under tension due to gravity. If taken in an upright posture, whilst the skin was under strain, there is a distinct possibility that we would have seen greater differences in skin stiffness due to the action of gravity. Future research should consider measuring breast skin stiffness in different postures to further our understanding of skin mechanical properties in this tissue.

- ### Conclusion

The results of this study demonstrate a dynamic interplay between breast size, skin stiffness, tactile sensitivity, and exercise. Breast size-dependent differences in skin stiffness exist in the upper breast at rest, such that the larger the breast, the greater the skin stiffness. Further research is required to investigate whether this effect impacts tactile sensitivity in this region. Exercise in the heat led to reduced skin stiffness and tactile sensitivity to a meaningful extent (i.e. between ~37 and 45 %). These findings expand our fundamental understanding of mechanical and sensory properties of the breast. Furthermore, this knowledge could help inform sports bra design that better meets the support needs of the skin of the upper breast in women of different breast sizes, both at rest and following exercise in the heat.

Chapter 7 Experimental Study 3: The effect of female breast surface area on cutaneous thermal sensation, wetness perception, and epidermal properties

Manuscript published in Experimental Physiology

Blount, H., Valenza, A., Ward, J., Caggiari, S., Worsley, P. R., & Filingeri, D. (2024). The effect of female breast surface area on cutaneous thermal sensation, wetness perception and epidermal properties. Experimental Physiology, 1–13. https://doi.org/10.1113/EP092158

○ Abstract

Female development includes significant size changes across the breast. Yet, whether differences in BrSA modify breast sensitivity to warm, cold, and wetness, and the associated epidermal properties (skin thickness and surface roughness) remain unclear.

We investigated the relationship between BrSA and thermal and wetness perception, as well as epidermal properties, in 21 females (28±10y) of varying breast sizes (BrSA range: 147-502cm^2), at multiple breast sites (i.e. nipple, above and below the nipple, and bra triangle). Associations between BrSA and the perceptual and epidermal variables were determined via correlation analyses. Differences across test sites were assessed by repeated-measures ANOVA.

Our results did not support the hypothesis that larger breasts present reduced thermal and wetness sensitivity, except for the above nipple site, which presented reduced warm sensitivity with increasing BrSA (r=-0.61, *p*=0.003). We also found a heterogeneous distribution of cold, but not warm nor wetness, sensitivity across the breast, with the above nipple site presenting lower cold sensitivity than any other site (*p*<0.015). Our findings did not indicate any association between BrSA and epidermal properties (thickness and roughness), nor any site-dependent variation in these anatomical parameters (*p*>0.15).

We conclude that, while some skin-site (i.e. above the nipple) and perceptual modality-dependent (i.e. warm sensitivity) differences were observed, BrSA-dependent variations in thermal and wetness sensitivity were not a generalised feature of the skin covering the breast. These observations advance our fundamental understanding of breast sensory function, and they could inform the design of user-centred clothing such as bras.

○ Introduction

The ability to sense changes in body temperature and to consciously experience thermal sensations is a fundamental cutaneous sensory attribute that is necessary for optimal interactions with our surrounding thermal environment, as well as with the objects that contact our skin, such as clothing (Havenith, 2002; Song, 2011) (See section 2.3). The perception of skin wetness, that is a synthetic perception arising from the integration of thermal and tactile cues originating at the skin when this is wetted (Filingeri, Fournet, et al., 2014b), also impacts the subjective experience of skin-clothing interactions, which can in turn lead to thermal and clothing discomfort (Gwosdow et al., 1986).

Empirical evidence indicates that innate differences may exist between men and women in their skin thermal and wetness sensitivity (Greenfield et al., 2023). For example, women have been shown to often report more intense thermal sensations than men for the same absolute temperature (Gerrett et al., 2014; Inoue et al., 2016; Li et al., 2008), as well as to present greater sensitivity to cold-wet stimuli (Valenza et al., 2019). However, it has also been proposed that sex-related differences in local thermal and wetness perceptions could be partly explained by differences in body morphology (Filingeri, Blount, & Valenza, 2024). Specifically, women often present a smaller (on average) BSA than men, and this may in turn result in a larger relative proportion of their BSA being stimulated by fixed-size thermal stimuli (Filingeri et al., 2018; Luo et al., 2020).

While the evidence above may (partly) explain some previously reported thermal sensitivity differences between man and women, it also opens to the question of how differences in body morphology within a specific group such as women may impact on individual responses to cutaneous thermal and wet stimuli. This question is relevant, as women undergo unique anatomical, physiological, and hormonal changes across the lifespan that impact their body morphology. For example, consider the impact of sexual maturation on breast development and the resulting breast size, which can vary greatly due to genetic factors, body-mass-index, and energy intake early in life (Trichopoulos & Lipman, 1992; Wade et al., 2010).

Variations in breast size lead to differences in BrSA, which could potentially translate to varying densities of thermoreceptors innervating the skin of the breast (Adair, 1999). It is indeed well established that the nervous system reaches maturity prior to breast development (Javed & Lteif, 2013). Hence, one may hypothesise that breasts with greater BrSA may present reduced density of thermoreceptors, and potentially lower thermal sensitivity (Moini et al., 2021). However, knowledge on how thermal and wetness sensitivity might differ amongst women varying in BrSA, and the implications that this might have for female-specific clothing comfort (e.g. in the context of wearing bras), continue to be lacking.

The available evidence on breast thermal sensitivity often lacks systematic measurements of (and/or control for) breast size and BrSA. For example, Luo et al. (2020) has recently reported a homogenous distribution of thermal sensitivity across the breast. By contrast, other studies have reported a more heterogenous thermal sensitivity distribution (Terzis et al., 1987; Valenza et al., 2023). Specifically, Valenza et al. (2023) demonstrated regional variation in warm thermal sensation with significantly greater sensitivity in the lower breast region compared to bra triangle, yet they showed no regional variation in response to cold thermal stimulation. Furthermore, an uneven distribution of thermal sensitivity was demonstrated by Terzis et al. (1987) who observed the lateral surface of the breast to demonstrate greater thermal sensitivity than the areola. These contrasting results have contributed to a certain level of ambiguity in the exact patterns of regional sensitivity across the skin of the female breast, particularly when this varies in size and surface area.

Regarding wetness perception, there is a paucity of evidence on how this may vary across the breast. Evidence is available on breast sensitivity to tactile stimuli, and this has indicated that larger breasts tend to have lower tactile sensitivity (Cornelissen et al., 2018; DelVecchyo et al., 2004; Tairych et al., 1998) and spatial acuity (Long et al., 2022). Owing to the dependence of wetness perception on thermo-tactile inputs, it could be hypothesised that size-dependent differences in thermal or tactile sensation may translate to a size-dependent difference in wetness perception. Yet, this hypothesis is yet to be tested empirically.

Variations in breast size, thus BrSA, can also lead to changes in breast skin stretch, with consequent implications for the mechanical properties of the breast skin. Acute skin stretching has shown to reduce skin surface roughness by up to 50% (Maiti et al., 2016). Furthermore, load-bearing skin regions have demonstrated greater epidermal thickness compared to non-load-bearing sites (Lundström et al., 2018; Maiti et al., 2020). When considering females with greater breast volume and mass, the supporting skin tissue will be exposed to greater load than in females with smaller breasts. However, it remains unknown how the effect of breast size may impact the epidermal properties of breast skin.

When modelling factors governing thermal sensation beyond the thermal characteristics of the skin and of the contacting material, evidence indicates that the mechanical properties of the skin could also influence heat exchange and the resulting thermal sensation upon contact with materials (Chen & Ding, 2019). For example, skin characteristics at the fingertip, namely epidermal thickness, and surface roughness, have been shown to impact thermal conductance. As surface roughness and thickness increase, there is greater thermal contact resistance, with a reduction in heat flux to the dermal tissues (Chen & Ding, 2019). Thus, differences in BrSA and the associated skin remodelling could lead to changes in thermal conductance, which could in turn impact local thermal sensitivity across breast sizes. However, whether local variations in epidermal properties across breasts of varying size contribute to individual differences in local thermal sensitivity, remain under investigated.

Breast thermal sensations play an important role in female thermal comfort at rest (Ayres et al., 2013). Furthermore, the perception of wetness will impact on perceptions of clinginess and comfort in this unique part of the female body, which is almost always covered by a bra (Song, 2011). Hence, broadening our fundamental understanding of the role of breast size and BrSA on thermal and wetness sensitivity, and on skin properties, could inform the design of user-centred garments such as bras that help improve the comfort of individuals with varying breast sizes.

The primary aim of this study was to investigate the relationship between BrSA and thermal and wetness perceptions over various breast regions in a cohort of healthy young to middle-aged females. We hypothesised that larger breasts would present reduced thermal and wetness perception than smaller breasts. The secondary aim of this study was to investigate the relationship between BrSA and epidermal properties in the same breast regions. We hypothesised that increased breast size would result in an increase in epidermal thickness, with potential implication for local thermal sensitivity.

○ Materials and methods

Ethical approval

This study was approved by the University of Southampton Ethics Committee (approval no.79007). All participants provided written informed consent prior to testing. The study conformed to the ethical standards set by the Declaration of Helsinki.

Participants

The same cohort of females who participated in the study outlined in Chapter 5 participated in this study following the same sampling approach and inclusion and exclusion criteria. One participants data were excluded from this section of the study due investigator error, resulting in a sample of 21 females of varying BrSA (age: 27.7 $\pm$ 9.6 years; weight: 72.2 $\pm$ 12.7 kg; height: 170.4 $\pm$ 4.8 cm) (Table 7-1)). Menstrual phase was not “controlled for” based on preliminary evidence that thermal sensation in females may not be independently modified by menstruation (Matsuda-Nakamura et al., 2015). However, self-reports of menstrual phase were collated. The participants were spread across a typical 28-day menstrual cycle (mean day of cycle: 13.6 ± 8.5) and two participants presented irregular periods at the time of the study.

To consider the potential effect of spatial summation (Courtin et al., 2023) in the investigation of thermal and wetness perception, it is necessary to account for the fixed-size stimulus probe (25 cm^2) and associated area of stimulated skin. Therefore, the proportional area of stimulated skin relative to BrSA and BSA was calculated following these equations:

$$\text{Proportion BrSA (\%)} = \frac{25}{\text{BrSA (cm2)}} \text{ x } 100$$

$$\text{Proportion BSA (\%)} = \frac{0.0025}{\text{BSA (m2)}} \text{ x } 100$$

where BSA was calculated as:

$$\text{BSA} = \text{Wt(kg)}^{0.425} \text{ x } \text{Ht(cm)}^{0.725} \text{ x } 0.007184 \text{ (Du Bois \& Du Bois, 1916)}$$

Proportional coverage relative to BrSA and body surface area (BSA) are reported in Table 7-1. It can be observed that while the proportional area of stimulated skin relative to BrSA decreased from smaller to larger breasts (i.e. from ~15 to ~6%), this translated in a much smaller difference between smaller and larger breasted females when expressed as proportional area of stimulated skin relative to BSA (i.e. from ~0.15 to ~0.12%).

Table 7-1. Participant demographics (n = 21). Mean, minimum and maximum values. BrSA = breast surface area. BSA = body surface area.

	Age (years)		Height (m)		Weight (kg)		BrSA (cm^2)		Proportional area of stimulated skin relative to BrSA (%)		BSA (m^2)		Proportional area of stimulated skin relative to BSA (%)	
Bra Size	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
Small (n=6)	23.3	18-30	1.67	1.63-1.72	60.8	56.4-68.9	168.0	147.2-230.1	15.2	10.9-17.0	1.68	1.60-1.75	0.15	0.14-0.16
Medium (n=5)	22.8	19-27	1.69	1.65-1.70	67.5	59.8-76.1	246.3	203.5-288.0	10.3	8.7-12.3	1.77	1.66-1.87	0.14	0.13-0.15
Large (n=6)	30.2	20-42	1.72	1.68-1.77	72.3	61.3-83.4	316.0	173.7-402.2	8.5	6.2-14.4	1.85	1.70-1.94	0.14	0.13-0.15
X-Large (n=4)	29.8	21-44	1.75	1.66-1.83	94.1	87.0-97.9	432.7	300.0-502.2	6.0	5.0-8.3	2.09	1.88-2.21	0.12	0.11-0.12

Experimental design

To establish breast size-dependent differences in thermal and wetness perception, participants visited the lab on one occasion in a quasi-experimental study design. Firstly, BrSA geometry was captured, then epidermal measures and thermal and wetness sensitivity were assessed at rest. This included multiple breast locations longitudinally down the breast, in line with the nipple (Figure 7-1). Spatial perception mapping was deemed important to capture potential regional differences in skin properties, as previously noted in the case of breast thermal sensitivity (Valenza et al., 2023). Evaluation of epidermal properties was also deemed important to provide insights into the potential causes of perceptual variation, as skin thickness and structure have been shown to impact the rate of heat transfer and to elevate perception thresholds (Chen & Ding, 2019; Lundström et al., 2018).

Thermal and wetness perception.

A single-blind psychophysical approach based on a well-established quantitative sensory test (QST) of skin thermal and wetness sensing (Valenza et al., 2019) was used. This enabled mapping of differences in regional thermal and wetness sensitivity at rest in a thermoneutral environment (21 $\pm$ 1.5°C and 37 $\pm$ 5.2 % RH). The QST involved participants having to report the perceived magnitude of local thermal sensations and wetness perceptions arising from a short-duration (i.e. 5s) static application of cold-wet (i.e. 5 ∘C below T_{skin}) or warm-wet (i.e. 5 ∘C above local T_{skin}) stimuli delivered with a hand-held, temperature-controllable probe (NTE-2A, Physitemp, USA; surface area: 25 cm^2; water content: 0.8 mL). Participants reported the extent of their local perceptions using two digital visual analogue scales (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). The study employed thermal stimuli relative to the local T_{skin} to account for inter-individual variability in local T_{skin}, such that the same relative thermal stimulus was applied to all participants (Darian-Smith & Johnson, 1977).

Sensitivity was mapped at three locations over the right breast (above the nipple, nipple-areola complex, below the nipple) and bra triangle (Figure 7-1). These locations were selected because: (i) the nipple is thought to be centre of breast sensitivity (Long et al., 2022), and (ii) thermal sensitivity differences have shown to be greatest in the longitudinal plane on the breast (Valenza et al., 2023). As with previous studies (Filingeri, Fournet, et al., 2014b; Filingeri et al., 2018; Valenza et al., 2023), participants were only informed of the location of stimulation and blinded to the nature of the stimuli to limit expectation biases. Moreover, participants underwent a systematic familiarization to the testing procedures and perceptual scales prior to testing (Valenza et al., 2019). The same investigator performed all testing to ensure internal consistency.

Epidermal measures

Epidermal properties of thickness and surface roughness were evaluated non-invasively using an optical coherence tomography (OCT) scanner (Vivosight, Michelson Diagnostics Ltd, Kent, UK). The VivoSight is a Fourier domain OCT system which captures image data at 20Hz. The OCT image volume obtained from each skin site was 6 x 6 x 2 mm^3 (width x length x depth). Epidermal properties were assessed at three locations that corresponded to the sites of sensitivity measurements. These properties were estimated using the proprietary software associated with the imaging system (VivoTools, Michelson Diagnostics Ltd, Kent, UK).

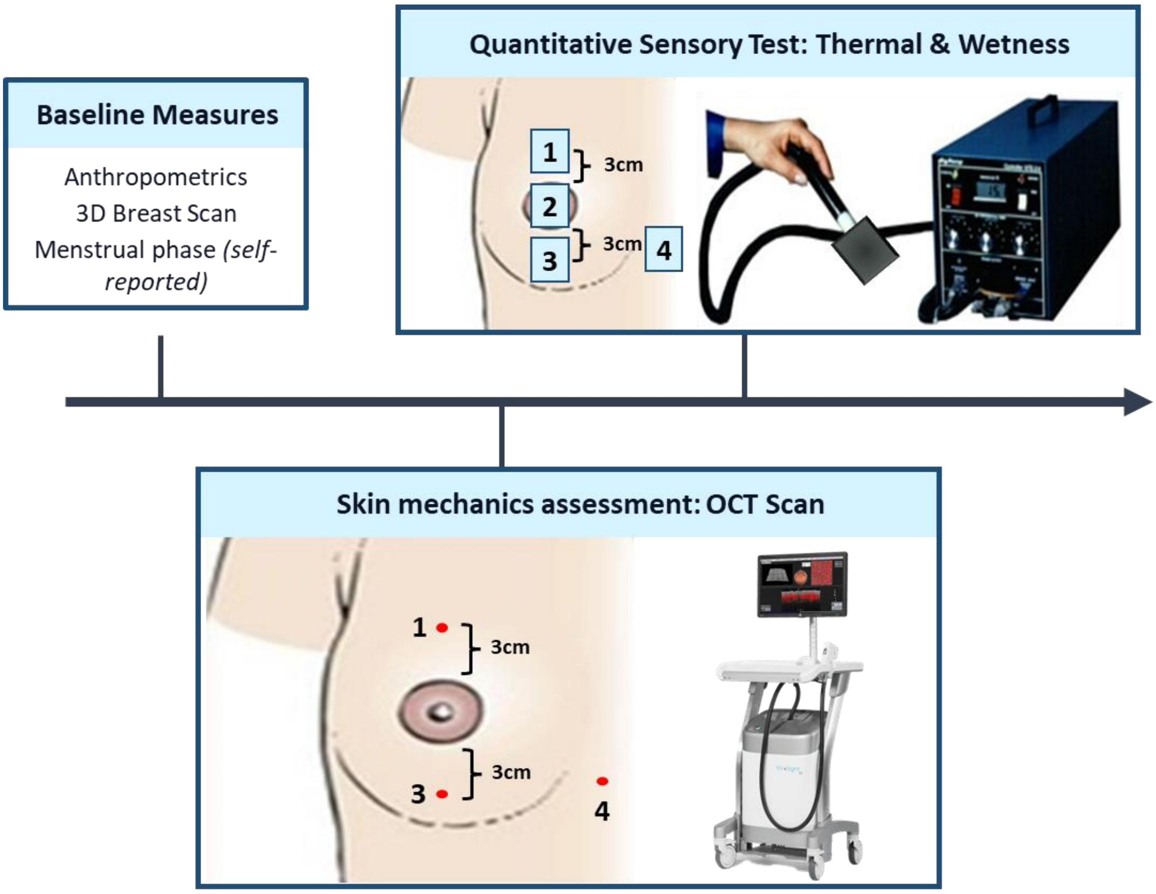

Figure 7-1. Schematic of experimental design and tested sites across the breast and bra triangle.

Experimental procedures

Upon arrival to the laboratory, participants completed a questionnaire to report estimated menstrual phase and contraceptive use. Anthropometric measures of height, weight and BrSA were taken in a thermoneutral laboratory (21 ± 1.5°C and 37 ± 5.2 % RH). Height was measured on a wall stadiometer and weight on a precision scale (KERN 150K2DL, Balingen, Germany). Participants were then asked to remove their bra and position themselves in a 4-point prone position. BrSA was then estimated using a 3D white-light surface scan (EinScan H, Shining 3D Tech. Co. Ltd., Hangzhou, China) with a calibrated surface height accuracy of 0.05 mm. Markers were placed around the breast border based on a validated breast volume model (Göpper et al., 2020), from which surface area was extracted using MeshLab (Visual Computing Lab, CNR-ISTI, Pisa, Italy). This allowed a 15-minute period of rest to adjust to the internal environmental conditions.

Following the 3D scan, participants were asked to lie in a supine position, and the epidermal measurements were taken using the OCT scanner. Test sites were marked with a washable marker, and participants were familiarised with the procedure. Figure 7-2 demonstrates an example OCT scan. Clearly visible are features such as the epidermis and dermis. Upon completion of the OCT imaging, thermal and wetness perception were assessed. Participants were familiarised with the experimental procedures and VAS for the thermal and wetness QST. The local T_{skin} was recorded with an infrared camera for each test site (ER53, FLIR Systems, Wilsonville, OR USA). A 100% cotton fabric patch was applied to the thermal probe which was then wetted with 0.8 ml of water using a pipette to ensure full saturation. The order of stimulus modality (i.e. warm vs. cold) and site (i.e. skin region) was randomised to minimize order effects. A verbal warning was given, and the stimulus applied for 5s, during which the participant was asked to rate their immediate thermal and wetness perception using the VAS. Probe application pressure was not measured but was controlled to be sufficient to ensure full contact without causing pronounced skin indention. Following the submission of the perceptual rating, the stimulus was removed, skin dried and local T_{skin} was recorded again, before proceeding to the next skin site.

[A] [B]

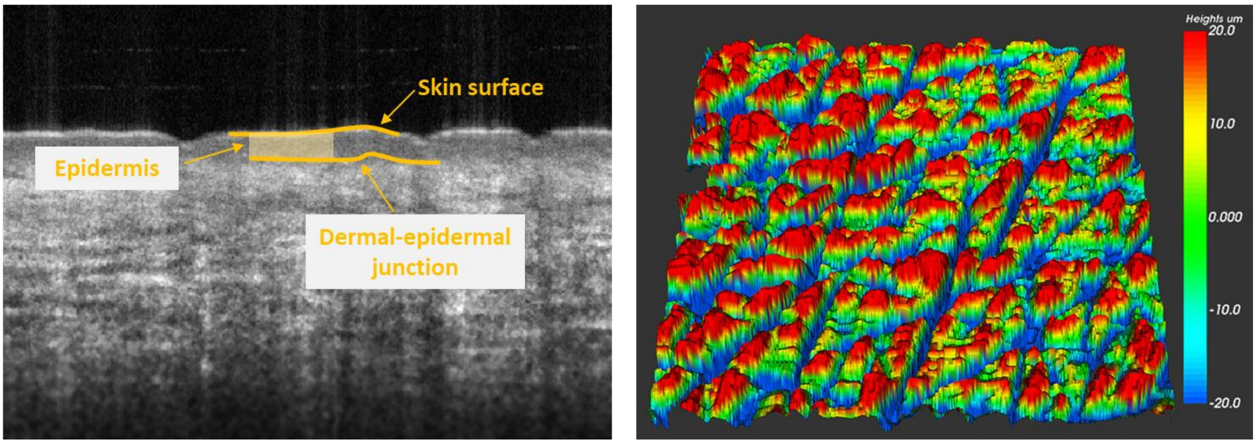

Figure 7-2. [A] Annotated 2D-OCT scan of the breast skin. [B] 3D surface roughness scan with scale.

Statistical analysis

Data normality was assessed using the Shapiro–Wilk tests. Thermal and wetness sensitivity and surface roughness were identified to be normally distributed, hence parametric tests were used for analysis. Epidermal thickness data were identified to be non-normally distributed, so non-parametric descriptors and tests were applied. Statistical analysis was completed using SPSS statistical analysis software package (version 28.1, Chicago, USA) with significance set at $p < 0.05$.

We assessed the relationship between BrSA with thermal sensation and wetness perception, as well as with epidermal measures using Pearson's correlation and Spearman's rank correlation analyses, respectively. Correlation coefficients were calculated separately for each of the skin site tested.

Regional variations in thermal sensation and wetness perception across the breast were analysed separately for the effects of stimuli temperature (2 levels, i.e. warm and cold) and skin site (4 levels) by means of 2-way repeated measures ANOVA. Regional variation in surface roughness was analysed using a repeated measures ANOVA (3 levels; skin site). To investigate site effects on epidermal thickness, a Friedman test was used. In the event of statistically significant main effects, post-hoc analyses were conducted with Bonferroni correction.

To explore inter-individual variability in the sensory outcomes (thermal and wetness perception) and epidermal measures, coefficient of variations [i.e., (SD/mean)*100] were calculated for each skin site and stimulus modality (cold-thermal [CT], cold-wetness [CW], hot-thermal [HT], hot-wetness [HW]). Data were summarized into heat maps to display skin locations of the breast with high and low inter-subject variability.

To determine whether any regional differences in perception were related to any changes in epidermal properties, Pearson's correlation analyses were performed between each stimulus modality (CT, CW, HT, HW) and epidermal outcome (epidermal thickness, surface roughness) at the 3 cross-over test sites (above nipple, below nipple, bra triangle).

○ Results

Breast size-dependent differences in thermal and wetness perception

The relationships between BrSA with thermal sensation and wetness perception at all skin sites are presented in Figure 7-3. The data analysis indicated that the only statistically significant correlation occurred between BrSA and warm sensation at the above the nipple site (Pearson r = -0.61, p = 0.003). No other statistically significant correlation was identified for any other skin site or perceptual modality (p > 0.12).

Regional variations in thermal sensation and wetness perception

Regarding thermal sensation, there was a statistically significant effect of skin site ($F(3,60)$ = 6.07; p = 0.001), no effect of stimuli temperature ($F(1,20)$ = 4.07; p = 0.057), and an interaction between skin site and stimuli temperature (interaction: $F(3,60)$ = 8.3; p < 0.001). Specifically, it was found that cold (Figure 7-4A), but not warm (Figure 7-4B), sensations varied across skin sites, such that less intense cold sensations were reported when stimulating the above nipple site (35.1 $\pm$ 28.7 mm) than the nipple (72.7 $\pm$ 24.6 mm; p < 0.001), below nipple (67.5 $\pm$ 26.9 mm; p = 0.014), and bra triangle sites (65.2 $\pm$ 27.8 mm; p = 0.010).

Regarding wetness perception, no significant effect of skin site ($F(3,60)$ = 0.90; p = 0.445), stimuli temperature ($F(1,20)$ = 0.11; p = 0.747), nor interaction ($F(3,60)$ = 0.73; p = 0.538), was found at any test site (Figure 7-4C & D).

With respect to inter-individual variability in perceptual responses (Figure 7-4E), we found this to vary from: 1) a minimum of 34% (nipple) to a maximum of 71% (above the nipple) for cold sensations; 2) a minimum of 37% (bra triangle) to a maximum of 48% (below the nipple) for warm sensations; 3) a minimum of 67% (below the nipple) to a maximum of 94% (bra triangle) for cold-wet perceptions; 4) a minimum of 73% (above the nipple) to a maximum of 93% (nipple) for warm-wet perceptions.

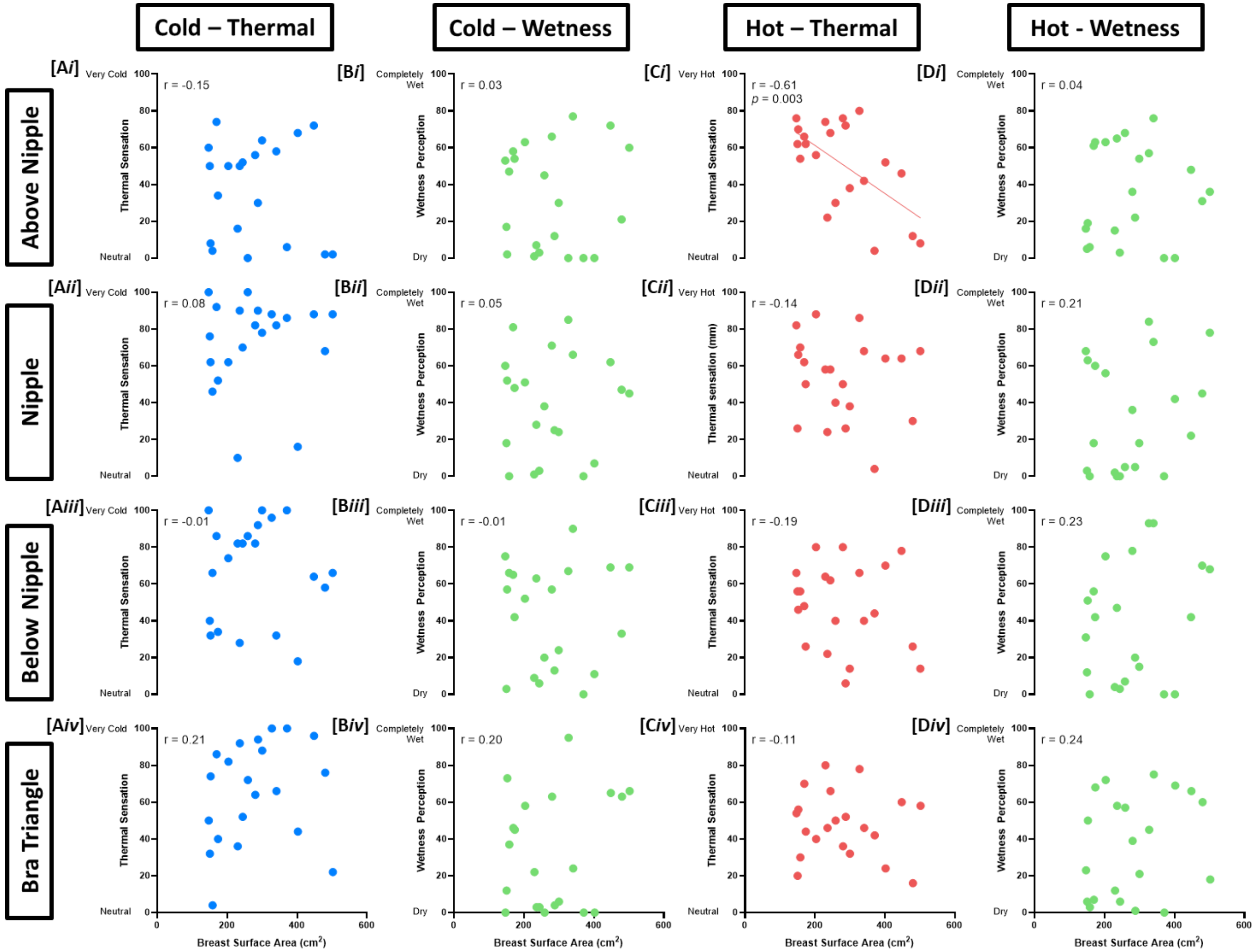

Figure 7-3. Relationships between breast surface area and 4 stimuli (cold-thermal [A], cold-wet [B], hot-thermal [C], hot-wet [D]) at 4 skin sites (above nipple [i], nipple [ii], below nipple [iii], bra triangle [iv]) (n = 21).

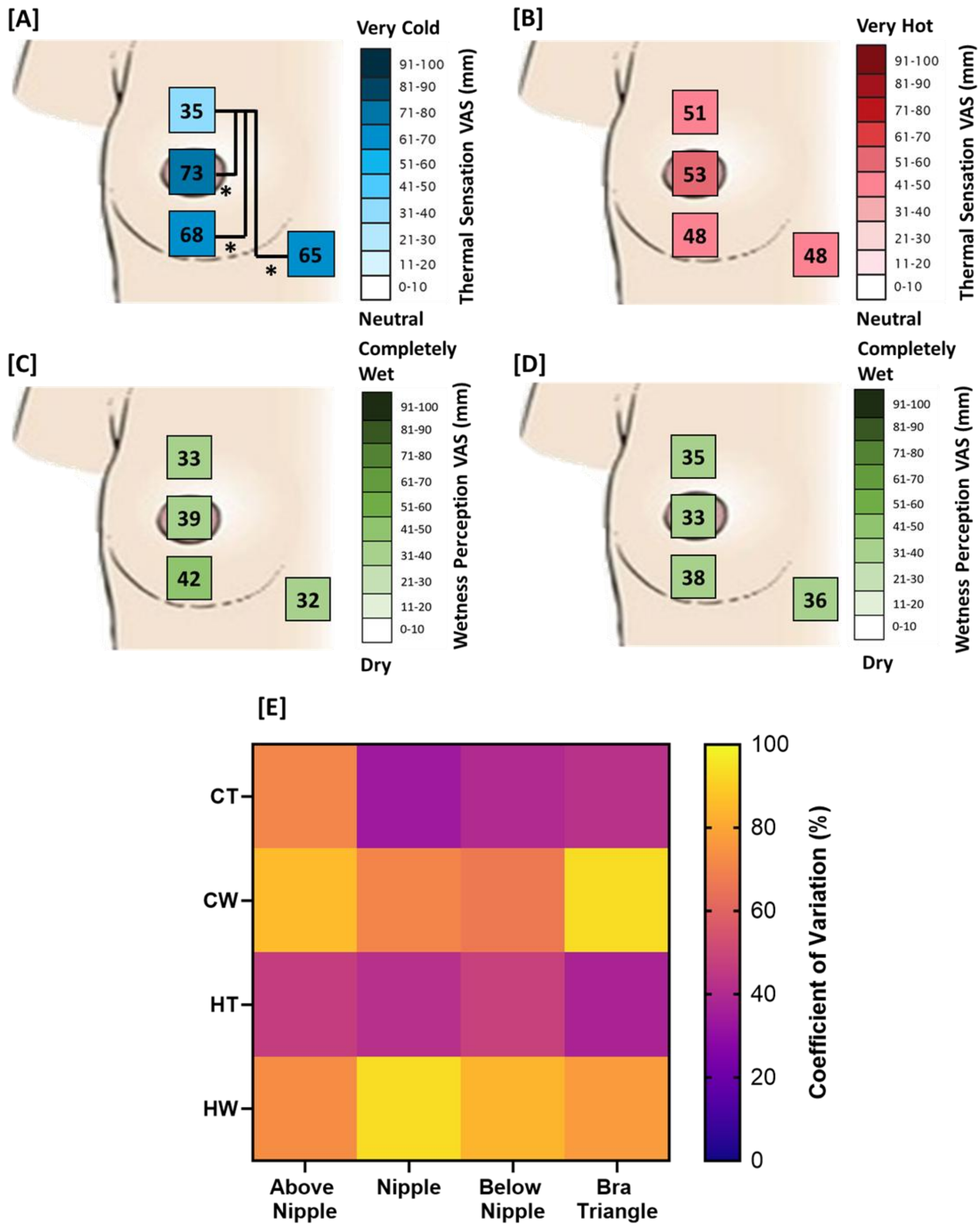

Figure 7-4. Mean (n = 21) cold-thermal (A), hot-thermal (B), cold-wet (C) and hot-wet (D) sensitivity for the 4 locations tested. Statistically significant multiple comparisons are pictured (*$p < 0.05$). (E) Coefficient of variations (%) at each test site for cold-thermal (CT), cold-wet (CW), hot-thermal (HT) and hot-wet (HW) sensations.

Breast size-dependent differences in epidermal measures

The relationships between BrSA with epidermal thickness and surface roughness at all skin sites are presented in Figure 7-5. Correlation analyses between BrSA and epidermal thickness indicated no statistically significant associations at any breast sites (*p* >= 0.195). A statistically significant negative correlation between BrSA and skin roughness was found only at the bra triangle (r = -0.64, *p* = 0.005).

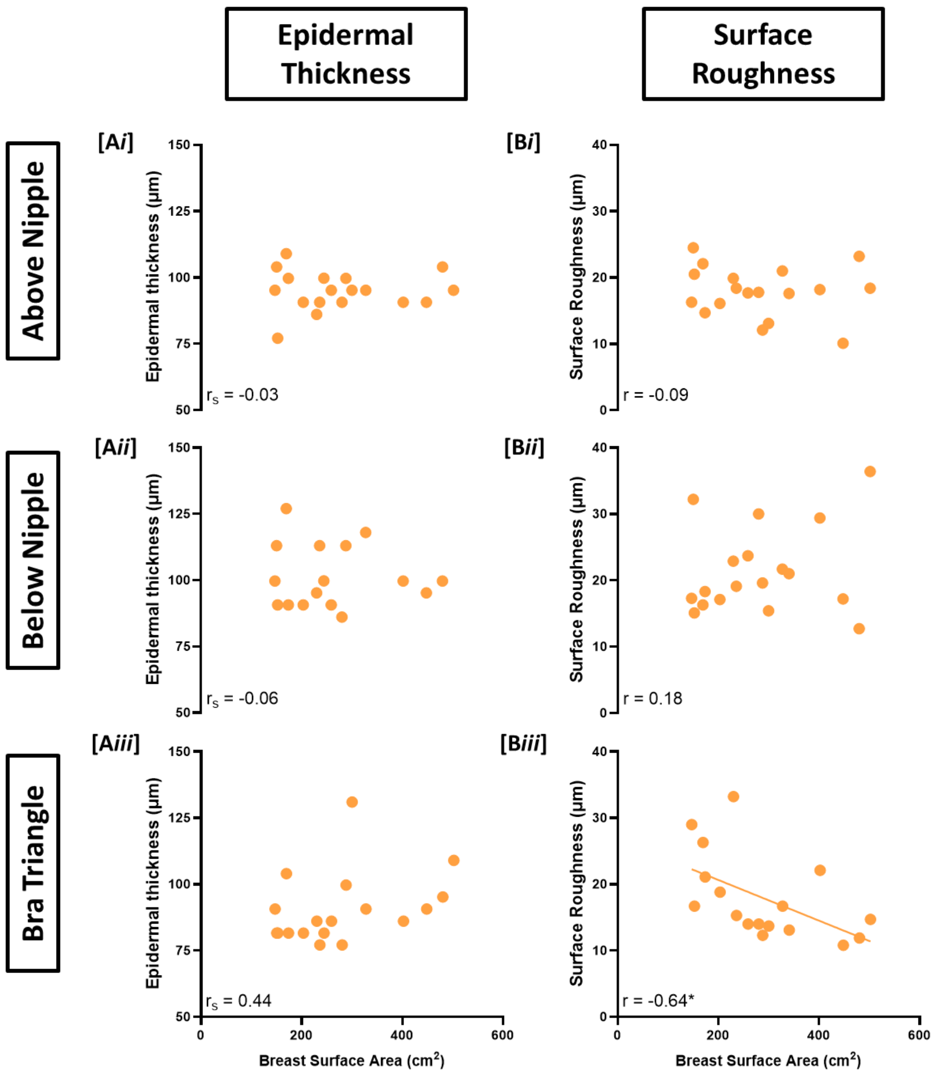

Figure 7-5. Relationships between breast surface area and epidermal measurements (epidermal thickness [A], surface roughness [B]) at 3 skin sites (above nipple [i], below nipple [ii], bra triangle [iii]) (n = 21).

Regional variations in epidermal measures

There was no significant effect of test site on epidermal thickness (p = 0.421, Figure 7-6A) nor on surface roughness (p = 0.158, Figure 7-6B).

Inter-individual differences in epidermal thickness ranged from 8% (above the nipple) to 34% (below the nipple), while variability in surface roughness ranged from 21% (above the nipple) to 36% (bra triangle) (Figure 7-6C).

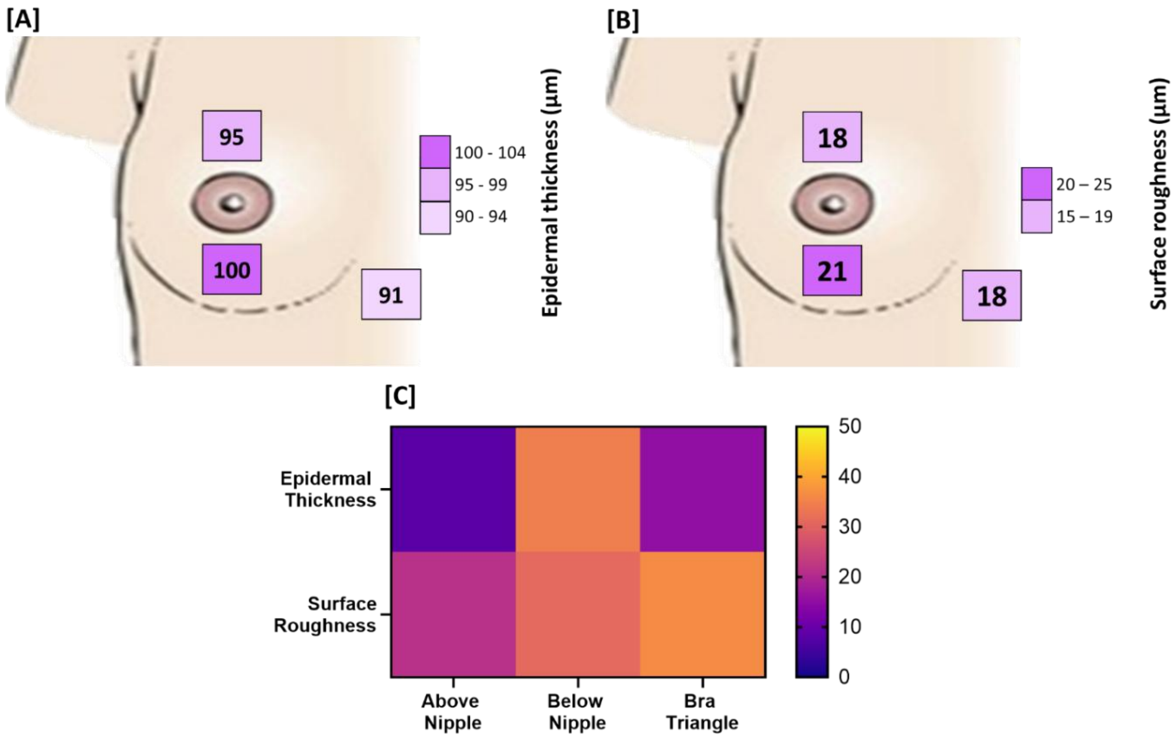

Figure 7-6. Mean (n = 21) [A] epidermal thickness, [B] surface roughness at the 3 skin sites. Statistically significant comparisons are pictured (*p < 0.05). [C] Coefficient of variations (%) at each test site for epidermal thickness and surface roughness.

Relationship between perception and epidermal properties

The correlation coefficients between epidermal properties and thermal sensation and wetness perception at all skin sites are presented in Table 7-2. Overall, no significant associations were found between epidermal thickness and surface roughness with any perceptual variable at any test site.

Table 7-2. Pearson correlation coefficients and p-values between epidermal properties with thermal sensation and wetness perception at all skin sites. *p < 0.05.

		Cold Thermal		Cold Wetness		Hot Thermal		Hot Wetness	
		r	p	r	P	r	p	r	p
Above Nipple	Epidermal Thickness	0.13	0.614	0.23	0.373	-0.15	0.559	0.17	0.527
	Surface Roughness	-0.35	0.159	-0.37	0.136	-0.01	0.955	-0.24	0.347
Below Nipple	Epidermal Thickness	0.23	0.380	-0.29	0.263	-0.04	0.888	-0.28	0.269
	Surface Roughness	-0.16	0.538	-0.19	0.455	0.16	0.649	-0.11	0.659
Bra Triangle	Epidermal Thickness	0.16	0.552	-0.09	0.728	0.04	0.887	-0.45	0.067
	Surface Roughness	-0.47	0.057	-0.22	0.398	0.42	0.095	-0.34	0.178

- ## Discussion

The primary aim of this study was to investigate the relationship between BrSA and thermal sensation and wetness perception over various breast regions. Our findings did not support the hypothesis that skin sites across larger breasts present reduced thermal and wetness sensitivity, except for the site above the nipple, which instead exhibited a reduction in warm sensitivity with increasing BrSA. Our findings also indicated a heterogeneous distribution of cold, but not warm nor wetness, sensitivity across the breast, with the site above the nipple presenting lower cold sensitivity than any other tested site. Regarding our secondary hypothesis, our findings did not indicate any association between BrSA and epidermal properties (i.e. thickness and roughness), nor did they indicate any site-dependent variation in these anatomical parameters. Finally, the lack of any meaningful association between any perceptual response and their site-specific epidermal parameters indicated that the observed body-regional and inter-individual variability in sensitivity in unlikely to be dependent on epidermal parameters. These observations are discussed in detail in the sections below.

BrSA- and skin-site dependent differences in perception

The relationship we observed between increasing BrSA and decreasing warm sensitivity at the site above the nipple is interesting and it may be underlined by a size-dependent variation in the density of warm thermoreceptors with spot-like receptive field (Kenshalo & Gallegos, 1967) that may innervate the skin of larger breasts. This hypothesis is not entirely speculative, if one considers that the nervous system reaches maturity prior to breast development (Javed & Lteif, 2013). Furthermore, this hypothesis would align with our previous findings of a reduced sweat gland density at the breast with increasing BrSA in the same cohort of females tested in the present study (Chapter 5) (Blount et al., 2024b). A size-dependent relationship between tactile sensitivity and BrSA has also been previously reported, and it demonstrated that larger breasts tend to have overall lower tactile sensitivity (Cornelissen et al., 2018; DelVecchyo et al., 2004; Tairych et al., 1998) and spatial acuity (Long et al., 2022) than smaller breasts (note: this effect is particularly evidence at the upper and lateral breast regions) (Tairych et al., 1998). However, it is important to note that we recently failed to replicate these mechano-sensory findings when stimulating the lower breast of the same cohort of females tested in the present study (Chapter 6)(Blount et al., 2024c). These contrasting findings may highlight the heterogeneity of such size-dependent perceptual mechanisms across skin sites, as well as their individual variability. This is clearly demonstrated by our observation that, out of the 16 possible combinations of perceptual assessments (i.e. cold, warm, cold-wet, and warm-wet) by skin site (i.e. above the nipple, nipple-areola complex, below the nipple and bra triangle), a statistically significant size-dependent association was identified in one instance only (i.e. warm sensitivity at the site above the nipple). Despite the relevance of the warmth-related findings at the site above the nipple, we therefore believe that a BrSA-dependent variation in thermal and wetness sensitivity may not be considered a robust and generalised feature of the skin covering the female breast.

Besides size-dependent differences, it also worth-noting that the site above the nipple was the only region to differ substantially from the other tested sites, by presenting a meaningfully lower thermal sensitivity to cold only. As we did not observe any other site-by-perceptual modality difference, one may argue that, albeit varying at an individual level (see Figure 7-4), thermal and wetness sensitivity across the breast sites tested in this study is rather homogenous. To date, only a few studies have investigated regional variations in breast thermal sensitivity (Luo et al., 2020; Terzis et al., 1987; Valenza et al., 2023). Our findings somewhat correspond to those of Luo et al. (2020), who found a homogenous thermal sensitivity distribution across the breast. However, this is in contrast with the findings of Valenza et al. (2023), who demonstrated differences in warm thermal sensitivity between the lower breast and the bra triangle. Furthermore, the lower cold sensitivity at the site above the nipple that we observed, was not identified by Luo et al. (2020) or Valenza et al. (2023). While methodological differences amongst these studies may underlie some contrasting results [e.g. Luo et al. (2020) used a thermal probe with a coverage of 1.32 cm^2 compared to the 25 cm^2 probe used in this study], these do not apply consistently (e.g. both our study and that of Valenza et al. employed the same size probe). In this respect, inter-individual variability in study participants (e.g. individuals with varying breast sizes were considered only in our study) as well as in their cold sensitivity at the site above the nipple (see Figure 7-4), may have also contributed to the heterogeneity of the breast sensorial data reported in the literature. Given the upper breast is being highlighted as a region where perceptual differences may exist relative to BrSA and compared to other chest sites, future studies should investigate what drives the perceptual differences in this area of the breast, particularly as this is commonly under greater tensile strains compared to the lower breast (Norris et al., 2020).

BrSA- and skin-site dependent differences in epidermal parameters

No relationship was found between BrSA and epidermal thickness at the breast. Maiti et al. (2020) used an OCT scanner to map skin morphology of 21 skin sites across the body and found epidermal thickness at the chest to average around 93 ± 5 μm, which corresponds to the values found in this study. However, this previous study only contained 4 females and made no mention of breast size. Work by Sutradhar and Miller (2013) specifically investigated variations in breast epidermal and dermal thickness at 16 breast locations in 23 females using high-frequency ultrasound. While this study made no mention of breast size, it demonstrated that skin thickness in the medial region was greater than in the lateral region of the breast (p = 0.001). Sutradhar and Miller (2013) also found no differences in skin thickness between the superior and the inferior region of the breast (p = 0.70), which supports the findings of our study. In contrast, other research has demonstrated that skin thickness (measured using mammography) in the superior breast region was lower than that in the inferior breast region (Ulger et al., 2003; Wilson et al., 1983). Ulger et al. (2003) also observed that skin thickness decreases with increases in age and size in all tested regions. While our study did not infer whether differences in skin thickness are size- or age-driven (Oriba et al., 1996; Waller & Maibach, 2005), it is likely that contradictory finings between the literature and our dataset may be primarily due to differences in measuring techniques (e.g. mammography measurement and OCT techniques present different resolutions of imaging and attenuation of dermal tissues). Future studies should investigate epidermal parameters across all breast regions, in an age-matched cohorts of females with varying sizes, or BrSA size-matched cohorts of females of varying ages, to better identify which parameter may play a greater role in individual variation in skin thickness.

Regarding surface roughness, we found no relationship with BrSA, nor skin site variations. Skin stretch has been shown to cause the undulations of the epidermal surface and the epidermal-dermal junction to become flattened (Ferguson & Barbenel, 1981). Skin surface folds provide a reserve of tissue, thus allowing the epidermis to stretch without disrupting the epidermal cells. We had hypothesised that the skin of larger breasts, which supports a greater breast volume and mass, may be in a greater state of stretch, which would in turn have reduced its surface roughness. However, this was not observed. We cannot exclude that this lack of an effect may be partly due to the roughness measurements being collected while participants were lying in a supine posture, which would have reduced gravitational tension at the breasts.

Finally, we found no meaningful association between any perceptual response and their site-specific epidermal parameters. We believe that this finding may be due to the relatively narrow range of inter- and intra-individual variations observed in epidermal thickness (i.e. 0.08 to 0.12 mm) and in surface roughness (i.e. 10 to 33 μm). Indeed, previous evidence has indicated that variations in epidermal thickness in the range of 0.1 to 0.5 mm and in surface roughness in the range of 0.4 to 100 μm may be required to observe a meaningful impact of epidermal thickness and surface roughness on the rate of heat exchange between the material in contact with the skin and the cutaneous thermal receptors that contribute to conscious thermal sensations (Chen & Ding, 2019). As a result, we believe it reasonable to conclude that the observed body-regional variations in sensitivity observed in this study is more likely to be dependent inter-individual variability in the subjective assessment of a thermal stimulus (e.g. lived experiences) than on epidermal parameters.

Limitations

The primary limitation of this study is that we used a stimulating probe of fixed size (i.e. 25 cm^2) to assess thermal and wetness sensitivity across varying BrSA(s). This approach resulted in a proportional area of stimulated skin relative to BSA ranging between 0.12 and 0.15% (i.e. from the largest to smallest breasted female). We have long known that, given the same local thermal stimulation of the skin, the resulting thermal sensation can vary in magnitude depending on the size of the stimulated area (i.e., the larger the area, the more intense the resulting hot or cold sensation) (Hardy & Oppel, 1937; Stevens et al., 1974). Specifically, previous studies investigating spatial summation in thermal sensitivity have found this phenomenon to occur with differences in proportional area of stimulated skin relative to BSA as little as of 0.04% (Kenshalo & Gallegos, 1967). The difference in proportional area of stimulated skin relative to BSA between the largest (~0.12% of BSA) and smallest breasted females (~0.15% of BSA) in the current study corresponded to 0.04% (see Table 7-1). Hence, it cannot be excluded that this methodological limitation could have somewhat biased our perceptual outcomes towards a scenario where larger breasted females may have reported less intense thermal sensations. However, a BrSA-dependent relationship was found in only one perceptual modality (warm-thermal above the nipple). Hence, if a spatial summation bias had occurred in this study, then we would have expected to observe it for all perceptual modalities. It should nevertheless be recognised that an ideal, yet challenging, methodological approach would have been one where proportional area of stimulated skin relative to BSA is fixed, by increasing the probe size in line with BrSA. Under that scenario and considering our results (i.e. sensation did not generally vary with BrSA), one may envisage that larger breasted women may have in fact presented greater thermal sensation for the same temperature stimulus. However, this consideration remains speculative, and future studies are therefore warranted to better characterise the complex relationship amongst stimulated skin area, probe size, and resulting sensations across individuals varying in body morphology. Furthermore, the implications of using a fixed-size probe over the nipple-areola complex should also be considered. The nipple-areola complex has been shown to be the anchor of breast sensitivity (Kasielska-Trojan et al., 2021). In the present study, thermal sensitivity was assessed over the nipple-areola complex when the nipple was not erect, and the probe was placed on the skin such that it would be in full contact with the skin surface. Our qualitative observations indicated that individuals presented different size nipples and areolas. Hence, we cannot exclude that e.g. individuals with larger nipples (i.e. larger area of greater sensitivity) may experience variations in thermal and wetness sensitivity independently of breast surface area. Future studies should therefore consider additional measurements of the size of the nipple-areola complex.

○ Conclusion

We conclude that BrSA-dependent variations in thermal and wetness sensitivity are not a generalised feature of the skin covering the female breast, as these appeared to be primarily skin-site (i.e. above the nipple) and perceptual modality-dependent (i.e. warm sensitivity). Irrespective of BrSA, thermal and wetness sensitivity over the breast did also appear to be rather homogenous, with only the skin site above the nipple presenting reduced cold sensitivity. Inter-individual differences may play a greater role in determining such perceptual patterns than epidermal parameters (e.g. skin thickness and roughness), as the latter did not vary neither with BrSA nor with skin site. Altogether, these observations advance our fundamental understanding of the sensory properties of the female breast. Furthermore, our findings carry applied implications to improve the design and comfort of clothing items such as bras, which may account for the observed interaction between breast size, warm sensitivity and regional differences (i.e. upper vs. lower breast) at rest.

Chapter 8 Experimental Study 4: The maturation of regional sweating patterns from childhood to young adulthood in females

Accepted for publication in Experimental Physiology

Abstract

Children are considered heat vulnerable, with the belief that maturation of sweating occurs throughout childhood. Indeed, young children demonstrate distinct patterns of regional sweating compared to adults, but little is known about this pattern maturation throughout puberty. This study aimed to investigate the maturation of regional sweating patterns and thermal perceptions in females during exercise.

28 females aged 8-25 years, representing 5 Tanner stages (preadolescent to adult) were recruited. Local sweat rates (LSR), sweat output per gland, and thermal perceptions, were measured during cycling exercise at a fixed evaporative requirement for heat balance (154±10 W/m^2) in a climatic chamber (36°C and 50% RH).

Results indicated that LSR across the torso (chest, abdomen, back), but not the limbs (hand, thigh, shin), increased linearly with age, due to increases in sweat output per gland. The transition of regional sweating patterns from children-like (higher LSR at extremities) to adult-like (higher LSR at torso) became meaningful (2-fold difference) at Tanner stage 3 and age 14. Perceptions of temperature, wetness and thermal comfort did not differ across age-groups.

Our findings provide the first detailed evaluation of regional sweating pattern maturation in females while exercising in the heat. This could inform person-centred public health and sportswear applications.

○ Introduction

As discussed in the Literature Review, body temperature regulation in humans is an important homeostatic process resulting from a combination of feedback and feedforward mechanisms aimed at maintaining optimal cellular function during thermal challenges, such as heat stress (Mitchell et al., 2025). In adults, following behavioural thermoregulation (Attia, 1984), the production and evaporation of sweat from the skin surface represents the principal and most powerful method of heat loss during exercise and heat stress (Havenith, 1999; Havenith et al., 2008)(Section 2.2.2). It is generally believed that the complete maturation of sweating mechanisms in humans may occur throughout puberty. This consideration is largely derived from empirical observations that children present lower whole-body sweat rates than adults during exercise and heat stress as discussed in section 2.5.3 (Bar-Or, 1998; Drinkwater et al., 1977; Inoue et al., 2004; Meyer et al., 1992). Furthermore, recent sweat mapping studies in children have indicated that regional sweating patterns observed in pre-pubertal girls (~8 years old; yo) do not resemble those observed in women (i.e. >18yo) (Arlegui et al., 2021; Smith & Havenith, 2012), whereby girls present their highest LSR at the extremities (forehead, hands, feet) instead of the torso (the latter being a body region presenting the highest LSR in women) (Blount et al., 2024b; Smith & Havenith, 2012).

This perception of a paediatric "thermoregulatory disadvantage", combined with evidence that children may find it challenging to verbalise their thermal perception and comfort (Fabbri, 2024), has shaped public health messaging that emphasises heightened heat vulnerability in children (UKHSA, 2025). In contrast, the American Academy of Paediatrics have argued that youth have an equally effective thermoregulatory ability as healthy adults (Bergeron et al., 2011), challenging the notion of an inherent disadvantage. These divergent views highlight a critical knowledge gap: it remains unclear how and when complete maturation of local sweating mechanisms across the body occurs throughout puberty, and how such maturation relates to age-dependent differences insensitivity to thermal discomfort, during both endogenous (i.e. exercise-mediated) and exogenous (i.e. environment-mediated) heat stress. This represents a significant fundamental and applied knowledge gap, which hinders the ability to a) establish critical age thresholds beyond which heat vulnerability may align with that established in adults;

and b) inform the design of interventions, such as age-appropriate sportswear, which accommodate the sweating and comfort needs of children throughout puberty.

The implications of this knowledge gap are particularly important for the female population, who continue to be largely underrepresented in thermoregulatory studies (Filingeri, Blount, & Valenza, 2024; Filingeri, Blount, & Ward, 2024; Hutchins et al., 2021). This is despite undergoing unique morphological and physiological change (i.e. consider menarche and thelarche) that could impact the development of autonomic thermoregulatory mechanisms, including regional sweating patterns (Biro et al., 2008; Breehl & Caban, 2024).

The aim of this study was therefore to investigate how and when complete maturation of local sweating mechanisms across the whole-body occurs throughout puberty in females. A secondary aim was to explore how these age-dependent changes may relate to variations in children’ sensitivity to thermal discomfort, during exercise in the heat. Leveraging validated methodologies for exercise prescription that accommodates an unbiased comparison of sweating responses in paediatric and adult populations (Smallcombe et al., 2025), we hypothesised that LSR across the torso may increase to a greater extent than peripheral sites over the limbs, secondary to changes in sweat output per gland, as recently observed at rest (Amano et al., 2025). We also hypothesised that meaningful changes in regional sweating patterns may occur at specific developmental stages associated with hormonal development in females.

○ Materials and methods

Ethical approval

This study was approved by the University of Southampton Ethics Committee (approval no.99072) and all procedures conformed to the ethical standards set by the Declaration of Helsinki. All participants, and guardians of those aged under 18, completed a health screen questionnaire and provided written informed consent prior to testing.

Experimental design

This observational cohort study was conducted in a climatic chamber at the University of Southampton between November 2024 and February 2025. Recruitment involved the purposeful sampling of girls from a range of adolescent age groups and comparison with a control group of adult women. Participants underwent one preliminary trial and one experimental trial, separated by >48 hours.

Participants

Twenty-eight healthy 8- to 25yo females volunteered to participate in this study. Participants were purposefully recruited by age group to accommodate appropriate representation across pubertal development: 8-9yo (*n*=4), 10-11yo (*n*=4), 12-13yo (*n*=6), 14-15yo (*n*=6), 16-17yo (*n*=4), 18-25yo (*n*=4). Pubertal development was determined via self-assessed Tanner staging in order to assess the level of physical and physiological maturation, which provides a more nuanced and accurate assessment of development rather that solely relying on chronological age (Section 2.5.2) (Breehl & Caban, 2024). Stage 1 represents pre-puberty and stage 5 indicates adult-level development. Participant physical and physiological characteristics spanned the full range of Tanner staging, as presented in Table 8-1. Participants were not heat acclimatized and seasonal variation was limited (Amano et al., 2025). They included physically active females (i.e. performing moderate intensity exercise >3 days per week), who were free of any injury or illness. Of those who had begun menarche (n = 15), 6 participants presented irregular periods at the time of the study and 9 were distributed across a typical 28-day menstrual cycle (mean testing day of cycle: 13 ± 4).

Preliminary session

Body mass (KERN 150K2DL, Balingen, Germany; accurate to 0.005kg) and height (Seca 213 Stadiometer, Birmingham, UK) were measured. Body surface area (BSA) was calculated using the Du Bois and Du Bois (1916) equation which is appropriate for use in children and adults (Haycock et al., 1978). Body fat percentage was estimated from skinfold thickness measured at 4 sites (abdomen, suprailiac, triceps, thigh) (Jackson & Pollock, 1985).

Participants performed a submaximal incremental exercise test of five 3-min stages in temperate conditions (air temperature: 24.0 ± 0.2 °C; relative humidity: 50.7 ± 7.0%) on a cycle ergometer (Lode Corvial Recumbent, Groningen, Netherlands) (Figure 8-1). Expired gases were measured via indirect calorimetry (Quark CPET, Cosmed, Rome, Italy) to determine the individual exercise workload required to elicit the target E_{req} for the experimental trials, as previously described (Cramer & Jay, 2019). Equations used to calculate partitional calorimetry parameters, including E_{req}, rate of convective and radiative heat exchange (C + R), rate of respiratory convective and evaporative heat loss (C_{res} + E_{res}) and H_{prod}, are presented in the Methods (Chapter 4: Partitional calorimetry) (Parsons, 2014).

Experimental session

Participants were asked to refrain from strenuous exercise 24h prior to the experimental trial. Upon arrival they provided a urine sample to measure urine specific gravity (USG)(Digital refractometer, KERN, Balingen, Germany) with euhydration confirmed by a USG <1.025 (Casa et al., 2005). A standardised ensemble of shorts, sports bra and t-shirt was provided to the participants, and shoes and socks were worn (~0.3 clo). All clothing items were weighed to the nearest 0.1mg (PCB 350-3, KERN, Balingen, Germany).

Prior to entering the climate chamber participants were familiarised with the whole-body perceptual assessment scales for thermal sensation (TS), wetness perception (WP) and thermal comfort (TC), leveraging adapted Likert scales for paediatric use (Teli et al., 2013). Likert scales ranged from 1 to 4 (TS: 1=neutral/ok, 4=hot; WP: 1=dry, 4=dripping wet; TC: 1=comfortable, 4=very uncomfortable). Upon entry to the climate chamber (air temperature: 36.6 ± 0.2 °C; relative humidity: 48.4 ± 2.2%), clothed body mass was measured (KERN 150K2DL, Balingen, Germany; accurate to 0.005 kg) (Figure 8-1). Whole-body sweat rate (WBSR) was calculated by subtracting post-trial clothed body mass from pre-trial clothed body mass, corrected for sweat trapped in clothing. This method was used instead of pre- and post- nude weights for ethical reasons. Participants were then equipped with an optical heart rate (HR) monitor (Verity Sense, POLAR, Kempele, Finland) and 7 skin temperature (T_{skin}) sensors (iButtons, Maxim, San Jose, USA; 0.2Hz) were fixed on the abdomen, shoulder, upper breast, upper back, lower back, thigh and shin. Weighted mean T_{skin} was calculated as the weighted average of measurements at the chest (0.3), shoulder (0.3), thigh (0.2) and calf (0.2) (Ramanathan, 1964).

Participants sat for 5 min such that baseline measures of HR, tympanic temperature (T_{tym}), and perceptual measurements were taken, then they cycled for 36 + 5 min, alternating between 3-min intervals of higher (E_{req}: 170W/m^2) and lower (E_{req}: 140W/m^2) intensities. Exercise prescribed at a fixed E_{req} in W/m^2 allows for the most unbiased investigation of LSR differences by accounting for biophysical differences in body size (Cramer & Jay, 2015), thus ensures that possible LSR differences would be due a true independent effect of maturation and not differences in heat production. VO_2, HR and T_{skin} were measured continuously throughout exercise. TS, WP and TC were measured at baseline then at 10-min intervals and T_{tym} at 5-min intervals (Figure 8-1). T_{tym} (ThermoScan 7+, Braun, Bussigny, Switzerland) was used due to ethical restrictions on the use of more invasive techniques, such as rectal sensors or ingestible telemetric pills with children.

Following the initial 36-min of cycling, participants briefly stopped to allow the set-up of LSR collection for the final 5-min of exercise, via the absorbent patches technique (Smith & Havenith, 2012). Prior to the trial, absorbent patches (max absorption = 4655 ± 220 g.m^{-2}) were cut to size (9cm^2), individually sealed in Ziplock bags, marked, and weighed to the nearest 0.1mg (PCB 350-3, KERN, Balingen, Germany). The skin was dried then patches were applied using a waterproof film dressing (Tegaderm, 3M, Minnesota, United States) to the palmar surface of the hand, bra triangle, abdomen, upper back, lower back, thigh, and shin on the contralateral side to the T_{skin} sensors**.** Following application, participants cycled for 5-min then the patches were removed, sealed in Ziplock bags, and weighed. LSR (g.m^{-2}.h^{-1}) was calculated from the relative change in pre- to post-patch weight, divided by the surface area and application time.

Following cessation of exercise and immediately after removal of the LSR pads, heat activated sweat gland density (HASGD) was assessed non-invasively at the bra triangle site using the modified iodine technique (Gagnon et al., 2012). HASGD was quantified to estimate maturation-dependent changes in sweat output per gland. The bra triangle site was selected as previous work demonstrated this site to have one of the highest levels of LSR and HASGD across the female torso (Blount et al., 2024b). Cotton paper patches were cut to 3x3cm squares and sweat glands were identified through a standardised image processing tool (ImageJ; (Schneider et al., 2012)), with a sub-set of images assessed by two raters to ensure rigor in the analysis (Peel et al., 2022). When raters agreed (<10% variation), the primary investigator's measurement was taken, where disagreement between raters was >10%, an average from the two raters was used. An estimation of sweat output per gland could then be calculated by dividing the sweat rate by the density of heat-activated sweat glands for the bra triangle site.

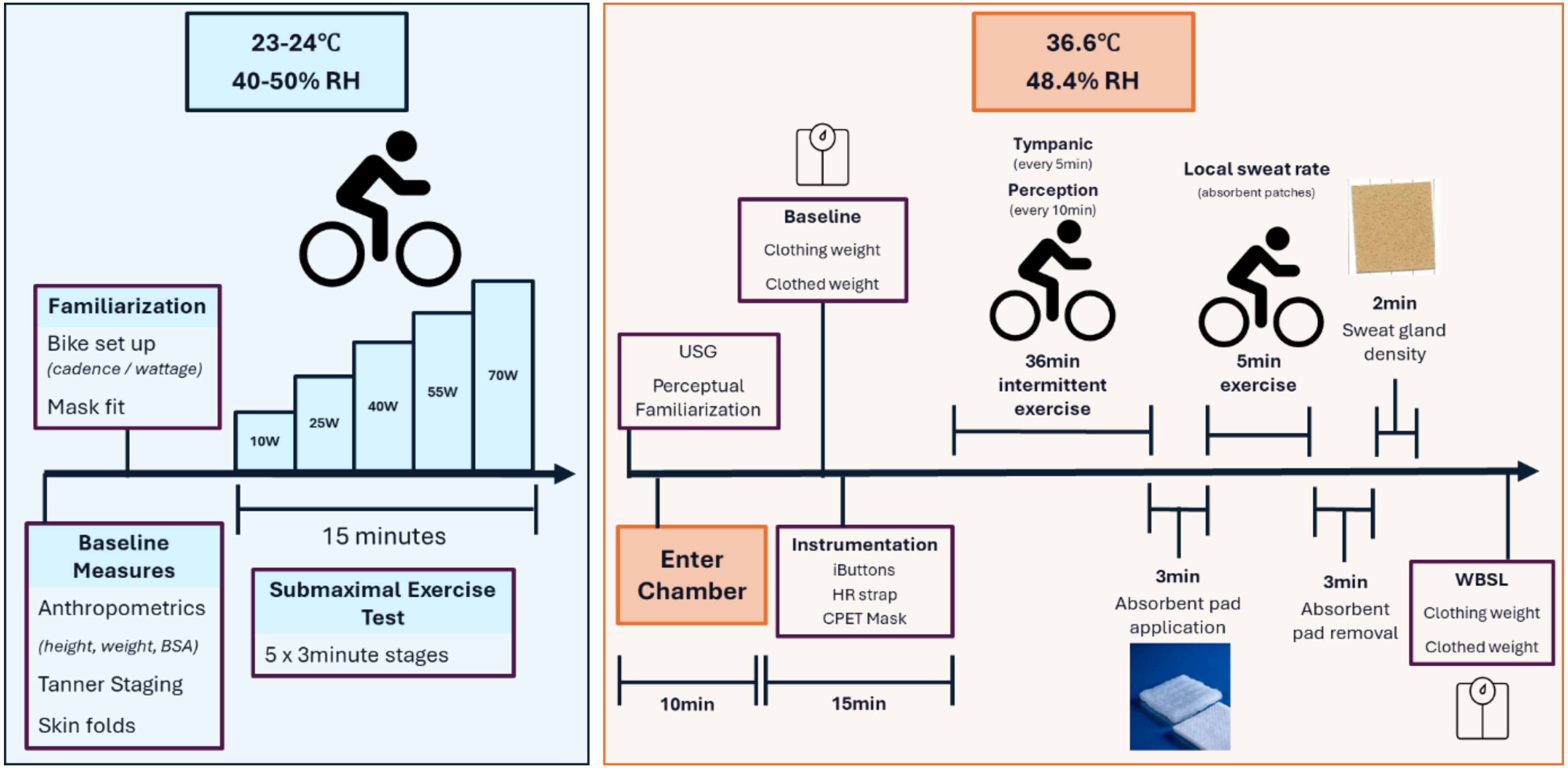

Figure 8-1. Schematic of experimental design. Preliminary session (left) and experimental session (right).

Statistical analysis

Statistical analyses were carried out using SPSS (version 28.1; Chicago, USA). Normality testing using the Shapiro–Wilk test was performed for all datasets, and significance was set at p<0.05. Subsequently, descriptive data are reported as means and standard deviations (SD).

Partitional calorimetry was performed to ensure exercise prescription at a fixed E_{req} in W/m^2 and to assess the relative contribution of evaporative and dry heat exchange in relation to age. One-way analyses of variance (ANOVA) were performed to assess the impact of age groups on E_{req}, H_{prod} and T_{skin} throughout exercise.

To address the primary aim, Pearson correlation analyses were performed to assess the relationships between age and local sweating responses at each skin site (i.e., LSR, heat activated sweat gland density and sweat output per gland). To assess the evolution of regional sweating patterns with aging / development, skin sites were grouped into torso and extremity sites to allow comparison between central vs. peripheral body regions. Two levels of grouped body sites were selected for two reasons: i) to investigate the hypothesis that LSR across the torso would increase to a greater extent than the periphery to align with sweating patterns seen in adulthood; and ii) to consider applications to sportswear, for which one predominantly designs separate clothing items for the torso and lower body. Two separate two-way ANOVAs were used with the factor of either age groups (6 levels: 8–9, 10-11, 12–13, 14-15, 16–17, 18-25) or Tanner staging (1-5), and body site (2 levels: torso and extremities). When a significant interaction was observed, a post hoc analysis for multiple comparisons was conducted using Bonferroni's multiple comparisons test.

Kruksal-Wallis Tests were used to investigate the impact of age (6 levels: 8–9, 10-11, 12–13, 14-15, 16–17, 18-25) on perceptual outcomes (TS, WP, TC) at each time point. The effect of time on perceptual outcomes (TS, WP, TC) were analysed using Friedman Tests.

Results

Descriptive exercise, physiological and calorimetric data

Anthropometric, heat exchange and exercise intensity data for all participants are presented in Table 8-1. Pubertal stage defined by Tanner staging, had a statistically significant positive correlation with age (r = 0.85, p < 0.001).

As per the study design, there was no statistically significant effect of age group on E_{req} ($p = 0.488$) or H_{prod} ($p = 0.383$) in W/m^2, nor on mean T_{skin} ($p = 0.307$). By contrast, there was a statistically significant effect of age on: i) absolute H_{prod} in W ($p < 0.001$), with the youngest girls having lower H_{prod} in W than adults; and ii) H_{prod} in W/kg ($p = 0.005$), with the youngest girls having greater H_{prod} in W/kg than adults (Table 8-1).

Table 8-1. Anthropometric, heat exchange and exercise intensity during exercise (*n*=28).

	All (n = 28)	8 - 9yo (n = 4)	10 - 11yo (n = 4)	12 - 13yo (n = 6)	14 - 15yo (n = 6)	16 - 17yo (n = 4)	18 - 25yo (n = 4)
Age (years)	14.1 ± 4.4	8.8 ± 0.5	10.3 ± 0.5	12.7 ± 0.5	14.3 ± 0.5	16.8 ± 0.5	22.5 ± 2.4
Tanner Stage (min-max)	1 – 5	1	1 - 3	2 - 4	3 - 4	4 - 5	5
Height (m)	1.60 ± 0.12	1.40 ± 0.09	1.49 ± 0.06	1.60 ± 0.07	1.71 ± 0.03	1.66 ± 0.05	1.68 ± 0.02
Body mass (kg)	54.1 ± 16.8	33.2 ± 2.6	36.9 ± 6.2	54.0 ± 17.8	62.4 ± 10.3	63.5 ± 12.2	70.5 ± 8.3
BSA (m^2)	1.54 ± 0.28	1.15 ± 0.06	1.25 ± 0.12	1.54 ± 0.23	1.72 ± 0.14	1.70 ± 0.17	1.80 ± 0.10
BSA:Mass (m^2/kg)	0.030 ± 0.004	0.035 ± 0.002	0.034 ± 0.003	0.030 ± 0.005	0.028 ± 0.002	0.027 ± 0.003	0.026 ± 0.002
Body fat (%)	17.5 ± 4.6	14.4 ± 4.1	14.1 ± 2.9	17.8 ± 6.0	17.5 ± 4.0	20.0 ± 3.9	21.2 ± 2.8
E_{req} (W/m^2)	154 ± 10	157 ± 13	150 ± 9	153 ± 14	157 ± 9	149 ± 9	162 ± 9
H_{prod} (W/m^2)	160 ± 10	164 ± 9	157 ± 10	159 ± 13	162 ± 10	153 ± 5	168 ± 9
H_{prod} (W/kg)	4.78 ± 0.75	5.72 ± 0.70	5.40 ± 0.78	4.72 ± 0.64	4.53 ± 0.43	4.16 ± 0.31*	4.31 ± 0.49*
H_{prod} (W)	247 ± 2	189 ± 21	196 ± 6	247 ± 50	280 ± 31*#	261 ± 35	301 ± 15*#
Mean T_{skin} (°C)	36.3 ± 0.3	36.6 ± 0.2	36.4 ± 0.2	36.1 ± 0.5	36.3 ± 0.2	36.2 ± 0.2	36.2 ± 0.3
$\Delta T_{Tympanic}$ (°C)	0.57 ± 0.27	0.62 ± 0.10	0.50 ± 0.27	0.63 ± 0.25	0.48 ± 0.32	0.68 ± 0.45	0.50 ± 0.16
WBSR (L/hr)	0.25 ± 0.09	0.20 ± 0.11	0.24 ± 0.08	0.21 ± 0.06	0.25 ± 0.08	0.30 ± 0.09	0.33 ± 0.07

*Values are presented as means ± SD, except for Tanner stage. BSA, body surface area; H_{prod}, rate of metabolic heat production; T_{skin}, mean skin temperature during exercise; E_{req}, rate of evaporation required for heat balance; $\Delta T_{Tympanic}$, delta change in tympanic temperature from start to end of exercise; WBSR, whole body sweat rate. *Denotes significant difference from 8 – 9yo, # denotes significant difference from 10 – 11yo ($p<0.05$)*

Relationship between age, local sweat rates, activated sweat gland density and sweat gland output

A statistically significant positive linear correlation was found between age and LSR at the 4 torso sites, namely the bra triangle (r = 0.858, $p < 0.0001$), abdomen (r = 0.602, $p < 0.001$), upper back (r = 0.481, $p = 0.010$), and lower back (r = 0.519, $p = 0.005$) (Figure 8-2). In contrast, no statistically significant correlation was found between age and LSR at the extremities, namely the hand (r = -0.295, $p = 0.127$), thigh (r = 0.242, $p = 0.215$), and shin (r = 0.242, $p = 0.214$) (Figure 8-2).

Subset analyses of HASGD at the bra triangle (n = 9) demonstrated no statistically significant correlations with age (r = -0.087, $p = 0.824$). Conversely, estimated sweat output per gland at the bra triangle had a statistically significant positive linear correlation with age (r = 0.865, $p = 0.003$) (Figure 8-3).

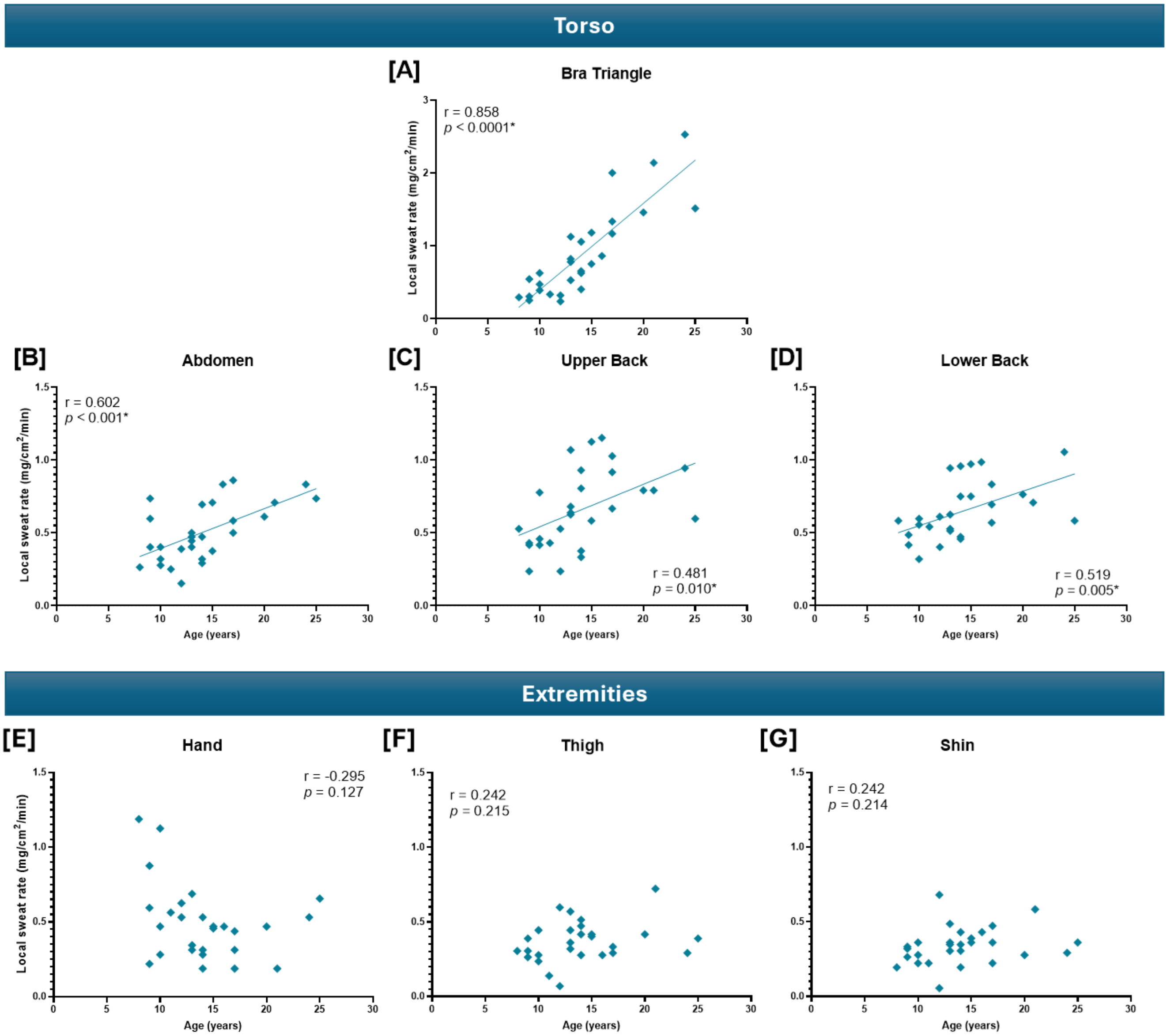

Figure 8-2. Relationship between age and local sweat rate at the torso sites (bra triangle [A], abdomen [B], upper back [C], lower back [D]) and the extremities (hand [E], thigh [F], shin [G]) (n = 28).

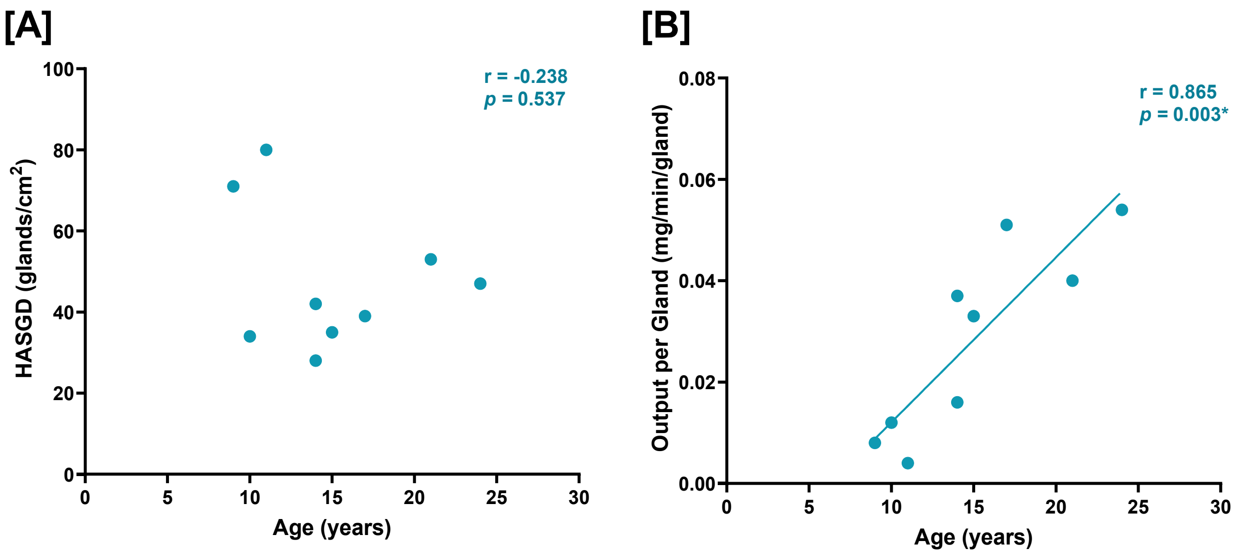

Figure 8-3. Relationship between age and [A] heat activated sweat gland density (HASGD), and [B] sweat output per gland at the bra triangle (n = 9).

Regional patterns of local sweat rates

Age groups: Statistically significant main and interactive effects of age groups and grouped body sites (torso vs. extremities) were observed for LSR (all $p \leq 0.001$). Post hoc analyses of interaction effects indicated no statistically significant differences in LSR between the torso and extremity sites for the 8-9yo ($p = 0.956$), 10-11yo ($p = 0.565$), and 12-13yo groups ($p = 0.095$). In contrast, a statistically significantly difference in LSR was found at the torso relative to the extremities, such that the torso had a 1.8-fold higher LSR than the extremities in the 14-15yo ($p = 0.003$); a 2.8-fold higher LSR than the extremities in the 16-17yo ($p < 0.001$); and a 2.4-fold higher LSR than the extremities in the 18-25yo ($p < 0.001$) (Figure 8-4A).

Tanner stages: Statistically significant main and interactive effects of Tanner stage and grouped body sites (torso vs. extremities) were observed for LSR (all $p \leq 0.001$). Post hoc analyses of interaction effects indicated no statistically significant differences in LSR between the torso and extremity sites at Tanner stage 1 ($p = 0.717$) and 2 ($p = 0.786$). In contrast, a statistically significantly difference in LSR was found at the torso relative to the extremities, such that the torso had a 1.9-fold higher LSR than the extremities at stage 3 ($p = 0.003$); a 1.7-fold higher LSR than the extremities at stage 4 ($p = 0.001$); and a 2.6-fold higher LSR than the extremities at stage 5 ($p < 0.001$) (Figure 8-4B).

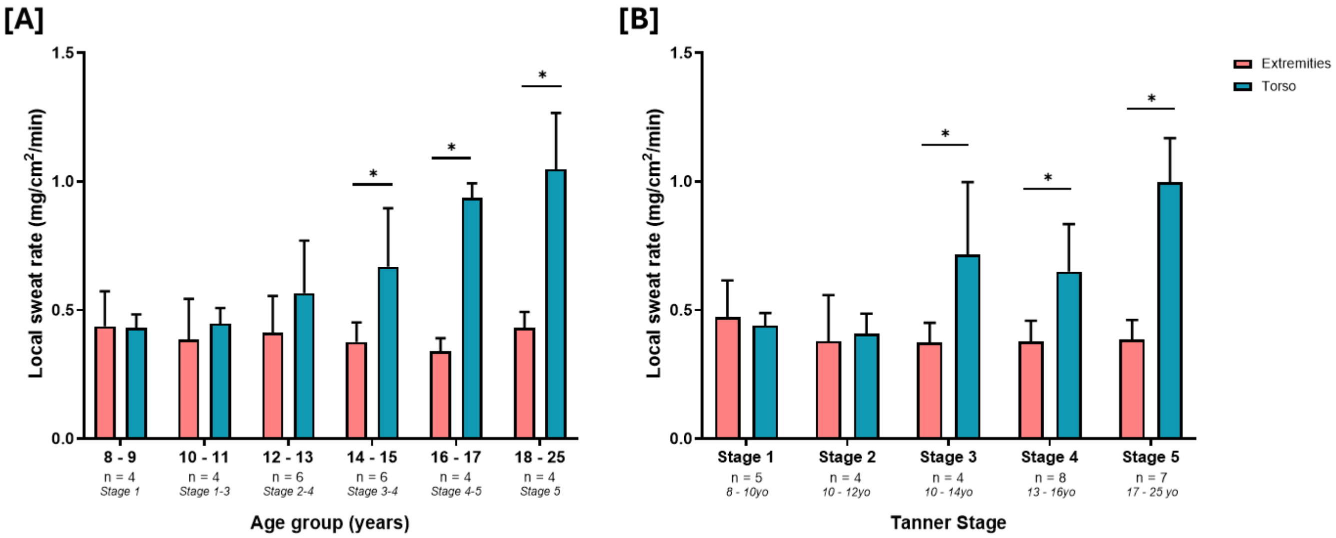

Figure 8-4. The effect of age [A] and tanner stage [B] on grouped local sweat rates (extremities vs. torso). Presented as mean and SD. *Significant difference between sites ($p \leq 0.05$).

Perceptual measures

Time was identified to have a statistically significant effect on TS ($p < 0.001$), WP ($p < 0.001$), and TC ($p < 0.001$) (Figure 8-5). Post hoc tests indicated no statistically significant effect of age group at any time point for TS or TC ($p > 0.05$). On average, participants felt “a bit warm” at baseline (median ± IQR; 1 ± 0) and increased to between “warm” and “hot” by the end of exercise (2 ± 1). All participants also felt “comfortable” at baseline (0 ± 1) and increased to between “a bit uncomfortable” and “uncomfortable” by the end of exercise (2 ± 1). Post hoc tests for WP showed no statistically significant effect of age group at min 0, 20, 30 ($p > 0.05$), with all participants feeling “dry” at baseline (0 ± 0.25) and increasing to “wet” by the end of exercise (2 ± 0). However, at minute 10, WP was statistically significantly lower in 10-11 yo (0 ± 0.25) than all other age groups (1 ± 0) ($p = 0.012$).

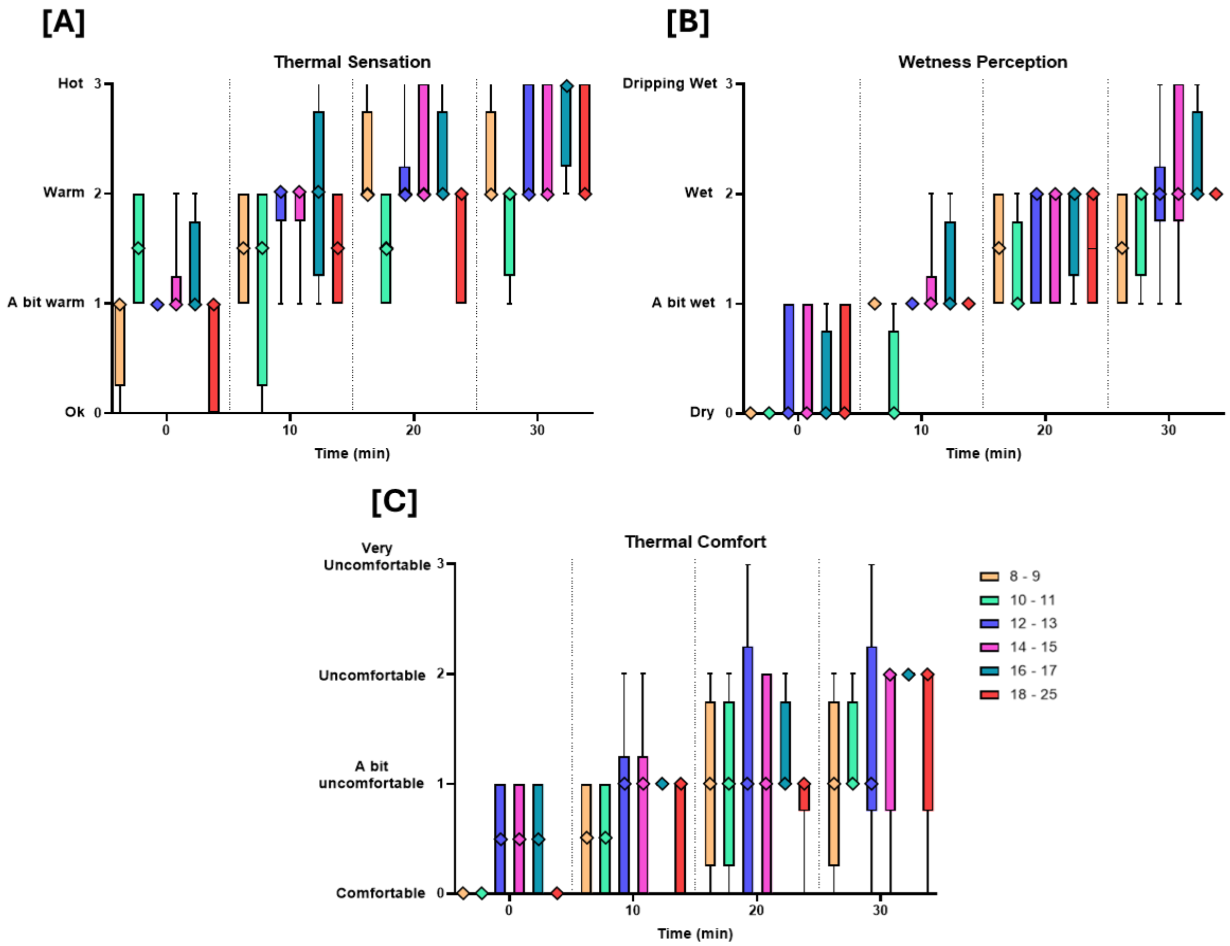

Figure 8-5. Box plots displaying thermal sensation [A], wetness perception [B] and thermal comfort [C] measured at 4 time points and grouped by age. Data presented as median (diamond symbol), interquartile range (box) and min/max (error bars).

○ Discussion

The aim of this study was to investigate how and when complete maturation of local sweating mechanisms across the whole-body occurs throughout puberty in females, and how these age-dependent changes may relate to variations in children' sensitivity to thermal discomfort, during exercise in the heat. In line with our primary hypotheses, our results indicated that LSR across the torso (i.e. chest, abdomen, upper and lower back), but not the limbs (hand, thigh, shin), increased linearly with age (see Figure 8-2), due to age-dependent increases in sweat output per gland (see Figure 8-3B). The transition of regional sweating patterns from children-like (i.e. higher LSR at extremities than torso) to adult-like (i.e. higher LSR at torso than extremities) became apparent and meaningful (i.e. 2-fold difference between torso and limbs) at a specific developmental stage associated with Tanner stage 3 and a chronological age of 14-15yo (see Figure 8-4). Our results also indicated that perceptions of temperature, wetness and thermal comfort during exercise in the heat did not differ across age-groups. Altogether, these findings are novel and important, as they provide the first detailed accounting of the maturation of regional sweating patterns across the body in females exercising in the heat.

Maturation of sweating

The regional sweating patterns observed in our oldest female cohort (i.e. 18-25 yo) aligns with the findings of Smith and Havenith (2012), who reported women (i.e. 21±1 yo) to present higher LSR at the torso than the limbs. Similarly, the regional sweating patterns observed in our youngest female cohort (i.e. 8-9 yo) support the findings of Arlegui et al. (2021), who reported girls (i.e. 8 yo) to present higher LSR at the extremities (forehead, hands, feet) than the rest of the body. Our detailed evaluation of regional sweating patterns across the full pubertal development period in women (i.e. age range 8 to 25yo and Tanner stages 1 to 5) critically extends those previous insights to demonstrate a specific developmental stage associated with sweating maturation in women, who are a group that undergo unique hormonal changes during puberty and throughout the lifespan.

Previous evidence has indicated that key hormonal changes occur when girls reach Tanner stage 3, such as a 20 to 40-fold increase in luteinizing hormone relative to pre-pubertal stages, which in turn causes a rise in circulating oestradiol levels for the first time in female development (DiVall & Radovick, 2009; Rosenfield et al., 2013). Increased circulating oestrogens in humans have been demonstrated to increase heat dissipation responses, including cutaneous vasodilation and sweating (Stephenson & Kolka, 1999). Elevated oestrogen levels during the female menstrual cycle, unopposed by progesterone, have also been associated with small decreases in female body temperature; an observation which further highlights the role of oestrogens in modulating heat exchange and body temperature in females (De Mouzon et al., 1984; Marshall, 1963). While hormone levels were not measured in this study, oestrogen levels have been previously shown to correlate well with Tanner staging (Frederiksen et al., 2019). Hence, our observation of a critical maturation stage for changes in regional sweating patterns coinciding with Tanner stage 3 in our female cohort is likely to be associated with hormonal changes occurring at this stage of puberty. This may have led to the observed upregulation of sweat output per gland over the torso (i.e. bra triangle) of our participants. It is important to note that the onset and rate of pubertal development can vary individually based on genetics, intrauterine events, stress, nutrition and socioeconomic conditions (Day et al., 2015; Hochberg, 2009). Future mechanistic studies may incorporate evaluation of the levels of circulating sex hormones to more directly establish causality between hormonal development and sweating maturation.

The observation of an upregulation of sweat output per gland during pubertal development of girls (see Figure 8-3B) greatly extends our current understanding of the mechanisms underlying maturation of evaporative heat loss responses in humans. Our observations correspond with the findings of Amano et al. (2025), who has recently reported increases in sweat output per gland at the forearm during puberal development in children. In their study, the authors used pharmacological (i.e. cholinergic agonist) stimulation of sweat glands in resting children to evaluate maturation of post-synaptic sweating, independently of the centrally-mediated drive to sweat production that occurs during exercise-induced elevations in body temperature (Saltin & Gagge, 1971; Shibasaki & Crandall, 2010). By adopting an exercise model in the heat, our study provides novel evidence that the upregulation of sweat output per gland during pubertal development observed by Amano et al. (2025), is also observed when a centrally-mediated drive to sweat production occurs during exercise in the heat. Although both studies were not designed to interrogate the mechanisms underlying the observed upregulation of sweat output per gland, similar hypotheses can be proposed such that age-dependent changes are likely the result of a combination of anatomical development of the sweat gland (sweat gland duct length and secretary coil area) (Sato & Sato, 1983) and an increased exposure to circulating growth and sex hormones, for which eccrine sweat glands express receptors (Choudhry et al., 1992; Lobie et al., 1990; Pelletier & Ren, 2004).

From a methodological standpoint, the present study provides a more rigorous mechanistic evaluation of age-dependent change in LSR patterns during exercise than previous research to date. For example, Smith and Havenith (2012) and Arlegui et al. (2021) leveraged experimental models using exercise prescribed at a fixed percentage of maximal HR or VO_{2max} to study LSR patterns. Conversely, our study adopted an exercise prescription designed to achieve equal levels of E_{req} in W/m^2 across all age groups (see Table 8-1). This is because individual variations in E_{req} in W/m^2 (which can occur when exercise is prescribed at a fixed percentage of maximal HR or VO_{2max}) have been demonstrated to drive the greatest proportion of variance in LSR. Indeed, if exercise is not prescribed at a fixed E_{req} in W/m^2 across all groups, potential group-dependent biases in sweating mechanisms may occur (e.g. children vs. adults) (Cramer & Jay, 2014, 2015).

Maturation of thermal perception

Our observations on the maturation of sweating in girls, and their relevance for our basic understanding of autonomic body temperature regulation, is well complemented by our results on the perceptual responses of our female cohort during exercise in the heat. This is particularly important given the paucity of evidence on thermal sensation of children in the heat. Inoue et al. (2009) has previously observed similar thermal sensations between boys (9-11yo) and men during passive heat exposure (from 28°C to 40°C), for the same change in T_{sk}. Our results extend these findings to exercising females, as our girls presented equal thermal sensations and discomfort to adult females under exercising conditions resulting in similar elevations in mean T_{sk} (i.e. ~36 °C - see Table 8-1). These observations indicate that younger girls are likely to be equally as sensitive to warmth and discomfort than their older counterparts. Furthermore, our findings indicated that perceptions of whole-body wetness during exercise in the heat did not differ across age-groups. One could speculate that this provides evidence that younger girls may have a greater wetness sensitivity than older girls as this same magnitude of perceived wetness in the younger girls occurred in the presence of much lower LSR at certain body sites. This theory may not be entirely speculative, as our group has recently observed boys and girls aged 7 to 12 yo to report greater wetness perceptions than adults during the application of the same local wet stimuli onto their skin while at rest (Valenza et al., 2025). However, future studies would have to investigate further whether this potential age-dependent variation in whole body wetness perception in girls is indeed robust and whether this impacts meaningful age-dependent differences in thermal behaviours under a paradigm that allows free behaviour (e.g. cool-seeking, drinking, etc.) (Schlader & Vargas, 2019).

Public health and industrial applications

Beside their relevance to understand the basic biological mechanisms underlying sweating maturation and perception in females, we believe that our findings have important implications for public health and industrial applications.

From a public health messaging standpoint, the American Academy of Paediatrics (Bergeron et al., 2011) has recently issued a position statement suggesting youth have an equally effective thermoregulatory ability as healthy adults and therefore are not at a "thermoregulatory disadvantage" during exercise in the heat (Davies, 1981; Drinkwater et al., 1977; Meyer et al., 1992; Rivera-Brown et al., 2006; Wilk et al., 2013). Our observations on the presence of lower LSRs across the torso in our youngest girls, secondary to lower sweat output per gland and despite the same E_{req} in W/m^2, may at first appear in contrast with the American Academy of Paediatrics' position, i.e. those younger girls were locally secreting less sweat than needed to meet the evaporative requirements for heat balance. Yet, despite these lower LSRs across the torso, and the fact that these younger girls were exercising at a greater level of heat production per unit of body mass than the older girls (i.e. 5.72 vs. 4.31 W/Kg – see Table 8-1), they did not develop a greater change in core (tympanic) temperature than their older counterparts (see Table 8-1). This observation aligns with recent evidence from Smallcombe et al. (2025), who also found children aged 10-16 to be at no greater risk of hyperthermia than adults during exercise in ambient temperature of up to 40°C. We speculate that this apparently effective maintenance of heat balance in children, despite developing sweating mechanisms, may be supported by a body morphology (e.g. higher body surface area to mass ratio – see Table 8-1), which could favour heat distribution across the body and dissipation with the environment.

From an industrial standpoint, our observation of a critical age for changes in regional sweating patterns in girls has important applied implications for the sportswear industry, which leverages knowledge of LSR patterns to guide the design of clothing that satisfies the thermal requirements of the user. It is important to note that clothing is commonly designed based on age ranges for specific consumer groups (i.e., kids vs. adults), rather than stages of hormonal development (e.g. Tanner stages). As age and tanner stages were strongly correlated in our study cohort, it allowed us to consider the critical stage for changes in regional sweating patterns in girls as a function of chronological age (see Figure 8-3A). This analysis indicated that a ~2-fold difference in LSR between torso and extremities became apparent in the age group 14-15 yo, which included girls spanning Tanner stages 3 to 4. Consequently, we believe that the meaningful shift in regional sweating patterns observed at 14 yo could inform design considerations such as the need for greater moisture management for the torso vs. limbs from this age onwards, to help maximise comfort for adolescent girls. This approach may have broader benefits, such as improving exercise participation at a time when factors such as body appearance (e.g. perceived sweatiness) may in part contribute to sport drop out in girls (Eime et al., 2016; Ogden et al., 2025). This may ultimately increase clothing comfort and performance, thus reducing barriers to participation in sport for women of all ages in a warming climate.

Limitations

There are limitations to this study. First, our study cannot establish the extent by which the observed differences in LSRs in younger vs. older girls may differentially impact the maintenance of heat balance at both lower ambient temperatures than we tested, as well as under greater thermal stress, i.e. uncompensable heat stress. Indeed, previous research has indicated that children may have an increased dependence on dry heat loss mechanisms to compensate for a less developed sweating capacity (Davies, 1981; Drinkwater et al., 1977). Our experiment was designed to maximise the reliance on evaporative heat exchange and minimise reliance on dry heat exchange, which was achieved by setting the environmental temperature to a level equal to skin temperature during exercise (i.e. 36°C). Future studies may therefore consider exposure to ambient conditions that may highlight a “thermoregulatory advantage” of children under less warm conditions, where the larger body surface area to mass ratio of younger children may favour dry heat exchange mechanisms and facilitate water conservation. Future studies may also consider different exercise modalities such as running, which may facilitate achieving greater levels of heat production than cycling and associated sweating requirements. We indeed noted in our investigation that the absolute level of cycling workload was primarily limited by the level of leg strength of our youngest participants (i.e. higher workload to induce higher thermal loads were not achievable due to early onset fatigue).

- ## Conclusion

Our study provides the first detailed accounting of the maturation of regional sweating patterns across the female body, a commonly underrepresented cohort in thermoregulatory studies. We provide novel evidence that the maturation of regional patterns of LSR occurs primarily because of linear increases in LSR across the torso but not the limbs; and at a particular stage of maturation, which we identified to coincide with Tanner stage 3 and 14-15 years of age. We also provide evidence that perceptions of temperature, wetness and thermal comfort during exercise in the heat did not differ across age-groups. Our results advance our fundamental understanding of the maturation of sweating in females, and they also have important applied implications for person-centred public health messaging and sportwear design.

Chapter 9 Industrial Placements – Nike World HQ

Throughout the course of my PhD studentship, I completed two 3-month secondments to the Nike Sport Research Lab (NSRL) in Portland, Oregon in the USA (Figure 9-1). During these periods working at the NSRL, I performed 3 studies using new, inter-disciplinary techniques that would have otherwise been unavailable to me, I presented results to senior leadership audiences - including product innovation teams thus translating science into practical product-oriented insights for stakeholders and gained great insight into how research is performed in an industry setting.

Included in this chapter is the outline of one of the studies I delivered at the NSRL as well as a brief overview of the findings (Section 9.1). However, due to industry confidentiality, information from the other two studies undertaken at the NSRL has been redacted. Following this is an executive summary on the impact of PhD and secondment research written by Dr Grant Simmons, Nike Senior Principal Researcher – Thermoregulation (Section 9.2).

Figure 9-1. Nike World Headquarters, including the LeBron James Innovation Centre that houses the NSRL.

9.1 Determining wind speeds for thermal manikin testing of apparel innovations.

This study was the second of two studies I performed during my first visit to the Nike Sport Research Lab, Portland, USA between October 2023 – December 2023. This experience allowed for training on the use of thermal manikins in for applied apparel research and the chance to conduct a study investigating the effect of different levels of air flow on thermal and evaporative resistance.

ABSTRACT

Evaporative resistance (R_{ET}) is a widely used metric to describe clothing evaporative heat transfer properties. Sweating thermal manikins allow for fast and controlled evaluations of clothing R_{ET}. The ASTM standard recommends performing manikin testing at a wind speed of 0.4m/s. However, when evaluating the evaporative properties of sportswear, which may be used when running for example (i.e. at higher wind speeds), testing at different wind speeds could provide greater ecological validity. We aimed to investigate the effect of wind speed and garment ventilation on thermal manikin R_{ET}.

Upper body R_{ET} was measured using a male and female articulated thermal manikin (Thermetrics, Seattle, USA) (Figure 9-2). Testing was performed at 3 wind speeds (0.4, 1.6, 2.8m/s), comparing 2 garments (two versions of a light mid-layer shirt; solid and 20% perforated for ventilation), with each condition tested in triplicate. R_{ET} was averaged over replicates; mean and SD values were compared to investigate wind speed and garment ventilation effects.

R_{ET} decreased with increasing wind speeds in the male (0.4m/s = 15.9 ± 0.3Pa.m^2.W^{-1}; 2.8m/s = 7.8 ± 0.2Pa.m^2.W^{-1}) and female (0.4m/s = 18.5 ± 0.7Pa.m^2.W^{-1}; 2.8m/s = 10.6 ± 0.1Pa.m^2.W^{-1}) manikin. Perforations reduced R_{ET} at all wind speeds for both male and female manikins. A greater difference in R_{ET} due to perforations was observed at lower windspeeds than higher windspeeds in the male (ΔR_{ET} at 0.4m/s = 3.34 ± 0.7Pa.m^2.W^{-1}; ΔR_{ET} at 2.8m/s = 1.52 ± 0.3Pa.m^2.W^{-1}) and female manikin (ΔR_{ET} at 0.4m/s = 4.12 ± 0.5Pa.m^2.W^{-1}; ΔR_{ET} at 2.8m/s = 2.87 ± 0.1Pa.m^2.W^{-1}).

Our findings indicate that changes in windspeed can have considerable effects on R_{ET} as previously shown. When considering sports apparel design, for which ventilation is an important factor, testing at lower windspeeds facilitates greater R_{ET} discrimination between garments. Yet

application depends on the experimental goal; discrimination (i.e. lower windspeeds) or ecological validity (i.e. wind speeds relevant to the garment purpose).

Figure 9-2. Male and female thermal manikins in the climate chamber.

9.2 Executive Summary of Nike Impact – Dr Grant Simmons

NIKE EXPLORE TEAM
SPORT RESEARCH LAB

As part of this PhD programme, Hannah Blount undertook two "Scholar in Residence" placements embedded within the Thermoregulation Research Team at the Nike Sport Research Laboratory (NSRL), Beaverton, USA, during Fall 2023 and Spring 2025. In total, these placements amounted to six months of in-residence research collaboration within an advanced industrial innovation environment.

The goal of these NSRL residency periods was twofold: deliver value to Hannah through experience conducting athlete- and product-focused research in an advanced innovation setting; and deliver tangible value to Nike through interaction and collaboration with an energetic trainee, complementing her academic training at the University of Southampton. A further benefit of the residency periods was extended academic and applied research engagement across North America, including visits and invited presentations at leading academic and military research institutions, notably:

- University of Oregon
- US Army Research Institute of Environmental Medicine (USARIEM)
- Brock University

These engagements strengthened knowledge exchange between academic, military, and industrial research communities.

Developmental Opportunities for the Doctoral Researcher

During her residence within the NSRL, Hannah gained advanced technical, methodological, and translational research experience, including:

- **Advanced product evaluation techniques**
    - Training in the use of sweating thermal manikins to quantify the thermal properties of apparel under controlled environmental conditions (Section 9.1).
- **Integrated, multidisciplinary research design**
    - Design and execution of studies combining biomechanical (motion capture), physiological, and thermoregulatory methods to address priority questions for female athletes.
    - Leadership of the first study conducted at Nike to integrate motion capture with environmental chamber testing, examining the intersection of breast motion during running and thermoregulatory sweating responses (Figure 9-3).
- **Translation of physiology to product innovation**
    - Direct exposure to how physiological research is used:
        - Strategically, to guide future product innovation pathways.
        - Tactically, to inform current product development decisions linked to measurable athlete benefits.
- **State-of-the-art thermal measurement**

- Hands-on experience with advanced thermal assessment techniques used to characterise athlete heat responses and apparel performance within NSRL environmental chambers (Figure 9-3).

Figure 9-3. Climate chamber equipped with VICON motion capture.

Value Delivered to Nike

Hannah's residency periods generated clear and actionable value for Nike's research and product innovation objectives, including:

- **Experimental design guidance**
    - Provision of evidence-based recommendations for thermal manikin testing protocols. The results of a thermal manikin study conducted by Hannah set the target windspeeds for testing products based on their intended use (e.g. running apparel vs. lifestyle / sportwear) (Section 9.1).
- **Novel research on sports bra performance**
    - Execution of a first-of-its-kind study investigating the effect of sweat on sports bra support during running, using innovative experimental methods.
- **Identification of new innovation opportunities**
    - Execution of a research study examining the impact of performance tops on sweating efficiency in humid heat.

- This study identified a previously unrecognised opportunity for innovation and athlete benefit in humid conditions.
- This finding was exciting and has since been replicated in three independent studies (as of January 2026), confirming the robustness and relevance of the original finding.

Strategic Relevance of the Doctoral Research to Nike

The central focus of Hannah's doctoral research aligns closely with Nike's product innovation strategy of leveraging scientific insight into athlete–product interactions to create disruptive products and services that improve athlete experience and performance.

At Nike we recognise that the interaction of sweat with the sports bra is a major challenge and opportunity for our women's consumer. However, it isn't clear when developmentally – in the transition from KIDS consumer to WOMEN'S consumer – this product problem emerges. Hannah's research was designed to expand our understanding of female consumers, and their product needs, across their developmental journey. This work has the potential to open the door for new product designs, possibly expanding material options based on the relative importance of moisture management (over the chest) at a given age or developmental stage.

Chapter 10 Conclusions, Applications & Further Research Directions

○ Thesis summary

The aim of this PhD project was to broaden our fundamental understanding of how females regulate their body temperature during exercise in the heat and of how the complex hormonal and developmental stages of a female's life impacting their morphology (e.g. breast development and puberty) alter these thermophysiological responses. These findings can have multiple applications, including the improvement of female sports apparel design, from childhood to adulthood, the improvement of bra design for women of varying breast sizes, and the improvement of thermoregulation models for females that include a more evidence-based approach to the investigation of heat transfer and sweat production during female puberty and across the female breast.

The literature review found gaps in our current knowledge and understanding of thermoregulation related to specific characteristics of female hormonal and morphological development. From here, experimental methodologies were designed to firstly investigate the impact of breast size-related differences under the lens of thermoregulation, perception and skin mechanical properties at rest and during exercise in a warm environment. The breast being an area of unique and understudied female anatomy which develops during puberty with large heterogeneity across females and can act as a significant barrier to exercise participation. Following on from this, the second study investigated how patterns of sweating responses develop during female puberty - a significant time of exercise drop out for girls. Together, these findings provide a novel and insightful overview of how thermoregulation is impacted by female hormonal and morphological development when exposed to warm environments, which is of substantial value when one considers our warming climate. A schematic summary of the PhD can be seen in Figure 10-1.

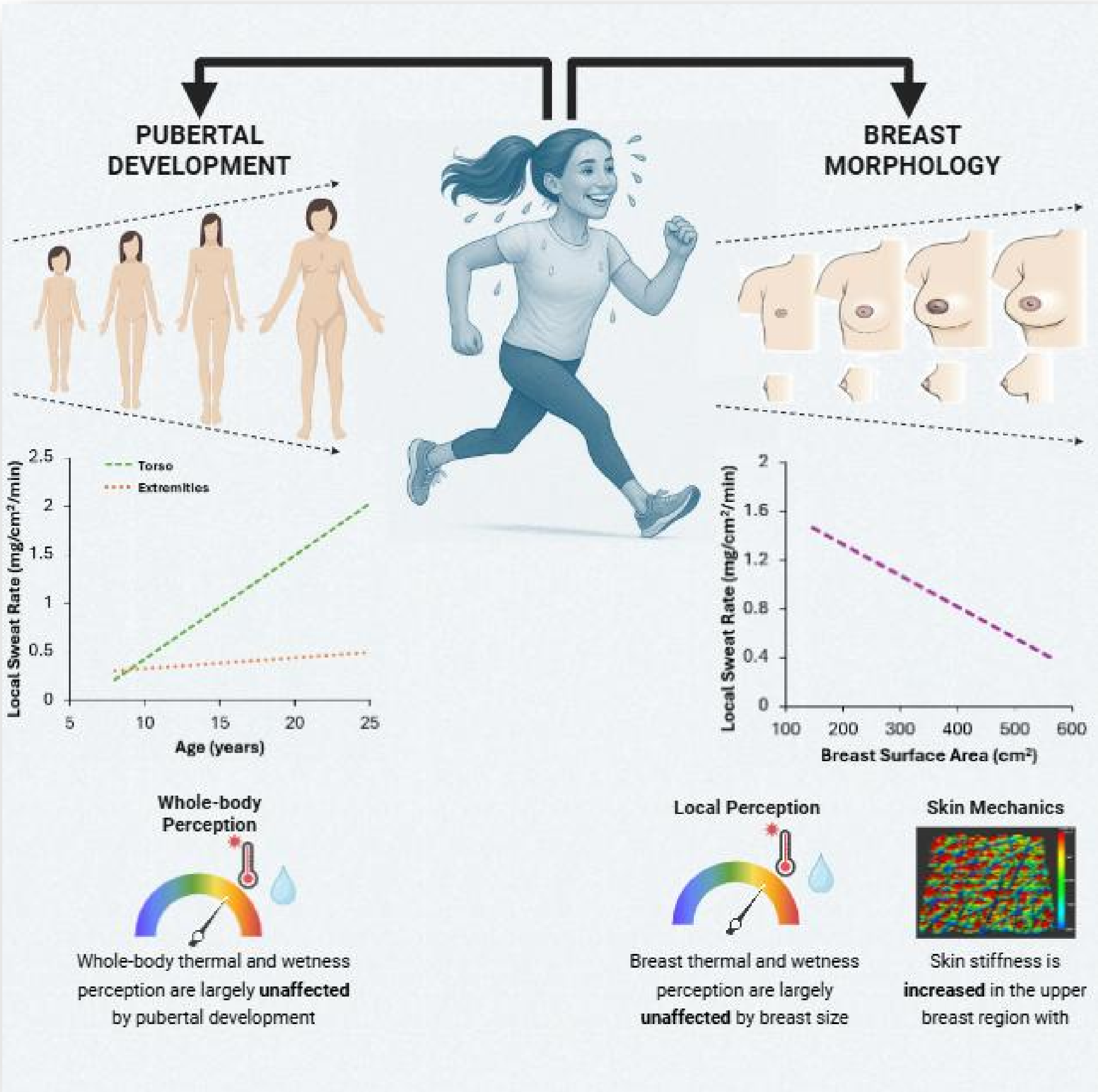

Figure 10-1. A summary of the PhD project key take-home messages.

○ Original contributions to knowledge

The PhD project was broken down into two main experimental blocks to assess female thermoregulation across the life span during exercise in hot environments; the impact of breast size variation (Chapter 5, Chapter 6, Chapter 7), and the impact of puberty (Chapter 8).

- **Breast size variations**

The series of studies presented above (Chapter 5, Chapter 6, Chapter 7) (i.e. (Blount et al., 2024a, 2024b, 2024c) aimed to shed light on this multidimensional question; how and when does breast size matter when considering thermoregulatory, mechanical and perceptual properties of the breast? By integrating findings on sweat regulation, sensory perception, and mechanical skin properties, these studies collectively aimed to address gaps in knowledge about female-specific thermoregulation and sensation influenced by breast size. Broadening this fundamental physiological knowledge aimed to improve activewear design to mitigate barriers to exercise, enhance comfort, and support an active lifestyle for women.

Using exercise heat stress to drive sweating, individual differences in breast surface area were observed to modulate both sweat gland density and local sweat rates in healthy young to middle-aged females. Sweat production was concentrated at the bra triangle - an area where sweat gland density and local sweat rate are unaffected by breast size. Yet, when looking across the actual breast, as breast size increases, sweat gland density and local sweat rates decreased (Chapter 5)(Blount et al., 2024b). These findings confirmed the established relationship between sweat gland density and body morphology (Section 2.5.7), and they further extended this observation to the female breast. Previous evidence in the literature would suggest that biophysical parameters (i.e. sweat gland density) often share similar patterns to neural receptor density, such that perceptual sensitivities may mirror the sudomotor (i.e. sweating) relationship with changes in morphology across the breast (Cotter & Taylor, 2005). As the breasts grow in later life, following nervous system development (Javed & Lteif, 2013) and when the number of sweat glands is set (i.e. age 2)(Kuno, 1956), it is possible these relationships may have been similar. However, this was not consistently found to be the case. Variations of thermal sensitivity and wetness perception due to breast size appear to be skin site specific (i.e. above the nipple) and perceptual modality dependant (i.e. warm sensitivity), rather than being a generalised feature of the skin covering the female breast (Chapter 6)(Blount et al., 2024a). Such that as breast size increased, warm sensitivity measured through quantitative sensory testing decreased in the upper breast region only. These findings align to previous studies which have also reported uneven thermal sensitivity across the breast (Terzis et al., 1987; Valenza et al., 2023). Furthermore, irrespective of breast size, thermal and wetness sensitivity over the breast did also appear to be homogenous, except for, again, the skin site above the nipple which presented reduced cold sensitivity compared to other breast sites. From a skin mechanics perspective, the above nipple region was also found to be the main area of interest, as skin stiffness was found to increase with increased breast size (Blount et al., 2024c), likely due to higher skin strains in larger breasted women. Yet no effect of breast size on skin stiffness was found in the lower breast region.

A consistent finding across my experimental chapters relating to the breast (Chapter 5, 6, 7) is that the upper breast region is an area whose thermoregulatory, perceptual and mechanical properties are regularly impacted by breast size. Yet, the extent to which these changes are related is open to questioning. It seems logical that a reduction in sweat gland density with increased breast size demonstrates an amount of skin stretch, which in turn, is likely to cause increased skin strain and thus stiffness (Choo et al., 2010; Joodaki & Panzer, 2018). This relationship was clearly observed in the upper breast region in our studies. Yet despite a size-dependent relationship with sweat gland density in the lower breast region, we observed no size-dependent relationship with skin stiffness in this area. The observed site differences in skin stiffness in relation to breast size are likely due to variability in breast skin strain which have previously been shown to be are greatest in the upper, lateral breast region (Norris et al., 2020). As such, we hypothesised that, despite being stretched with growth, the lower breast region is likely to be under lower mechanical load (i.e. it is required to bear less of the breast tissues load) which could in turn reduce any size-dependent effect on skin stiffness (Choo et al., 2010). What remains somewhat ambiguous is the observation that thermal and wetness sensitivity did not consistently change with breast size. If a size-dependent relationship existed with thermal and wetness sensitivity, one would expect to see this pattern across the whole breast, similar to the relationship between sweat gland density and breast surface area. However, given only one breast region, with one thermal modality reflected a relationship with breast size, we can infer that this size-dependent relationship is not a generalised feature of the breast. A plausible reason for this would be due to the breast's secondary role in sensory function. We hypothesize that the dispersion of thermoreceptors may be sparse such that the ability to quantify sensation is more limited across this region compared to other body sights which are more thermally sensitive, such as the hands. Hence, we are less likely to see a breast size-dependent effect.

When considering the question "does breast size matter?", in light of our collective findings, the answer appears to be 'yes' in relation to the sweating apparatus and the skin mechanical properties of the upper breast region only. However, the answer may also be "no", in the case of breast thermal and wetness perceptions at rest.

These initial, fundamental findings have increased our understanding of the impact of breast size on skin properties, and this knowledge could inform tailored considerations in sportswear design, targeting specific regions of the breast to optimize comfort and function from a thermal and mechanical perspective for women of varying breast sizes.

- **Puberty**

Within the literature, there is currently limited knowledge on how regional sweating patterns develop from childlike to adultlike patterns during puberty. No studies have directly assessed how and when regional patterns of LSR in girls start to resemble those of women throughout pubertal development, nor have these studies prescribed exercise at an intensity to allow unbiased comparisons of sweating responses. Within Chapter 8 of this thesis, regional sweating patterns (LSR and heat activated sweat gland density) in girls from age 8 to young adulthood were assessed in a warm environment (36 ± 0.2°C; 48 ± 2% RH) when exercising at a fixed E_{req} (154 W/m^2) to minimise the biophysical bias when comparing local sweating responses. Technical absorbent pads were applied to the skin to measure LSR over a 5-minute period at the end of exercise, followed by the modified iodine technique to measure heat activated sweat gland density.

The results of this provide the first detailed accounting of the maturation of regional sweating patterns across the body in females, building upon the previously known discrete differences between pre-pubertal and adult female sweating patterns (Section 2.5.3)(Arlegui et al., 2021; Smith & Havenith, 2012). We provide novel evidence that in females, LSR across the torso (i.e. chest, abdomen, upper and lower back), but not the limbs (hand, thigh, shin), increased linearly with age during adolescence, due to age-dependent increases in sweat output per gland. These results advance our understanding beyond that of Amano et al. (2025) by demonstrating that age-dependent increases in sweat output per gland occur not only during cholinergic-agonist-induced local sweating, but also through heat-stress–induced autonomic stimulation. Furthermore, the results of this study showed that the transition of regional sweating patterns from child-like (i.e. higher LSR at extremities than torso) to adult-like (i.e. higher LSR at torso than extremities) became apparent and meaningful (i.e. 2-fold difference between torso and limbs) at a specific developmental stage associated with Tanner stage 3 and a chronological age of 14-15 years old. The results also indicated that perceptions of temperature, wetness and thermal comfort during exercise in the heat did not differ across age-groups. The results therefore advance our fundamental understanding of the maturation of regional sweating patterns in females, as well as having important applied implications for person-centred public health messaging and sportwear design.

Applications of the findings

As discussed in each chapter, the outcomes of this Thesis have several fundamental and applied implications.

From a fundamental perspective, the findings of this Thesis expand our knowledge on the thermoregulatory responses (physiological and perceptual) occurring in females in warm environments, with the consideration of the hormonal and morphological development unique to the female life course.

The principal application of this research was to inform the design of improved and more user-centred sportswear for females. The findings of this Thesis have proven useful to Nike, as outlined in their impact statement (Section 9.2). This research has provided Nike with information to leverage scientific insight into athlete–product interactions and allow them to create products and services that improve athlete experience and performance. The assessment of local sweating patterns, thermal and wetness perceptual ratings and skin temperatures have considerable value in the design process. For example, local sweating data across the breast of women with varying breast size (Chapter 5) indicated that women with larger breasts had lower local sweat rates across this area than women with smaller breasts. Hence highlighting the need for size-based sports bra design, whereby larger bras should be designed to focus less so on moisture management, and more so on providing mechanical sport to reduce movement and skin strains (McGhee & Steele, 2020; Scurr et al., 2010), whereas smaller bras - where discomfort due to movement is less common - should focus more on moisture management due to their higher LSR. In addition, these results underscore the importance of incorporating region-specific material selection. For example, using targeted water-vapour-transfer fabrics in areas of higher sweat production could better accommodate the heterogeneous sweating patterns observed across the breast.

Furthermore, regarding the development of sweating patterns during female puberty (Chapter 8), the data in this Thesis indicated that at a particular stage of maturation, which we identified to coincide with Tanner stage 3 and age of 14, LSR across the torso became significantly greater than that across the limbs, to reflect sweating patterns seen in adult females. Thus, highlighting a critical age at which sportswear product characteristics, relating to clothing thermal insulation and moisture management properties, needs to adapt to better support adolescent females during a time of increased exercise drop-out (Howard, 2024; Slater & Tiggemann, 2010; Zarrett et al., 2020). Again, region-specific design to incorporate targeted material technologies over the torso in adolescent sportswear - where sweat production increases markedly - may better align garment performance with physiological needs.

Lastly, the findings highlighted in this Thesis have application into the design of thermal manikins and thermoregulatory modelling by providing empirical data of sweating distribution patterns at different stages during female puberty, as well as highlighting thermoregulatory and mechanical variations in relation to breast size. Thermal manikins are regularly used in the clothing design validation phases (e.g. moisture management or insulation assessment – Section 9.1). In order to perform an effective product validation, it is first necessary to understand the unique physiology of the user.

- **Recommendations for future research**

The current research has expanded our knowledge on female thermoregulatory responses and perception. However, as with any research study, there are a series of limitations which have generated potential avenues for future research studies as described below.

From an applied perspective, a limitation of the present work is that it did not fully examine how sweat produced at the skin migrates into and interacts with clothing systems. Future research should investigate how the variations in local sweat rates identified in this Thesis - both across different breast sizes and throughout puberty - affect sweat accumulation patterns within garments. Understanding how these physiological and morphological differences influence moisture retention, fabric clinging, mechanical support, thermal comfort, and perceived discomfort would provide critical insights for sportswear designers. Such work would support the translation of these physiological findings into evidence-based, user-centred design solutions, enabling the development of bras and garments that better match the thermoregulatory and mechanical needs of diverse female populations.

A further limitation relates to the mechanistic understanding of why regional sweating patterns change during puberty. While, the results from Chapter 8 provided novel insights into the clear developmental shifts in local sweat rates, the underlying drivers of these changes could not be fully explored because hormonal development was assessed using self-reported Tanner staging rather than direct physiological measures. Future research should incorporate endocrine assessment, such as serum hormone sampling, to examine how hormonal fluctuations contribute to the maturation of sweating pathways. Furthermore, the results from Chapter 8 only provide us insight to sweating responses during compensable heat stress, when the requirement for sweating can be achieved. What would be of interest would be to design an exercise protocol to elicit higher metabolic heat, or to manipulate environmental conditions to induce a state of uncompensable heat stress. Such an approach would force near-maximal sweating responses, thereby allowing us to examine how maximal sweating capacity develops across puberty in females - a question that currently remains unexplored. Unlocking this information would provide important insight into the upper limits of heat loss through sweating during maturation, as well as the relative contribution of dry heat loss pathways in children. This is particularly relevant given the hypothesis that dry heat exchange plays a more prominent role in younger children (Section 2.5.4), before sweating capacity is fully developed. However, these proposals may come with possible ethical restrictions. Ethical review boards may be challenged to accept study designs that have increased invasiveness with regards to blood sampling and the need to measure core temperature (i.e. rectal probes or gastro-intestinal pills) if pushing children to uncompensable heat stress, as well as the safety concerns and health risk when pushing children to uncompensable heat stress.

A final limitation concerns the breadth of female life stages included in this Thesis. Due to the constraints of the PhD timeframe, the work focused on selected developmental periods, leaving considerable gaps in our understanding of thermoregulation, heat tolerance, and thermal comfort at other key phases of the female life course. Notably, there remains limited evidence relating to pregnancy, peri-menopause, and post-menopause. These female groups remain underserved by the research which can carry considerable health risks and barriers to exercise participation to maintain an active lifestyle. For example, current advice for pregnant women with regard to heat exposure is sparse, inconsistent and not evidence based (Samuels et al., 2022). Important questions remain to be answered including does heat exposure at different gestational ages cause different effects; is there a dominant physiological mechanism relating to increased heat risk during pregnancy that can be targeted for an intervention; does heat-stress exposure exert an effect on pregnancy outcomes in a dose-dependent manner. It is important to understand the mechanisms by which pregnant women and babies are impacted by heat stress for interventions to avoid poor outcomes. Further research is therefore essential to ensure that clear, evidence-based guidance can be provided to females across all stages of life, as well as to healthcare professionals, policymakers, and clothing designers. Such work is crucial to helping females stay active and healthy in a warming climate, where heat tolerance will be increasingly challenged.

○ Conclusions

To conclude, this PhD project provides novel fundamental evidence showing how female hormonal and morphological development can shape thermoregulatory, perceptual, and skin mechanical responses in the heat. The research offers the first integrated characterisation of breast-specific sweating, perceptual sensitivity, and mechanical properties, as well as the first detailed mapping of the transition from child-like to adult-like regional sweating patterns in girls. These findings fill critical gaps in female-centred thermophysiology and generate empirical data of direct relevance for improving sportswear and bra design, refining thermoregulatory models, and informing user-centred product development for females across life stages. Collectively, this work establishes a foundational evidence base that advances scientific understanding of female thermoregulation and enables more informed support for female comfort, health, and exercise participation in increasingly warm environments.

Appendix A Participant Information Sheet – Breast Study

Study Title: Impact of breast size on sweat gland density, sweat gland output and breast sensation during exercise heat stress

Researcher: Hannah Blount

ERGO number: 79009

You are being invited to take part in the above research study. To help you decide whether you would like to take part or not, it is important that you understand why the research is being done and what it will involve. Please read the information below carefully and ask questions if anything is not clear or you would like more information before you decide to take part in this research. You may like to discuss it with others, but it is up to you to decide whether or not to take part. If you are happy to participate you will be asked to sign a consent form.

What is the research about?

During physical activity (e.g. running or jumping), the breasts move up and down depending on the level of support offered by the bra. It is unknown whether the amount of breast movement changes during prolonged physical activity in heat and how this may impact breast comfort or pain. This knowledge could be very useful in the context of sports bra design.

Furthermore, breast size differs greatly across females. In response to heat stress or exercise, evaporation of sweat is the body's main method to lose heat. From the age of 2, the number of sweat glands does not change with age, so as we grow, the density of our sweat glands reduces. This raises the question as to how sweat gland density may differ across the breast of females with different breast sizes, and how this may impact females' ability to regulate their temperature and remain comfortable. Our thermal and clothing comfort is governed by the sensation at the skin. Given the breast area is almost always covered by a bra or t-shirt it could be valuable to know how sensation of comfort across the breast is also related to breast size.

This study is part of an industry co-funded PhD studentship in partnership with a global sportswear manufacturer, Nike. By better understanding of regional sweat gland and sensation differences across the breast and the impact of different breast size, this could influence sports bra design to improve thermal comfort during exercise or activity in hot conditions.

Why have I been asked to participate?

You have been asked to participate because you meet the study's inclusion criteria. Inclusion and exclusion criteria are as follows:

Inclusion criteria:

- Female;
- Physically active (i.e. performing 30 minutes regular exercise of moderate intensity, physical activity on at least 3 days each week for at least 3 months).
- Can comfortably run at a self-selected speed corresponding to a rate of perceived effort (RPE) of "somewhat hard" for 45 minutes in heat;
- 18 to 50 years old

Exclusion criteria:

- Pregnant
- Post-partum or breast feeding
- Have breast implants or augmentation
- Have breast reduction
- Neuro-diverse participants with diagnosed attention disorders (e.g. ADHD, Autism, Dyslexia)
- Family history of cardiovascular diseases
- Suffering from heart diseases
- Suffering from cardiovascular, metabolic, and neurological disorders
- Suffering from skin conditions (e.g. eczema)
- Presence of conditions altering thermoregulation and blood flow (e.g. Raynaud's disease)
- Taking prescribed medications for a health condition associated with cardiovascular, metabolic, or neurological disorders, which could alter thermoregulatory (e.g. sweating) or cardiovascular (e.g. blood flow) functions.
- Smoker or Vaper
- Iodine allergy

What will happen to me if I take part?

Participants will be required to visit our laboratory in the Clinical Academic Facility (south block) at Southampton University Hospital on three different days, separated by a minimum of 48 hours. The three experimental sessions will differ in terms of the sports bra level of support. The low and high support bra sessions will last 90-120mins. The medium support bra sessions will last 120mins but requires you to take a pill that measure core temperature l at least 3-4hrs prior to data collection. Total testing time commitment will be ~5.5-6.5 hours. There is also an optional extra session which will take place at building 67 at The University of Southampton that will last approximately 60mins.

For each experimental session we will ask you to arrive with running shoes, a water bottle, a towel and long hair tied up. You will be given a sports bra and shorts for the data collection sessions.

Breast sensory measures (thermal, wetness, tactile) will be taken by an experienced researcher prior to exercise in thermoneutral conditions. A urine sample will be taken to assess your hydration status then disposed of immediately. Following this, you will enter a warm climate chamber (32°C) and run for 15-45mins on the treadmill at 70% perceived effort. During this you will have 3 small sensors affixed to both breasts and the back of your neck which measure body movement. A survey of thermal, wetness and stickiness sensation, breast pain, bra support and wear comfort will be asked at intervals throughout the run. Immediately before and after the run we will take a nude body weight measurement. For this measurement you will go behind a privacy screen, and we will ask you to remove all of your clothing and stand on the scales which will record your weight. You will then put your clothes back on behind the screen so full privacy is maintained. Then following the run, tactile sensation at the breast will again be assessed when resting. Tactile sensation measures will be done at 3 points on the breast, including the nipple. To ensure your safety, your temperature will be monitored following testing until it begins to drop and has reached a level close to that measured before the testing session, after which you will be free to leave. This decline will likely occur during the first 30 minutes following exercise termination. All testing will be performed by an experienced female researcher, unless you would prefer a male researcher, which can be arranged. We are also able to provide a chaperone of either gender for the duration of the testing upon request. If you would feel more comfortable with a chaperone please inform us prior to testing and this will be arranged.

The optional extra session aims to help us validate the breast movement measurements. This will involve a series of short 1min bouts of walking and running on the treadmill in neutral conditions with 6 extra sensors placed across your torso and breast region to collect 3D motion capture data.

If you have any questions about the data collection procedures etc then please get in touch via email (h.blount@soton.ac.uk). If you wish to participate, you will be required to complete a consent form. This can be completed in person on the first day of data collection or emailed out prior to the data collection which can also be returned to the email address above.

Are there any benefits in my taking part?

With your participation, you will help advancing basic biological knowledge on female breast biomechanics, morphology and sensitivity. You will also receive a £105 Amazon voucher upon completion of all sessions, i.e. a £35 Amazon voucher per session completed to cover for the time and inconvenience caused by data collection.

Are there any risks involved?

As this study focuses on morphological and sensation differences across the breast region, this could cause some embarrassment for the participant. To reduce this risk, data collection will be performed by a researcher with the gender of your choice and will take place in a closed laboratory equipped with privacy screens. The researcher will do their best to help ensure you are comfortable, but participants are encouraged to verbalise any discomfort or uneasiness at any time and can stop the data collection at any point if they are not happy.

There are no risks associated with the perception testing although you will be told to expect mild sensations of wetness and warmth/cold during the data collection.

The hazards of this experiment include those associated with heat stress and with exercising when this is undertaken. The participants will be healthy volunteers exercising sub maximally, so no exercise related problems are foreseen. Also, the extent of heat stress is limited so there are no heat stress-related problems foreseen either. The combination of clothing, climate and physical activity will be carefully chosen to avoid excessive stress.

The heat exposures do usually result in a moderate increase of deep body temperatures. As a safety precaution, no participant can leave the laboratory until internal body temperature (however measured) has reached a level close to that measured before the experiment. It is not possible to wait until the temperature is fully restored because this may, because of circadian changes, take up to 24 hours. If necessary rapid cooling and warming facilities are available in the form of electric fans and/or cool and warm showers. First aid cover will be provided throughout and following each exposure.

All body temperature and heart rate data will be recorded at 1minute intervals and monitored constantly. Environmental variables will be recorded and monitored in a similar manner. Subjective measures of sensation, discomfort and rate of perceived exertion will be requested of the participant at 10minute intervals. Experimental tests will be terminated in any of the following instances:

1. At the request of the participant.
2. At the discretion of the researcher.
3. At completion of pre decided duration for exposure.
4. If the participant's internal body temperature rises by 3℃ or increases to an absolute value of 39.5℃ during heat exposure.
5. If the average skin temperature rises above 38℃ during heat exposure
6. If participant heart rate rises above 85% of the age-related predicted maximum for that participant (85% of [220 age] beats per minute).

Similar to the risk involved in other activities involving face-to-face contact with other people, there is a risk of COVID-19 transmission and infection when taking part in this study. Steps have been taken to reduce these risks and these will be explained to you before you take part in the study. Please consider this risk particularly if you are pregnant or have an underlying condition. If you exhibit symptoms related to COVID-19 in the 7 days prior to taking part in the study, then we ask you to not take part in the study. If we, the researchers, exhibit symptoms within 7 days of you taking part in the study then we will cancel or postpone your participation. If you have a particular requirement that researchers are screened for Covid-19 before face-to-face contact, please contact the study team (Hannah Blount, h.blount@soton.ac.uk) giving at least two working days' notice before any booked appointments.

What data will be collected?

We will collect some demographic (e.g., sex, age, ethnicity) and anthropometric data (e.g., height, weight) about you. In addition, we will collect data about your physiological and perceptual responses to heat and cold exposures, as described in the "What will happen to me if I take part?" section of this sheet. All data collected will be anonymised at the earliest opportunity and analysed as such.

Will my participation be confidential?

Your participation and the information we collect about you during the research will be kept strictly confidential. Only members of the research team and responsible members of the University of Southampton may be given access to data about you for monitoring purposes and/or to carry out an audit of the study to ensure that the research is complying with applicable regulations. Individuals from regulatory authorities (people who check that we are carrying out the study correctly) may require access to your data. All these people have a duty to keep your information, as a research participant, strictly confidential.

The project will comply with the Data Protection Act 2018 (DPA) and Southampton University policies. All data covered by the DPA will be encrypted and kept on secure Microsoft OneDrive, or Office 365 Groups. Southampton's IT Storage (including the Microsoft services) uses ISO 27001 accredited cloud suppliers with specific data sharing agreements, and model clause contracts. The infrastructure is protected by an appropriate number of security controls and has achieved the UK government Cyber Essentials certification. The primary risk to your personal data is that of unintended disclosure. To mitigate this risk, informed consent will be required, and study data/results will be anonymised (ICO standards) at the earliest opportunity using unique identifiers accessible only by the researchers. All data will be assessed for deposit in liaison with the University's Research Data Managers.

Do I have to take part?

No, it is entirely up to you to decide whether or not to take part. If you decide you want to take part, you will need to sign a consent form to show you have agreed to take part.

What happens if I change my mind?

You have the right to change your mind and withdraw at any time without giving a reason and without your participant rights being affected. If at any time, before, during or after your two data collection sessions you wish to withdraw from the study please contact the main researcher via email. However, once the study has been completed it may not be possible to remove your data if it has been aggregated or published.

What will happen to the results of the research?

Your personal details will remain strictly confidential. Research findings made available in any reports or publications will not include information that can directly identify you without your specific consent.

This study is part of an industry co-funded PhD studentship in partnership with global sportswear manufacturer, Nike. The results of this study will be shared in anonymised form with Nike and used to support the development of a PhD thesis by Miss Blount on female thermoregulation across the life span and they will also support innovation by the project partner in the design of female-specific sportswear. Some of the results may also be presented at academic conferences and via peer-reviewed scientific publications.

Where can I get more information?

Please contact the study team:

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What happens if there is a problem?

If you have a concern about any aspect of this study, you should speak to the researchers who will do their best to answer your questions.

If you remain unhappy or have a complaint about any aspect of this study, please contact the University of Southampton Research Integrity and Governance Manager (023 8059 5058, rgoinfo@soton.ac.uk).

Data Protection Privacy Notice

The University of Southampton conducts research to the highest standards of research integrity. As a publicly-funded organisation, the University has to ensure that it is in the public interest when we use personally-identifiable information about people who have agreed to take part in research. This means that when you agree to take part in a research study, we will use information about you in the ways needed, and for the purposes specified, to conduct and complete the research project. Under data protection law, 'Personal data' means any information that relates to and is capable of identifying a living individual. The University's data protection policy governing the use of personal data by the University can be found on its website (https://www.southampton.ac.uk/legalservices/what-we-do/data-protection-and-foi.page).

This Participant Information Sheet tells you what data will be collected for this project and whether this includes any personal data. Please ask the research team if you have any questions or are unclear what data is being collected about you.

Our privacy notice for research participants provides more information on how the University of Southampton collects and uses your personal data when you take part in one of our research projects and can be found at http://www.southampton.ac.uk/assets/sharepoint/intranet/ls/Public/Research%20and%20Integrity%20Privacy%20Notice/Privacy%20Notice%20for%20Research%20Participants.pdf

Any personal data we collect in this study will be used only for the purposes of carrying out our research and will be handled according to the University's policies in line with data protection law. If any personal data is used from which you can be identified directly, it will not be disclosed to anyone else without your consent unless the University of Southampton is required by law to disclose it.

Data protection law requires us to have a valid legal reason ('lawful basis') to process and use your Personal data. The lawful basis for processing personal information in this research study is for the performance of a task carried out in the public interest. Personal data collected for research will not be used for any other purpose.

For the purposes of data protection law, the University of Southampton is the 'Data Controller' for this study, which means that we are responsible for looking after your information and using it properly. The University of Southampton will keep identifiable information about you for 10 years after the study has finished after which time any link between you and your information will be removed.

To safeguard your rights, we will use the minimum personal data necessary to achieve our research study objectives. Your data protection rights – such as to access, change, or transfer such information - may be limited, however, in order for the research output to be reliable and accurate. The University will not do anything with your personal data that you would not reasonably expect.

If you have any questions about how your personal data is used, or wish to exercise any of your rights, please consult the University's data protection webpage (https://www.southampton.ac.uk/legalservices/what-we-do/data-protection-and-foi.page) where you can make a request using our online form. If you need further assistance, please contact the University's Data Protection Officer (data.protection@soton.ac.uk).

Thank you for taking the time to read the information sheet and considering taking part in the research.

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