

Hands and feet: physiological insulators, radiators and evaporators

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Abstract The purpose of this review is to describe the unique anatomical and physiological features of the hands and feet that support heat conservation and dissipation, and in so doing, highlight the importance of these appendages in human thermoregulation. For instance, the surface area to mass ratio of each hand is 4–5 times greater than that of the body, whilst for each foot, it is ~3 times larger. This characteristic is supported by vascular responses that permit a theoretical maximal mass flow of thermal energy of 6.0 W (136 W m^2) to each hand for a $1 \text{ }^\circ\text{C}$ thermal gradient. For each foot, this is 8.5 W (119 W m^2). In an air temperature of $27 \text{ }^\circ\text{C}$, the hands and feet of resting individuals can each dissipate $150\text{--}220 \text{ W m}^2$ (male–female) of heat through radiation and convection. During hypothermia, the extremities are physiologically isolated, restricting heat flow to $<0.1 \text{ W}$. When the core temperature increases $\sim 0.5 \text{ }^\circ\text{C}$ above thermoneutral (rest), each hand and foot can sweat at $22\text{--}33 \text{ mL h}^{-1}$, with complete evaporation dissipating $15\text{--}22 \text{ W}$ (respectively). During heated exercise, sweat flows increase (one hand: 99 mL h^{-1} ; one foot: 68 mL h^{-1}), with evaporative heat losses of $67\text{--}46 \text{ W}$ (respectively). It is concluded that these attributes allow the hands and feet to behave as excellent radiators, insulators and evaporators.

Keywords Glabrous · Heat loss · Non-glabrous · Skin blood flow · Sudomotor · Sweating · Temperature regulation · Vasomotor

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Introduction

During the evolution of *homo sapiens*, selection pressures probably favoured individuals capable of regulating body temperature, and who possessed the intellectual capacity to develop behavioural responses that resulted in protection from, and the modification of, the thermal environment (Heinrich 1977; Crompton et al. 1978). One can only speculate regarding the dominant characteristics that ensured survival, but it is reasonable to assume that these co-existed with other favourable attributes, such as a sizeable endurance capacity (Ruben 1995; Bennett et al. 2000). Integral within this natural selection was the structural and physiological modifications of the hands and feet, and it is the roles that these appendages play in temperature regulation that is the focus of this review.

Hands and feet evolved through their roles in locomotion, food gathering, tool use and the provision of sensory feedback (Lovejoy et al. 2009). Indeed, hand evolution was probably linked with tool use (Marzke and Marzke 2000; Young 2003), with hands becoming tools with which the brain manipulated objects (Putz and Tuppek 1999; Marzke 1992; van Duinen and Gandevia 2011). The continual refinement of the intricate neural, vascular and musculo-skeletal structures provided appendages possessing remarkable dexterity. Similarly, the feet evolved from grasping appendages, driven by adopting bipedal locomotion (Harcourt-Smith and Aiello 2004; Preuschoft 2004; Wang and Crompton 2004). Thus, from small arboreal graspers evolved a relatively large, bipedal, homeothermic species with considerable physical endurance. However, *homo sapiens* could not have survived unless they also possessed effective autonomic and behavioural mechanisms for heat conservation and dissipation. Whilst much is known about these human capacities, detail pertaining to the roles of the

Table 1 The morphological characteristics and typical tissue compositions of one hand and one foot of an average adult man (79.1 kg, 1.72 m) and woman (66.2 kg, 1.60 m)

Attributes	Hand		Foot	
	Male	Female	Male	Female
Mass (kg) ^a	0.447	0.280	1.032	0.720
Surface area (m ²) ^{b, c, d}	0.044	0.037	0.071	0.060
Surface area to mass ratio (m ² kg ⁻¹)	0.098	0.133	0.069	0.084
Volume (mL) ^e	365.0	299.3	860.0	705.2
Bone mass (kg) ^f	0.093	0.085	0.296	0.226
Muscle mass (kg) ^g	0.144	0.058	0.227	0.148
Skin mass (kg) ^g	0.076	0.048	0.206	0.144
Thermonutral blood volume (mL) ^h	24.0	20.0	24.0	20.0
Other soft tissue mass (kg) ^g	0.089	0.062	0.268	0.187

Authors' compilation using data from 49 countries (height) and seven countries (body mass)

^a Shana and Bohn (2003)

^b Hand: Asian sample ($N = 270$; Hsu and Yu 2010) adjusted to the average male and female dimensions

^c Foot: Asian sample similarly adjusted ($N = 270$; Yu and Tu 2009)

^d The volar hand surface was assumed to represent 39 % of the hand (Hsu and Yu 2010), whilst the volar foot was taken as 79 % of the total foot surface area (Yu et al. 2010)

^e Mayrovitz et al. (2005, 2006)

^f Martin (1984)

^g Derived by subtraction using fractional mass (after Allwood and Burry 1954)

^h Derived using appendage volumes and basal volume-specific blood flows: hand = 6.7 mL 100 mL⁻¹ min⁻¹; foot = 2.8 mL 100 mL⁻¹ min⁻¹ (Caldwell et al. 2014)

hands and feet within these processes is fragmentary, and this review is an attempt to fill that gap as well as building upon existing knowledge. Also provided is a description of the morphological, physiological and biophysical characteristics of the hands and feet as participants within an integrated temperature regulatory system.

Morphological characteristics

The dry and evaporative exchanges of thermal energy within the body and with the thermal environment are dictated by temperature and water vapour pressure gradients, the size of each exposed surface relative to its mass, and by the convective (mass flow) and conductive delivery of heat to the superficial tissues. Thus, morphological characteristics exert a powerful influence on heat exchange.

Anatomical structures

The human hand contains 27 bones, and the foot 26, which are arranged in three groups, of which the digits can be wholly exposed to the surrounding environment (Standring 2008; for online and interactive hand and foot resources, see: Mahadevan et al. (2000) and McGrouther et al. (2000)). The bones make up ~20 % (males) and 30 %

(females) of the hand mass, and about 28 % (males) and 31 % (females) of the foot mass (Table 1). These tissues behave as heat sinks.

Active skeletal muscles can liberate large amounts of thermal energy. However, since the principal muscles that control the foot reside within the leg (Standring 2008), and since the 11 intrinsic foot muscles are only responsible for fine toe movements, there is no sizeable heat source within the foot. Thus, thermal energy for the feet comes mainly from other sources which, in combination with their frequently intimate contact with large heat sinks, increases their susceptibility to cold injury (Golden et al. 2013). Nevertheless, this configuration supports survival, since incapacitation of the foot due to protracted hypothermia does not result in immobilisation. This is not so for the hand. It has more than 30 muscles (Standring 2008), with ten controlling the thumb, and the rest producing hand and finger movements. Nineteen of these muscles are found within the hand, and these are responsible for precise finger movements and object manipulation. These muscles represent 20–30 % of the hand mass (female–male dimensions); they are relatively inactive and poorly insulated (Table 1). Consequently, the hand also has limited heat production capability, and when significantly cooled, hand functions become adversely affected (Hunter et al. 1952; Brajkovic and Ducharme 2003; Zander and Morrison 2008; Daanen

2009). Thus, lower-limb function can be retained, albeit impaired, long after losing fine hand movements.

Segmental surface areas and masses

The whole-body surface area to mass ratio for an average, adult man and woman is 0.024–0.025 m² kg⁻¹ [male–female: assuming 79.1 kg, 1.72 m; and 66.2 kg, 1.60 m, respectively (Table 1; also see ISO/TR 7250-2 2010)], with a larger ratio associated with a greater potential for heat exchange. When separate body segments are analysed, one finds considerable variability in these ratios. For instance, the surface area to mass ratio of the hand, relative to the whole body, is 4.1–5.2 times greater (male–female), whilst that of the foot is 2.9–3.2 times greater (male–female; Table 1). Yet the combined surface areas of both hands and both feet represent only 4.4–4.6 % (female–male) and 7.1–7.4 % (female–male) of the body's total surface area (respectively), making these appendages morphologically well suited for dissipating heat. Indeed, the feet, and especially the hands, are excellent radiators if sufficient heat can be delivered by the blood (convective delivery or mass heat flow).

Neural connections

A detailed description of the neurophysiology of the hands and feet is beyond the current scope. However, a brief overview of this topic provides important background information for understanding thermal sensory feedback, and the control of the thermoeffectors within these appendages.

Innervation of the hands and feet

The somatosensory nerves that innervate the hands and feet provide common pathways not only for autonomic and motor control, but also for sensory feedback. Three such nerves innervate each hand (Standring 2008). Firstly, and perhaps of greatest functional significance, is the ulnar nerve, which enters the hand ventrally, passing below the palmarcarpal ligament and dividing into deep and superficial segments. Since it innervates most of the intrinsic hand muscles, except those responsible for the delicate digit movements (Standring 2008), then the preservation of the functional integrity of the hand relies upon the protection of this nerve. The second major pathway is the median nerve. It also passes below the palmarcarpal ligament and is the most important sensory nerve of the hand (Standring 2008). In addition, it innervates the muscles that control fine thumb and finger movements. Finally, there is the superficial branch of the radial nerve, which enters the hand at the base of the thumb. It carries the cutaneous sensory

information from the dorsolateral surface of the hand as well as from parts of the thumb and the first two fingers (Standring 2008).

Each foot has five somatosensory nerves (Standring 2008). Branches of the tibial nerve (medial calcaneal, medial and lateral plantar nerves) innervate the heel, the sole and the first four toes. These enter from behind the medial malleolus, with the lateral plantar nerve controlling the intrinsic foot muscles (Standring 2008). Secondly, the superficial fibular nerve traverses the dorsal foot, carrying most of the cutaneous sensory information for that surface. The deep fibular nerve innervates three muscles and carries some sensory afferents from the first and second toes (Standring 2008). Finally, two nerves innervate the medial ankle and upper foot (saphenous nerve) and the lateral aspect of the foot (sural nerve; Standring 2008).

Thermoafferent feedback

Thermoreceptors

Thermoreceptors are located throughout the deep and superficial structures of the body (Boulant 2011; Pierau 2011) with the latter providing our first source of thermal awareness. The warm- and cold-sensitive receptors (free nerve endings) are not homogeneously distributed across the skin surface (Hardy and Opper 1938), and all are found in a three-dimensional configuration within the lower epidermis (Iggo 1969; Hensel et al. 1974; Ivanov et al. 1986).

One generally considers the volar (glabrous) aspects of the fingers to possess greater thermosensitivity, though this is perhaps more due to habitual hand use to obtain sensory feedback than it is to their thermoreceptor density. Indeed, Zotterman (1959) identified 7–9 cold-sensitive spots per cm² within the skin of the dorsal fingers and hands, but only 2–5 spots cm⁻² for the volar skin. The feet have a similar distribution (dorsal: 5.6 spots cm⁻²; volar: 3.4 spots cm⁻²), whilst the warm-sensitive sensors are more evenly distributed (0.4–1.7 spots cm⁻² across all sites; Zotterman 1959). Furthermore, the cold-sensitive receptors respond to temperatures ranging from –5 to 43 °C, whilst warm-sensitive sensors operate over 28–48 °C (Hensel 1981). This greater response range, in combination with their greater density, is of considerable functional significance during cold exposure and defence.

Thermoafferent pathways and thermosensitivity

Most cutaneous sensory flow from the hand occurs through the radial and median nerves, whilst that from the foot is carried in the tibial (plantar surface), superficial fibular (dorsal surface) and saphenous nerves (laterodorsal ankle surface; Standring 2008). Of these two appendages, the

nerves of the hands are better protected, with those of the feet being more vulnerable. For instance, the tibial and sural nerves pass behind the malleoli (Standing 2008), and are relatively well protected. However, poorly designed shoes that come into firm contact with the malleoli may impinge upon these nerves. Moreover, the superficial fibular nerve passes across the upper surface of the foot, so shoes that are tight across that surface may also adversely affect neural function.

Cutaneous thermoafferents travel to the spinal cord, with neurons from the hands entering the dorsal (sensory) roots of the sixth, seventh and eighth cervical spinal nerves, and those from the foot feeding into the first sacral and the fifth lumbar spinal nerves (Michael-Titus et al. 2007; Standing 2008). This arrangement means that anatomically related skin regions share common neural pathways (dermatomes). The spinal cord is thermosensitive, as well as being a relay through which signals pass and undergo some synaptic modification and convergence (Simon 1974; Simon et al. 1998).

Within the spinal cord, second-order thermal afferents ascend via the lateral spinothalamic tract (Willis et al. 1973; Brück and Hinkel 1990), eventually reaching the somatosensory cortex and the hypothalamus. We consciously perceive our environment from sensory feedback to the former, the organisation of which enables discrimination among different skin surfaces. Indeed, the sensory acuity of some surfaces is much greater than that of others, due to variations in peripheral innervation density and also the volume of the somatosensory cortex assigned to those regions. Thus, sites with superior acuity have a greater innervation density as well as a greater cortical representation (Penfield and Rasmussen 1952). These are both characteristics of the hands and fingers, which, along with the face, are our most sentient of structures. The feet and toes also have considerable sensory importance. Accordingly, feedback from any of these surfaces heavily influences thermal sensation, which appears to be age dependent (Taylor et al. 1995). In the hypothalamus, sensory neurons synapse with both the warm- and cold-sensitive hypothalamic neurons (Boulant and Hardy 1974), and the integration of these signals gives rise to the autonomic regulation of body temperature by controlling heat loss, heat conservation and thermogenesis (Werner et al. 2008).

At this point, it is necessary to briefly review the relative importance of thermal feedback from the hands and feet (physiological thermosensitivity), since animal research has established regional differences in cutaneous thermosensitivity (Hales and Hutchinson 1971; Ingram and Legge 1972; Necker 1977). In humans, however, differential cutaneous thermosensitivities have not been convincingly demonstrated, despite several attempts (Nadel et al. 1973; Crawshaw et al. 1975; Werner and Heising

1990; Bothorel et al. 1991). The problem was that thermosensitivity was evaluated using closed-loop methods, in which selected (relatively small) skin sites were heated and cooled, but the temperatures of the untreated surfaces were not controlled. Under such conditions, local heating or cooling will elicit generalised thermoeffector responses which, in turn, modify the temperatures of larger non-treated surfaces, modifying thermal feedback and altering thermoeffector function. For example, forearm heating can increase whole-body sweating and evaporative heat loss. This lowers the mean skin temperature and can counteract the sudomotor responses induced by the initial treatment.

To address this limitation, Cotter and Taylor (2005) examined cutaneous thermosensitivities for sweating in supine, resting individuals during the local warming and cooling of ten skin sites. Throughout each manipulation, the deep-body (core) and remaining skin temperatures were clamped above the sweat threshold (Cotter et al. 1995; Patterson et al. 1998), opening feedback loops from untreated skin and ensuring that changes in sweating could be assigned solely to feedback arising from the treated region. With respect to the hands and feet, neither site differed significantly in thermosensitivity from each other, or from any other treated site (Cotter and Taylor 2005). That is, local thermal stimulation displayed equivalent and minimal autonomic impact on whole-body sweating. However, these open-loop experiments have not yet been performed to evaluate local cutaneous thermosensitivities with respect to cutaneous blood flow.

Thermoeffector pathways

Sweating and cutaneous vasomotor responses are driven by both thermal (Kuno 1938; Johnson and Kellogg 2010; Roddie 2011) and non-thermal stimulations (Kenny and Journeay 2010; Kondo et al. 2010). Thus, whilst whole-body heating induces sweating and cutaneous vasodilatation, the subsequent initiation of exercise is accompanied by a reduction in cutaneous blood flow and a further elevation in sweat secretion (Christensen and Nielsen 1942; van Beaumont and Bullard 1963). In this case, neural feed-forward (central command) emanating from the rostral brain simultaneously activates the motor and sympathetic neurons (Kondo et al. 2010). These generalisations apply also to the thermoeffectors of the hands and feet, with the thermal sudomotor and cutaneous vascular responses being controlled by the preoptic anterior hypothalamus (Teague and Ranson 1936; Hardy et al. 1964; Boulant et al. 1989).

The thermally activated sudomotor efferents descend through the brain stem and spinal tract, terminating in the lateral horn region and synapsing with neurons that innervate the eccrine sweat glands (Sato 1977). The classical work of List and Peet (1938) first revealed the spinal

segments through which these efferents left the spine, with thoracic segments T2–T8 innervating sweat glands of the upper limbs, and the lower thoracic and lumbar segments (T11–L2) relaying sudomotor efferents to the lower extremities. These neurons are post-ganglionic, sympathetic fibres producing the neurotransmitter acetylcholine (Schotzinger and Landis 1988) which targets the muscarinic receptors of the clear cells. Efferent signals reach the sweat glands in waves, such that each sudomotor unit secretes sweat in a pulsatile fashion, with a period of 0.60–0.74 s (Bini et al. 1980; Nilsson et al. 1980). This secretion pattern occurs in synchrony with motor units innervating other skin regions (Nakayama and Takagi 1959; van Beaumont et al. 1966), thus confirming their autonomic linkage with the hypothalamus. Moreover, secretions from the volar and dorsal (non-glabrous) surfaces of the hands and feet are also synchronised (van Beaumont et al. 1966; Taylor and Machado-Moreira 2013), although this is not always observed (Nakayama 1969).

An absence of this sudomotor synchronisation between the volar and dorsal surfaces of the hands and feet is consistent with different pathways innervating each area, which may, in turn, be activated by different central mechanisms. Furthermore, it might indicate that different control centres modulate sweating from each skin surface, and some have hypothesised that dorsal secretion is driven by the hypothalamic thermoregulatory centre whilst a separate centre controls psychological sweating from the volar surfaces (Darrow 1937; Kuno 1956; Ogawa 1975). It has even been proposed that these psychological responses were noradrenergically mediated (Robertshaw 1977; Nakazato et al. 2004). Indeed, this hypothetical modulation of thermal and non-thermal sweating has become the frequently accepted teaching (Iwase et al. 1997), although those views are not held by the current authors, and these theories are explored and challenged within a subsequent section of this communication.

It has long been known that two separate neural mechanisms modify the dilatation of cutaneous arterial blood flow (passive and active dilatation: Kellogg 2006; Roddie 2011). Indeed, the research legacy behind this knowledge can be traced to Bernard (1852), and readers are directed to reviews by Rowell (1993), Charkoudian (2003), Kellogg (2006) and Roddie (2011), with the following text providing a distillation specific to the control of blood vessels that perfuse the skin of the hands and feet.

For the volar surfaces of the hands, and by default, also those of the feet, only one control mechanism modulates cutaneous blood flow (Roddie 2011), with this pathway first being identified through the research of Lewis and Pickering (1931) and then by Roddie et al. (1957b). This mechanism operates via active constriction during both thermoneutral and cold states, with strong vasoconstriction

also seen during various non-thermal stresses, such as exercise (Blair et al. 1961). Therefore, in thermoneutral conditions, blood flow to the volar skin surfaces is minimal, like that for the nose, lips and ears (Roddie 2011). Thus, the vasoconstricted state is normal for these areas, and venous pooling is also minimal. Constriction is brought about through the tonic release of noradrenaline from the sympathetic fibres that innervate these blood vessels (Roddie 2011). Noradrenaline activates both the α_1 and α_2 receptors that respectively dominate the arterial and venous vessels of the volar skin surfaces (Bodelsson et al. 1990). In warm-hot conditions, this sympathetic vaso- and venomotor tone is withdrawn, leading to a pressure-mediated (passive) dilatation (Blair et al. 1960).

On the dorsal surfaces of the hands, and again presumably the feet, there exist active vasodilatory mechanisms (Johnson et al. 1995). When the body is heated, the cutaneous arterioles actively dilate, with the corresponding smooth muscle activation reducing the vascular transmural pressure, and facilitating a cutaneous blood flow elevation (Roddie et al. 1957a). Under thermoneutral conditions, there is some tonic constrictor tone to these skin regions; however, the active dilatory pathways are silent (Roddie 2011). Cooling induces greater noradrenergic constriction, but does not influence the vasodilatory mechanism (Roddie 2011).

Vasomotor characteristics

Blood vessels of the hands and feet

The arteries

Blood flow to the hand is provided by the brachial artery, which terminates below the elbow, dividing into the radial and ulnar arteries (Standring 2008). The former passes over the wrist to the dorsal hand, then down through the first dorsal interosseous muscle to the palm. Near the fifth metacarpal, the radial artery forms the deep palmar arch and joins the deep branch of the ulnar artery. The superficial palmar branch of the radial artery provides blood to the thenar muscles. On the palmar aspect, the radial artery also gives rise to smaller vessels that feed the thumb and index finger. The deep palmar arch is formed by vessels from the radial and ulnar arteries. Three metacarpal arteries run along the second, third and fourth interossei, and join the digital branches of the superficial palmar arch (Standring 2008). The latter divides to form the common palmar digital branches that descend on the lumbricals and join the corresponding palmar metacarpal artery. The main blood vessels for the fingers now arise and run down both sides of each digit before eventually terminating in the subcutaneous tissues of the finger tips (Standring 2008).

Each foot receives blood from arteries that enter behind each malleolus (medial and lateral malleolar arteries), and across the dorsal foot surface (*dorsalis pedis* artery; Standring 2008), and their positioning, with respect to the bones, has significant implications for shoe design. Thus, poorly designed or incorrectly fitted footwear may reduce blood flow through these arteries. Along the dorsal foot, *dorsalis pedis* forms the medial and lateral tarsal arteries, the arcuate artery and the first dorsal metatarsal artery (Standring 2008). This last vessel supplies blood to the first and second toes, whilst the second, third and fourth dorsal metatarsal arteries supply both their respective digits plus one neighbour. Eventually, each gives rise to two dorsal digital arteries. On the plantar surface, the medial plantar artery (a sub-division of the posterior tibial artery) enters below the medial malleolus (Standring 2008). This vessel supplies the foot muscles, the skin of the medial sole and the three medial toes. The lateral plantar artery travels to the calcaneus, the adjacent muscles, the plantar tarsal and tarso-metatarsal joints, and the lateral sole. Eventually it joins *dorsalis pedis*, forming the plantar arch deep in the foot. The four plantar metatarsal arteries are now formed, feeding the digital arteries as per the dorsal metatarsal arteries. However, the plantar digital arteries are the major arterial source for the toes (Standring 2008).

Capillaries and arteriovenous anastomoses

Cutaneous capillaries typically have internal diameters of ~10 μm (Molyneux and Bryden 1981), and it is through the walls of these vessels that exchanges occur between the blood and the interstitial compartment (Starling 1896). In the skin, capillaries are in the papillary region, looping up towards the surface before descending to the superficial venous plexus (Standring 2008). In the fingers and toes, the density of these capillaries is quite variable. For instance, Zhong et al. (2000) reported a fingernail capillary density of ~65 vessels mm^{-2} , whilst Bukhari et al. (2000) found 6.5 vessels mm^{-2} on the nailfold. However, perhaps the most extensive work for the hand still remains that of Grant and Bland (1931), and these data are presented in Table 2. In the foot, Mørk et al. (2002) observed toenail bed capillary densities of 54 vessels mm^{-2} , and Zhong et al. (2000) reported 38 vessels mm^{-2} on the big toe. For the whole foot, Lamah et al. (1999) found average densities of 34 vessels mm^{-2} . From this evidence, one may conclude that capillary densities of the hands and feet are in the range 40–70 vessels mm^{-2} .

These papillary capillaries are aligned perpendicularly to their arterial (*rete subpapillare*) and venous connections (Standring 2008), optimising the gradient for heat exchange. Since the papillae are not well perfused, then epidermal temperatures are heavily influenced by ambient

Table 2 Capillary densities for the skin of the hand (Grant and Bland 1931)

Site	Capillary density (vessels mm^{-2})
Hand (palmar: fifth metacarpo-phalangeal joint)	77
Finger (volar, medial phalanx)	76
Hand (palmar: thenar eminence)	69
Finger (volar, distal phalanx)	57
Finger (dorsal, medial phalanx)	52
Hand (dorsal)	47

temperature, and heat exchange with the blood is maximised (Conrad 1971). Moreover, since capillary flow is very slow (Hales 1985), then the blood rapidly equilibrates with tissue temperature.

However, whilst the papillary capillaries facilitate heat dissipation, this function is enhanced in a multiplicative manner by the cutaneous arteriovenous anastomoses that exist within the hands and feet. These vessels, first described by Sucquet (1862) and Hoyer (1877), are found in the skin of the hands, feet, ears, lips and nose, and almost exclusively on the glabrous surfaces (Clark 1938; Nagasaka et al. 1987a). The most complex and largest anastomoses are believed to exist within the palms and the soles (Clark 1938; Abramson 1965). Although, Grant and Bland (1931) found that anastomoses were most abundant in the nail beds of the hands and feet (500–600 anastomoses cm^2), with the volar surfaces of the second toes being the next most plentiful sites (290 anastomoses cm^2), followed by the volar aspect of distal phalanges of the fingers (150 anastomoses cm^2). The palmar and plantar surfaces seem to possess widely variable distributions, ranging from 30 to 200 anastomoses cm^2 . However, most of the dorsal surfaces of the hands and feet appear not to have these arteriovenous anastomoses (Grant and Bland 1931). Readers are directed to Masson (1937) and Clark (1938) for both a critique of, and elaboration upon, these observations.

These anastomotic vessels are found deeper than the papillary capillaries, and they behave as capillary by-pass vessels and have internal diameters ranging from 25 to 125 μm (Hales 1985). These characteristics appear counter-intuitive, given the function of anastomoses in promoting heat loss. However, the paradox disappears when one considers volar blood flow during heat-induced vasodilatation. In this state, papillary blood flow rises, and the anastomotic vessels passively dilate, producing a much larger elevation in cutaneous blood flow. This occurs because dilatation of a vessel with a radius that is perhaps tenfold larger than a capillary, would, for the same pressure head, elicit a 10,000-fold greater blood flow elevation over the same tube length (Poiseuille's law: Nelms 1963; Molyneux

and Bryden 1981). Therefore, whilst this blood by-passes the more superficial papillary capillaries, it actually delivers more blood to the slower moving, deep venous plexus. Since the tissues surrounding these plexuses are poorly insulated, then heat exchanges with the ambient medium are enhanced (Midtgård 1980; Nuzzaci et al. 1999).

Conversely, maximal constriction of the arterioles and the anastomoses reduces acral cutaneous blood flow to levels less than required to support basal metabolism (Abramson 1965), and heat is conserved. Thus, extremes of cold can result in protracted under-perfusion, giving rise to potentially debilitating consequences, including disturbances to manual dexterity, peripheral pain, work performance, and non-freezing and freezing cold injuries (Enander and Hygge 1990; Heus et al. 1995; Stocks et al. 2004; Imray et al. 2011; Golden et al. 2013). However, the anastomoses will intermittently open (cold-induced vasodilatation), with each blood flow surge helping to protect the surrounding tissues (Wilson and Goldman 1970; Nuzzaci et al. 1999; Daanen 2003). Readers are directed to supplementary resources for further discussion on cold-induced vasodilatation (Edwards and Burton 1960; Livingstone 1976; Bergersen et al. 1999; Daanen and Ducharme 1999; O'Brien 2005; van der Struijs et al. 2008; Cheung and Mekjavic 2007; Flouris and Cheung 2009; Keramidis et al. 2010).

The veins

The veins are the vascular capacitance vessels and may contain 70–80 % of the total blood volume in thermoneutral individuals (Pang 2001; Mertz 2004). Thus, changes to venous tone can have a pronounced influence on central blood volume and systemic blood pressure (Rowell 1993; Halliwill et al. 2013). The cutaneous veins similarly have a considerable capacity (Rowell 1993; Roddie 2011), and are well innervated and quite responsive to sympathetic stimulation (Zimmerman 1966; Webb-Peploe and Shepherd 1968). These veins participate principally in temperature regulation by reducing the volume of blood within the cutaneous tissue beds (Rothe 1983; Rowell 1983). In addition, the close proximity of veins and arteries within the hands and feet, but perhaps more importantly within the forearms and legs, means that, during cold exposures, heat carried in the arterial blood is transferred to the veins. This counter-current heat exchange reduces peripheral heat loss, and it was first recognised by Bernard (1876), with Forster et al. (1946), Scholander and Krog (1957) and Weinbaum et al. (1984) elaborating on this heat conservation mechanism. However, it was the classical work of Scholander and Schevill (1955) that demonstrated its significance in heat conservation for diving mammals.

Each finger possesses a venous network, with most blood passing to the dorsal surface, and through the metacarpal

veins and the dorsal venous arch (Standing 2008). This latter structure is the largest superficial venous network of the hand and provides tributaries to the cephalic and basilic veins (Schmidt and Lanz 2004). On the palmar surface and within the limbs in general, there are three drainage routes: the deep and superficial palmar venous arches (draining into the radial and ulnar veins, respectively) and the more superficial venous plexus that feeds the median antebrachial vein (Schmidt and Lanz 2004). However, there exist numerous communicating conduits (perforator veins) between the palmar and dorsal vessels of the carpo-metacarpal region. These vessels pass through the interosseous spaces, permitting palmar blood to flow to the dorsal surface, but since 70 % of these vessels have valves, this flow is predominantly unidirectional (Zhang and Schmidt 1993). Thus, the perforator veins facilitate venous return that is assisted by muscle pumping during finger and hand flexion (Pegum and Fegan 1967b; Simons et al. 1996).

In the foot, blood drains from the toes through superficial veins on the dorsal and plantar surfaces (Standing 2008). The feet have several plantar and dorsal veins, the most significant of which are the two venous arches: the deep plantar arch and the more superficial dorsal arch (Standing 2008). The former runs the length of the metatarsal region and, as well as feeding into the posterior tibial vein, these vessels connect to the dorsal veins by perforating conduits at the foot margins (Pegum and Fegan 1967a). Perforating veins also join the plantar and dorsal veins, again with about half containing valves (Pegum and Fegan 1967a). Thus, venous blood from the plantar surface can return via the tibial veins and also through the foot fascia, mixing with blood from the dorsal surface, before leaving through the saphenous veins. This latter route is activated during lower-limb loading (compression pumping).

Since the veins are very compliant, a significant volume of blood within each appendage may be retained within these vessels (Levy et al. 1985), particularly when in a dependent position at rest. The resulting venous pooling increases blood vessel diameter and slows blood transit time, both of which optimise heat exchange. However, generalised or cutaneous venoconstriction shifts significant blood volumes away from the skin, preventing pooling and reducing vessel transit times. Therefore, the combination of these anatomical structures with the morphological configuration of the hands and feet allows these regions to potentially behave as radiators and insulators.

Mechanical modulation of hand and foot blood flow

Muscle pumping assists venous return from dependent regions (Halliwill et al. 2013), and this is particularly important for the hands and feet, both of which are susceptible to oedema. In addition, pressure loading and

load bearing also modify arterial inflow and venous stasis (Pegum and Fegan 1967b; Broderick et al. 2010).

Activation of the forearm flexors when gripping objects elevates venous pressure and flow in the hand (Simons et al. 1996). Similarly, standing compresses the plantar venous arch, as does foot flexor activation (Broderick et al. 2010). Thus, whilst the anastomoses increase blood flow to the palmar and plantar skin of supine, resting individuals, compression pumping diverts this blood through the perforating veins to the dorsal skin. One might therefore expect these surfaces to become prime heat loss avenues during physical activity, perhaps with the overall contributions from these appendages being reduced relative to the resting state.

If these local pressures are excessive, blood flow is impeded. For instance, finger flows can be reduced by 85 % when local pressures of 30–52 kPa are applied, whilst palmar flow can tolerate pressures up to 100 kPa before experiencing a similar decline (Johansson et al. 2002). However, a 70-kg individual bearing the full body mass on both hands will only experience a palmar pressure of ~16 kPa, or a plantar pressure of only ~12 kPa when standing. Furthermore, the hands, and presumably the feet, resist compression through a reactive, pressure-induced vasodilatation of the cutaneous vasculature (Abraham et al. 2001), and this sustains tissue perfusion, albeit at a reduced level.

Thermal modulation of cutaneous blood flow

Hand and foot blood flows are rarely stable (Grant and Pearson 1938; Blair et al. 1961). Indeed, it is often when people are thermally comfortable that appendage flows are the most variable, with the vaso- and venomotor tone to these appendages constantly changing within the thermoneutral zone (Mekjavic and Eiken 2006; Werner et al. 2008). These changes modify the convective delivery of thermal energy to the skin, and with the whole-body cutaneous blood flow in thermoneutral males averaging ~350 mL min⁻¹ (Rowell 1974, 1993), then ~5 kJ min⁻¹ (83 W) of thermal energy will be transferred to the skin for the 4 °C core-skin gradient that typically obtains under these conditions. In fact, in suitably clothed people resting at 22–27 °C, thermal homeostasis can be achieved entirely through subtle changes in cutaneous blood flow, particularly to the hands, face and feet.

Blood flow to the skin of the hands and feet is modified centrally (Boulant 2011), with deep-body temperature dominating this modulation (Wenger et al. 1975; Proppe et al. 1976; Jessen 2011). This also applies to sweating, but with cutaneous feedback rising in importance during thermal adaptation (Regan et al. 1996; Tipton et al. 2013; Taylor 2014) or when the skin temperature is rapidly changed (Libert et al. 1978). With the exception of the arteriovenous anastomoses (Hales 1985), cutaneous blood vessels are also

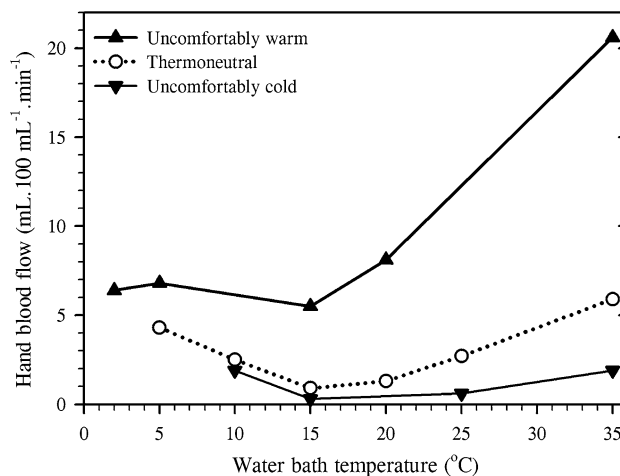


Fig. 1 Volume-specific hand blood flow during hand immersion at different water temperatures, but with the body uncomfortably warm (air temperature 32 °C), thermoneutral (air temperature 24 °C) or uncomfortably cold (air temperature 16 °C). Blood flow was powerfully modulated by the thermal state of the deep-body tissues when this temperature was elevated, regardless of local tissue temperatures. Data digitised from Spealman (1945) and used with permission

powerfully affected by local thermal changes (Taylor et al. 1984; Pérgola et al. 1993; Johnson and Kellogg 2010), the influence of which is related to the existing level of sympathetic tone (Spealman 1945; Pérgola et al. 1993; Caldwell et al. 2014). For instance, Spealman (1945) demonstrated that hand blood flow was always greatest when the deep-body tissues were warm (Fig. 1), and this deep-body dominance in the control of blood flow has recently been further verified for the foot (Caldwell et al. 2014).

At the hands or feet, local cooling can elicit strong vasoconstriction (Grant and Pearson 1938; Blair et al. 1961; Pérgola et al. 1993; Caldwell et al. 2014), with blood flow in previously cooled individuals decreasing to below that needed for normal cellular function (0.8 mL 100 mL⁻¹ min⁻¹; Abramson 1965). Local skin heating of thermoneutral subjects first produces a large flow increase (rapid vasodilatation), followed by a slight constriction, then a gradual dilatation over 25–30 min (Pérgola et al. 1993; Minson et al. 2001). However, whilst powerful, these local thermal influences can neither abolish nor dominate central autonomic drive (Johnson et al. 1976; Pérgola et al. 1993; Caldwell et al. 2014). Thus, whilst it is generally assumed that (local) heating the skin to 42 °C induces maximal vasodilatation (Taylor et al. 1984), maximal hand and foot blood flows can only be obtained if one first induces some level of hyperthermia (Spealman 1945; Caldwell et al. 2014).

In a thermoneutral state, vasoconstrictor tone within the hands and feet dictates blood flow, with active dilatation being minimal (Blair et al. 1961). During whole-body

cooling, cutaneous vasoconstriction is activated, driving a significant blood volume back to the deep-body tissues. Simultaneously, a generalised vasoconstriction reduces arterial flow to the hands and feet. This is associated with a relatively stronger constriction of the sub-papillary veins and the intermediate venous plexuses, which are closer to the skin surface, and this means that venous blood is directed into the deeper and better insulated vessels. The arteriovenous anastomoses also close, and tissue insulation increases to conserve heat. Indeed, under these influences, a temperature gradient is established along the skin surface (Freeman and Nickerson 1938; Werner and Reents 1980), and also through cutaneous cross-sections (Pennes 1948; Webb 1992). Thus, the appendages behave as a protective barrier, with a physiological amputation of the extremities conserving deep-body heat as one becomes progressively colder (Forster et al. 1946; Scholander and Krog 1957; Caldwell et al. 2014). Without this insulating capacity, primitive humans would probably not have migrated beyond the temperate regions, unless they possessed heavily insulated hand and footwear.

In warmer conditions, veno- and vasoconstrictor tones may be abolished and pressure-induced, passive dilatation occurs. During maximal heating, whole-body cutaneous blood flow can reach 7–8 L min⁻¹ (Rowell et al. 1970). Thus, for a 1 °C core-skin temperature gradient, this flow can now deliver thermal energy at a rate of 27 kJ min⁻¹ (450 W). This elevates the skin temperature, which has three consequences, the first two of which are beneficial. Firstly, it buffers against external heat gains and helps to defend the temperatures of the deep-body tissues. Secondly, there is an elevation in cutaneous water vapour pressure which increases evaporation without the need to increase sweat flow. Finally, it reduces the convective and conductive heat flow from the deep-body tissues.

These skin temperature increases are most dramatic at the extremities (Maddock and Coller 1933; Werner and Reents 1980; Webb 1992). For the hands and feet, passive dilatation occurs along the volar surfaces, reinforced by opening the arteriovenous anastomoses. On the dorsal surfaces, active vasodilatation can also be initiated (Lewis and Pickering 1931; Greenfield 1963; Johnson et al. 1995), and the resulting cutaneous blood flow is much greater than would accompany vasoconstrictor tone withdrawal. Indeed, approximately 80–95 % of the flow increase within non-glabrous (dorsal) skin occurs through active vasodilatation (Kellogg 2006; Johnson and Proppe 2011), and these mechanisms mean that the hands and feet have a considerable capacity to both reduce and elevate cutaneous blood flow.

It has been estimated that the minimal blood flow to support cutaneous tissues is ~0.8 mL 100 mL⁻¹ min⁻¹ (Abramson 1965). In resting, thermoneutral males,

basal (volume-specific) hand blood flow is approximately 6.7 mL 100 mL⁻¹ min⁻¹, whilst that of the foot is about 2.8 mL 100 mL⁻¹ min⁻¹ [Caldwell et al. 2014 (males)]. When normalised to segmental surface areas (Table 1), basal hand blood flow (550 mL m⁻² min⁻¹) is more than three times greater than might be observed for the rest of the body [79.1 kg, 1.72 m (Table 1), absolute blood flow 350 mL min⁻¹ (Rowell 1974, 1993); 183 mL m⁻² min⁻¹], and 1.6 times that observed in the foot (340 mL m⁻² min⁻¹). Such basal, area-specific flows emphasise the extent to which these appendages, particularly the hand, can function as radiators under thermoneutral states (Grant and Pearson 1938; Forster et al. 1946; Ferris et al. 1947).

Table 3 provides an historical summary of hand and foot blood flows across a range of treatments, revealing that the hands have an enormous potential for increasing blood flow and heat dissipation. If one assumes that volume-specific flows of 30 (hand) and 18 mL 100 mL⁻¹ min⁻¹ (foot) are maximal, with the respective minimal flows both approximating 0.2 mL 100 mL⁻¹ min⁻¹ (Table 3), then the hand supports a 150-fold blood flow increase over these extremes; for the foot, this is a 90-fold elevation. Indeed, both extremities can dramatically elevate tissue insulation by reducing blood flow to <25 % of their metabolic requirement. However, for lightly clad individuals resting in the cold, blood flows of ~0.4 (hand) and 0.2 mL 100 mL⁻¹ min⁻¹ are more typical (Table 3). Finger flows reveal even greater minimal-to-maximal ranges (0.2–120 mL 100 mL⁻¹ min⁻¹; Wilkins et al. 1938; Nagasaka et al. 1987b). Moreover, flow variations exist between the distal (higher) and middle phalanges of the fingers (Wilkins et al. 1938), and this is consistent with the distributions of both the arteriovenous anastomoses and eccrine sweat glands.

Notwithstanding the number of experiments in which hand and foot blood flows were investigated, until recently, a detailed description of these flows, across a range of whole-body thermal states, was not available. Indeed, most investigations focussed upon states approximating thermoneutrality. Therefore, the current authors developed water-displacement plethysmographs for the hand and foot that permitted independent control over local tissue temperatures (Caldwell and Taylor 2014). In combination with pre-experimental, whole-body cooling and heating (water immersion: Booth et al. 2001), followed by whole-body thermal clamping (Cotter and Taylor 2005), three steady-state thermal states were investigated: mild hypothermia [deep-body (oesophageal) temperature: 36.1 °C; mean skin temperature: 22.2 °C], thermoneutral (deep-body: 37.0 °C; mean skin: 33.6 °C) and moderate hyperthermia (deep-body: 38.5 °C; mean skin: 37.7 °C). Under each of these clamped conditions, five thermal treatments (5, 15, 25, 33,

Table 3 Hand and foot volume-specific blood flows reported across a range of experimental manipulations

Blood flow	Condition	Source
Hand blood flow (mL 100 mL ⁻¹ min ⁻¹)		
0.15–0.75	Whole-body: air temperature: 15.3 °C (rest)	Forster et al. (1946)
0.9	Hand immersion: 15 °C (rest)	Spealman (1945)
2.7	Hand immersion: 25 °C (rest)	Spealman (1945)
5.0	Hand immersion: 32 °C (rest)	Kunkel et al. (1939)
5.9	Hand immersion: 35 °C (rest)	Spealman (1945)
6.20–8.72	Whole-body: air temperature: 25 °C (rest)	Forster et al. (1946)
10.0	Hand immersion: 37 °C (rest)	Kunkel et al. (1939)
12.1–31.7	Whole-body: air temperature: 37–38 °C (rest)	Forster et al. (1946)
30–40	Hand immersion: local anaesthesia (neutral)	Roddie et al. (1957a)
32.0	Hand immersion: 43 °C (rest)	Kunkel et al. (1939)
34.0	Hand immersion: 44 °C (rest)	Roddie and Shepherd (1956)
Foot blood flow (mL 100 mL ⁻¹ min ⁻¹)		
0.2	Foot immersion: 17–20 °C (rest)	Kunkel and Stead (1938)
0.24	Foot immersion: 14–15 °C (rest)	Allwood and Burry (1954)
17.1	Foot immersion: 43 °C (rest)	Kunkel and Stead (1938)
17.8	Foot immersion: 44 °C (rest)	Allwood and Burry (1954)

Table 4 Hand and foot volume-specific blood flows (mL 100 mL⁻¹ min⁻¹) for semi-nude, supine subjects (resting $N = 8$) during three clamped thermal states: mild hypothermia, thermoneutral and moderate hyperthermia

Right hand				Left foot			
T_{core}	T_{skin}	Local T_{skin}	Blood flow	T_{core}	T_{skin}	Local T_{skin}	Blood flow
36.1	22.3	6.2	0.9	36.1	22.4	5.5	0.6
36.1	21.8	15.6	1.4	36.1	22.0	15.5	0.7
36.0	22.0	25.3	1.4	36.1	22.0	25.5	1.2
36.1	22.1	33.1	1.9	36.0	22.1	33.3	1.3
36.1	22.0	40.4	1.5	35.8	22.0	41.8	2.5
37.0	33.3	7.1	2.5	36.9	33.2	5.2	2.0
37.0	33.4	16.1	3.5	36.9	33.4	16.6	1.4
37.0	33.4	25.4	4.1	36.9	33.3	25.1	2.2
37.0	33.2	33.8	7.3	36.9	33.4	33.5	2.8
37.0	33.3	41.8	8.2	36.9	33.3	41.6	4.5
38.5	37.7	8.1	6.4	38.5	37.7	6.5	4.5
38.3	37.6	17.1	8.4	38.5	37.6	16.7	4.6
38.4	37.5	25.6	9.7	38.5	37.6	25.1	6.1
38.4	37.6	33.3	12.6	38.5	37.5	34.2	9.3
38.4	38.1	40.3	18.4	38.5	37.9	41.4	12.8

Thermal data are means (°C) for the clamped deep-body (oesophagus: T_{core}) and mean skin temperatures (T_{skin} : area-weighted, whole-body average), and localised whole-segment [hand and foot (local T_{skin})] temperatures during cooling and heating. Five local skin temperature treatments were applied to each limb segment using a water-displacement plethysmograph (Caldwell and Taylor 2014) that was also used to measure segmental blood flows. Data extracted from Caldwell et al. (2014) with permission

40 °C) were applied to the hand and foot of supine, resting participants using rapid changes in the water temperature of each plethysmograph (Caldwell et al. 2014). These data are summarised in Table 4. From this experiment, three-dimensional surfaces were created that described the interactions

of mean body and local tissue temperatures on segmental blood flows (Fig. 2a, b).

Volume-specific hand blood flows exceeded those of the foot during all treatments (Fig. 2), and flow elevations with increments in segmental temperature (sensitivity)

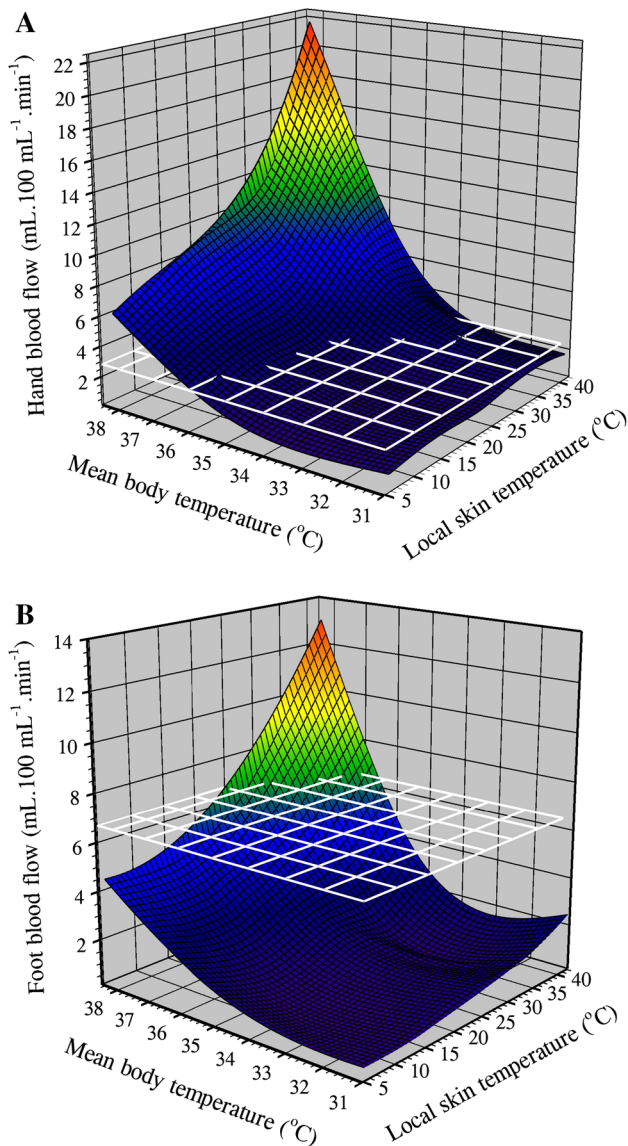


Fig. 2 Three-dimensional surfaces for hand (a) and foot blood flows (b) across mean body temperatures from 31.2 to 38.3 °C and segmental temperatures from 5 to 40 °C. Semi-nude, supine subjects (resting $N = 8$) were pre-treated (water immersion) and clamped in three thermal states (separate trials): mild hypothermia, thermoneutral and moderate hyperthermia. Mean body temperatures were calculated using the weighted sum of oesophageal and mean skin temperatures using the following deep-body coefficients (Vallerand et al. 1992): 0.65 (mild hypothermia), 0.70 (thermoneutral) and 0.80 (moderate hyperthermia). Five hand and foot thermal treatments were applied (5, 15, 25, 33, 40 °C). Segmental blood flows were measured using water-displacement, venous-occlusion plethysmography. Data are averages for the 15 three-dimensional coordinates with points between derived through extrapolation. The colour spectra indicate flow graduations (*red for highest*), whilst the transparent (*white*) planes are thermoneutral blood flows for the opposite limb segment (oesophageal temperature 37.0 °C **a, b**, mean skin temperature 33.6 °C **a, b**, and respective foot and hand skin temperatures of 33.7 and 33.4 °C). From Caldwell et al. (2014) and reproduced with permission

were significantly greater within each thermal state. When mildly hypothermic, these thermal treatments were barely able to override vasoconstriction. However, when hyperthermic, both segments demonstrated considerable sensitivity to these local temperature changes. Indeed, both appendages act as radiators when humans are hot, with the hands performing significantly better. This cutaneous vascular dilatation means that heat delivery to the skin is sustained even when hot individuals are immersed in cool, but not cold water (Caldwell et al. 2014), and this centrally mediated resistance to vasoconstriction provides a vascular mechanism that explains why immersion cooling of hyperthermic individuals can be achieved quite rapidly, even when using temperate water (26 °C; Taylor et al. 2008; Casa et al. 2010).

The descriptions above largely relate to blood flows measured during supine rest. However, during upright locomotion in the heat, it is highly likely that dilatation of the arteriovenous anastomoses within the feet will be much less effective, with load bearing redirecting plantar venous return to the dorsal foot surfaces, which may well be covered. When the hands are used for work, the contribution of the palmar surfaces is similarly reduced, and in both instances, the appendages are generally in dependent positions. Thus, whilst the hands and feet of unclothed, resting individuals can radiate large amounts of heat, this capacity is compromised during exercise and work.

Restoration of blood flow following hypothermia

Foot and hand blood flow within hypothermic individuals cannot be instantaneously restored (Wyndham and Wilson-Dickson 1951; Savard et al. 1985). In the early stage of recovery from acute hypothermia, this delay is due to the progressive reduction in deep-body temperature following rescue (afterdrop: Currie and Percival 1792; Currie 1797; Alexander 1945; Golden and Hervey 1977). Beyond this point, the combined influence of deep-body and peripheral cooling results in the maximal constriction of the arteriolar and venous vessels. If mean arterial pressure is normal, then peripheral blood flow restoration initially involves a release of this generalised constrictor tone. However, this only occurs if the deep-body tissues have first been warmed (Ferris et al. 1947; Savard et al. 1985; Brajkovic et al. 1998; Caldwell et al. 2014). The process involves sympathetic withdrawal (Freeman 1935), with a more complete disengagement occurring at the hands than at the feet (Pickering and Hess 1933; Caldwell et al. 2014). Thus, the feet retain constrictor tone, not only when thermoneutral (Caldwell et al. 2014), but also during rewarming, and even after the hands have dilated (Pickering and Hess 1933).

Cold-induced cutaneous vasoconstriction is maximal, even in moderate air temperatures (Bittel et al. 1988), and if this constriction has been protracted, then peripheral tissue temperatures will approximate ambient temperature. In this circumstance, smooth muscle relaxation will be impaired, even after constrictor tone has eased. Since the surrounding tissues have a relatively poor thermal conductivity, they will remain cool for some time, and this local impediment to the restoration of cutaneous blood flow is not immediately corrected (Bazett 1968). Indeed, blood flow is only fully restored when deep-body thermoneutral tissue temperatures have been re-established (Savard et al. 1985; Caldwell et al. 2014). However, the return of normal blood flow occurs faster to the hands than to the feet for an equivalent level of cold, physiological strain (Pickering and Hess 1933), with the application of external heating accelerating this process (Savard et al. 1985).

Sudomotor characteristics

Human skin is not impermeable, with both water and water vapour moving through the epidermis. In this section, the focus is primarily on eccrine sweating, but the hands and feet lose more water through transepidermal (insensible) water loss than any other body segment (Taylor and Machado-Moreira 2013).

In resting, thermoneutral individuals, whole-body transepidermal water loss occurs at approximately 20–43 mL h⁻¹ (Taylor and Machado-Moreira 2013). The *stratum corneum* has a uniform thickness (10–20 μm), except at the volar surfaces of the hands and feet (both 400–600 μm: Rushmer et al. 1966; Scheuplein and Blank 1971). This thickness appears not to dictate vapour diffusion. In fact, water vapour flux through abdominal skin, for instance, is only about 10 % of that observed from the sole, and 30 % that of the palm (Scheuplein and Blank 1971), and water loss from the hands and feet appears to be 2–4 times greater than that from all other skin surfaces. Thus, the dorsal hands and feet lose ~0.05 mg cm⁻² min⁻¹, whilst the corresponding volar surfaces lose 0.13 and 0.10 mg cm⁻² min⁻¹ (respectively: Taylor and Machado-Moreira 2013).

Thermal sweating

Eccrine sweat gland distribution

Recent analysis of investigations involving over 320 data sets has shown that a reference adult (70.0 kg, 1.702 m, body surface area 1.807 m²: Miller et al. 1980) will possess some 2.06 million functional eccrine sweat glands (Taylor and Machado-Moreira 2013). On the non-glabrous surfaces of the hand and feet, these glands are found at the

Table 5 The distribution of physiologically active eccrine sweat glands (glands cm⁻²) across the hand and foot surfaces

Sites	Gland density	Data sets
Finger (volar: distal phalanx)	530 (±113)	14
Toe (volar: distal phalanx)	526	2
Foot (plantar surface)	467	2
Hand (palmar surface)	307 (±94)	6
Hand (dorsal surface)	167 (±45)	14
Foot (dorsal surface)	119 (±41)	9

Data are means derived from 16 studies [with 95 % confidence intervals across studies (in parenthesis), unless fewer than three data sets were obtained]. Some studies contributed data to several sites, and sometimes more than one data set within a site. These total contributions are indicated in the rightmost column

Calculations: Site-specific means were computed as: regional density = $((N_1 \times \text{density}_1) + (N_2 \times \text{density}_2) + \dots (N_i \times \text{density}_i)) / N_{\text{Total}}$ (where: N is the sample size and subscript numerals refer to separate studies)

Sources: Clark and Lhamon (1917), Ogata (1935), Randall (1946), MacKinnon (1954: with that author's surface area error corrected), Thompson (1954), Hellon and Lind (1956), Silver et al. (1964), Juniper and Dykman (1967), Toda (1967), Bar-Or et al. (1968), Knip (1969), Roberts et al. (1970), Knip (1972), Schaefer et al. (1974), Catania et al. (1980), Amano et al. (2011)

intersections of the skin creases (Johnson et al. 1970) and participate extensively in thermal sweating. Conversely, the epidermal ridges of the palmar and plantar surfaces contain glands at much greater densities (Johnson et al. 1970; Taylor and Machado-Moreira 2013). These glands are powerfully activated by non-thermal influences (e.g. psychological sweating; Kuno 1956; Machado-Moreira and Taylor 2012a, b), although they also respond strongly to thermal stimulation (Taylor et al. 2006; Machado-Moreira et al. 2008a), and in a manner very similar to the torso and head (Machado-Moreira et al. 2008b, c). The distribution of sweat glands across the hands and feet is summarised within Table 5, with minimal evidence of ethnic differences (Taylor 2006). These gland counts were determined following thermal, exercise, psychological and pharmacological stimulations, and if one assumes that the volar surfaces represent 39 % of the total hand surface area (Hsu and Yu 2010), and 79 % of the total foot surface area (Yu et al. 2010), then one may predict local sweat gland densities (glands cm⁻²) for each hand and foot from these data (Taylor and Machado-Moreira 2013) from a knowledge of total body surface area and the relative contribution of each appendage to that total area. Thus:

$$\text{Dorsal hand} = \text{body surface area (cm)}^2 \times 0.0283 \times 166 \quad (1)$$

$$\text{Palmar hand} = \text{body surface area (cm)}^2 \times 0.0181 \times 518 \quad (2)$$

$$\text{Dorsal foot} = \text{body surface area (cm)}^2 \times 0.0364 \times 119 \quad (3)$$

$$\text{Plantar foot} = \text{body surface area (cm)}^2 \times 0.0290 \times 497 \quad (4)$$

One could expect to find our reference person (1.8 m²) to have about 270,000 eccrine glands across both hands, 67 % of which would occur on the palmar surfaces. For the feet, the corresponding values would be 410,000 glands, with 77 % on the plantar surfaces. Since these glands typically have a mass of ~35 µg (Sato 1977) and an approximate length of 6.1 mm (Kuno 1956; Sato and Sato 1983), then the hands and feet of this individual would contain glands with a combined mass of ~24 g, and if laid end-to-end, their combined length would be approximately 4.1 km.

Sweat composition

Eccrine sweat gland activation initiates a calcium flux into the clear cells, followed by an active pumping of sodium into those cells and the passive influx of chloride and water (Sato 1977; Morimoto 1978). On the luminal sides of these cells, sodium–potassium pumps increase their activity, now transporting sodium ions into the glandular lumen, with chloride and water again following passively (Hashimoto 1978). This primary (precursor) sweat rapidly accumulates, eventually elevating the intra-luminal pressure to the point that sweat starts to flow through the coiled duct. *En route*, the surrounding cells actively extract sodium, with an obligatory reabsorption of chloride and water (Sato 1973). The resulting hypotonic fluid that reaches the skin surface forms the discharged sweat, with its volume and composition dictated by its transit time within the duct (Schwartz and Thaysen 1956). Indeed, across the physiological range of secretion rates, sweat sodium concentrations can change at least twofold in some people (Allan and Wilson 1971; Costill 1977). Thus, the composition of sweat is widely variable across (Dill et al. 1966; Maughan and Shirreffs 2008) and within individuals (Dill et al. 1967; Patterson et al. 2000).

Four groups have studied the composition of discharged sweat from the hands and feet (Collins 1962; Emrich et al. 1968; Yousef and Dill 1974; Patterson et al. 2000). At secretion rates of about 0.05 mg cm⁻² min⁻¹, one may expect palmar sweat to contain 20.9 mmol L⁻¹ of sodium, 17.4 mmol L⁻¹ of chloride and 18.8 mmol L⁻¹ of potassium. On the dorsal surfaces of the hands, for which the corresponding sweat rate may be 0.50 mg cm⁻² min⁻¹, the respective ion losses would be 28.8, 28.3 and 5.7 mmol L⁻¹. Plantar sweat composition seems not to have been reported. However, when the dorsal foot sweats at 0.56 mg cm⁻² min⁻¹, its sodium, chloride and

potassium compositions approximate 24.3, 18.1 and 6.8 mmol L⁻¹ (respectively). For comparative purposes, whole-body electrolyte losses, derived across sweat rates from 0.72 to 3.65 mg cm⁻² min⁻¹, would range from 26.5 to 49.7 mmol L⁻¹ for sodium (95 % confidence interval), and chloride loss would be 26.8–36.7 mmol L⁻¹, with a potassium loss of 2.7–4.5 mmol L⁻¹ (Taylor and Machado-Moreira 2013). The palmar surfaces lose relatively small amounts of sodium and chloride, but potassium loss appears to be about five times greater than for the rest of the body. However, since only one data set was available for this electrolyte (Collins 1962), these data need to be verified and perhaps treated with caution at this time.

Sweat secretion during passive heating

The hydration state of the skin is essential for its normal function, and the *stratum corneum* contains about 0.9 mL water g⁻¹ dry tissue (Scheuplein and Blank 1971). This content is sustained through vapour fluxes from deeper layers as well as reabsorption from sweat ducts and plays an important role in protecting the skin from injury (Wilcott 1966). These generalisations also apply to the hands and feet, and in the former instance, hydration affects contact friction and grip (Adelman et al. 1975) as well as the tactile and thermal sensitivities of the volar surfaces (Edelberg 1961). Thus, these water fluxes interact with tool use, locomotion and temperature regulation, and it is assumed that these attributes evolved simultaneously as co-selected characteristics (Montagna and Parakkal 1974; Folk and Semken 1991).

During whole-body (passive) heating of resting individuals, a considerable range of sweat secretion may be observed across the body surface (Weiner 1945; Hertzman et al. 1952; Smith and Havenith 2011; Taylor and Machado-Moreira 2013). Readers may see a critique of the sweat-measurement techniques within Taylor and Machado-Moreira (2013). Herein, the focus centres entirely upon passive thermal sweating from the hands and feet, and data for these regions were collected from three studies, and reported in Fig. 3. Each project was undertaken under identical conditions (climatic chamber: 36 °C, 60 % relative humidity; water-perfusion suit: 40–46 °C), with local sweat rates measured using ventilated capsules positioned at 14 sites over the dorsal and volar surfaces of the hands, fingers, feet and toes (Taylor et al. 2006; Machado-Moreira et al. 2008a; Smith et al. 2013). This thermal load elevated deep-body temperature about 0.5 °C, and resulted in a mean skin temperature of 37.1 °C and resting heart rates of 84 beats min⁻¹ (see original manuscripts for details). Under these conditions, a threefold variation in the steady-state sweating was observed across the hand surfaces [dorsal finger (highest) to palm], with a twofold range across the feet

[dorsal toe (highest) to sole]. These changes occurred without introducing reactive errors, such as the cooling of skin below each sweat capsule.

These data confirm the presence of thermal sweating from the volar surfaces of both appendages, although some have suggested otherwise (Kerassidis 1994; Tronstad et al. 2008). Certainly the palms and soles are the least prolific sites (Fig. 3), as first described by Grew (1684), but this is not a universal attribute of the glabrous surfaces, with the volar fingers secreting only slightly, although not significantly less sweat than the dorsal hand (Machado-Moreira et al. 2008a). When the fingers and toes are included with the metacarpal and metatarsal surfaces, the glabrous sites are seen to secrete 60–67 % (foot-hand) of the thermal sweat produced from the dorsal surfaces. However, when the digits are excluded, these relative flows become 40 % (hand) and 66 % (foot), reflecting the greater thermoresponsiveness of the fingers. When all sites were considered, along with typical hand and foot surfaces areas (Table 1), then one may anticipate that, for a deep-body temperature elevation of ~ 0.5 °C above its thermoneutral level, a resting individual would lose approximately 20 mL h^{-1} of sweat from each hand and about 27 mL h^{-1} from each foot. Since whole-body heating significantly increases hand and foot blood flow (Caldwell et al. 2014), and skin temperatures (Maddock and Collier 1933; Werner and Reents 1980; Webb 1992), then cutaneous water vapour pressure rises, elevating evaporation. Thus, these appendages also behave as physiological evaporators, with

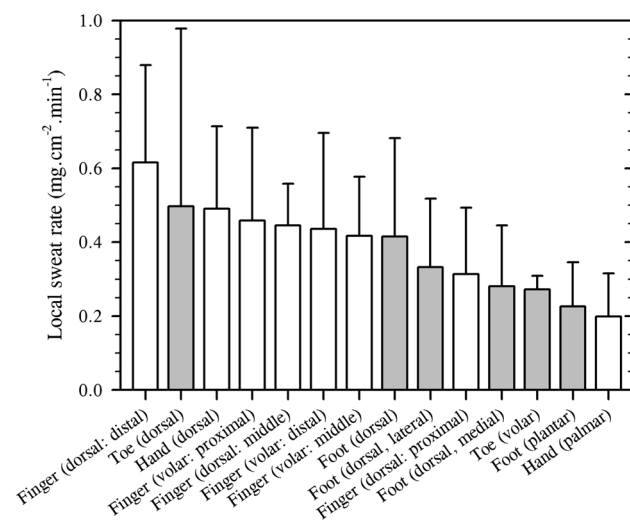


Fig. 3 Distributions of steady-state thermal sweating (ventilated capsules) across 14 sites within the hands and feet (shaded bars) of resting individuals (seated: air temperature 36 °C, 60 % relative humidity) wearing a heated, water-perfusion suit (40–46 °C). Data are means with standard deviations. Sources: Taylor et al. (2006), Machado-Moreira et al. (2008a), Smith et al. (2013)

these secretion patterns resembling segmental blood flow variations.

Sweat secretion during exercise in the heat

When exercising, whole-body water losses of $10\text{--}16 \text{ L day}^{-1}$ can occur under challenging climatic conditions (Eichna et al. 1945; Ladell 1945; Latzka and Montain 1999), with the hands and, to a lesser extent, the feet sweating copiously. In the trials reported above (Taylor et al. 2006; Machado-Moreira et al. 2008a; Smith et al. 2013), subjects exercised (cycling) in the same conditions after resting data were collected, and this was incremental in nature (25-W increase every 15 min), terminating at volitional fatigue. This forcing function resulted in final deep-body temperatures of 38.5–39.0 °C. Sweat data were averaged across all work rates to provide integrated responses for the same 14 sites (Fig. 4), representing flows when performing about 100 W of external work (36 °C, 60 % relative humidity). To facilitate inter- and intra-segmental comparisons, Figure 4 includes only those data collected using ventilated sweat capsules, although qualitatively similar outcomes have been obtained from most skin surfaces using the sweat-patch technique (Fogarty et al. 2007; Smith et al. 2013). Relative to the resting phase, sweat rates increased 1.5-fold (volar toe) to 9.4-fold (dorsal surface, proximal phalanx of index finger). Across the entire hand, sweating varied by a factor of 5.7 (lowest-highest), whilst for the foot there was a 2.8-fold variation.

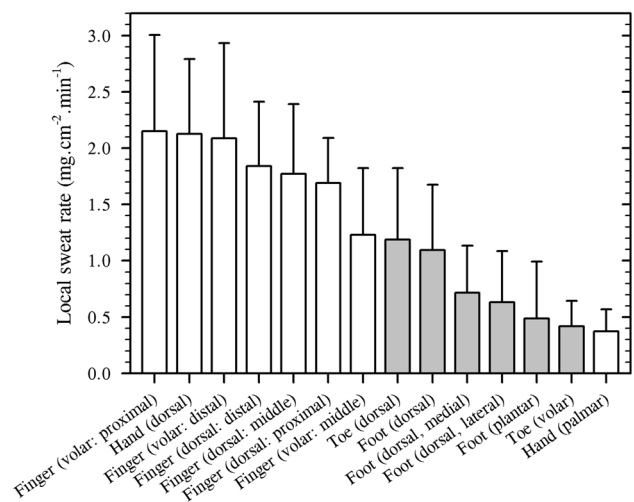


Fig. 4 Sweat secretion (ventilated capsules) from 14 sites on the hands and feet (shaded bars) during incremental exercise in the heat (cycling: air temperature 36 °C, 60 % relative humidity) whilst wearing a heated water-perfusion suit (40–46 °C). Data are means (with standard deviations) averaged across the entire exercise period, and equate with sweat rates that would obtain when working at 100 W. Sources: Taylor et al. (2006), Machado-Moreira et al. (2008a), Smith et al. (2013)

If one now combines the morphological data from Table 1 with these sweat rates, mean total sweat rates for each hand (80.7 mL h^{-1} or $1.52 \text{ mg cm}^{-2} \text{ min}^{-1}$) and each foot can be obtained (64.8 mL h^{-1} or $0.75 \text{ mg cm}^{-2} \text{ min}^{-1}$) for individuals exercising in the heat at an average external work rate of $\sim 100 \text{ W}$. Within each segment, the volar surfaces produced 43–57 % (foot-hand) of the sweat secreted from the dorsal regions, or 33–44 % (foot-hand) of total sweat from each segment. The relationship between the volar and dorsal surfaces is not identical for the hands and feet. For example, secretions from the sole and the volar surface of the big toe were uniformly lower than both the average dorsal foot and dorsal toe sweat rates. However, this generalisation did not apply to the hand, with the dorsal and volar surfaces of the fingers secreting significantly more sweat than the palm, but not the dorsal hand (Machado-Moreira et al. 2008a).

Finally, one may combine the regional glandular densities with these data to derive sweat gland outputs: an approximation of discharged sweat from individual glands. Within each appendage, the surfaces with the lowest glandular densities (dorsal hand and foot) produced the greatest glandular flows: 12.7 and $7.6 \mu\text{g gland}^{-1} \text{ min}^{-1}$ (respectively). The palms and soles possess intermediate gland densities, but displayed the lowest flows when exercising in the heat: 1.2 and $1.0 \mu\text{g gland}^{-1} \text{ min}^{-1}$ (respectively).

Psychological (non-thermal) sweating

The eccrine sweat glands are stimulated by both thermal and non-thermal mechanisms, and readers are directed to recent reviews on the latter (Kenny and Journey 2010; Kondo et al. 2010). However, a particular form of non-thermal sweating that was once believed to dominate secretion from the hands and feet is that which accompanies changes in emotional and affect states (Harrison and MacKinnon 1966; Homma et al. 2001); psychological (psychogenic) sweating.

The widely accepted view has been that such sweating is modulated by a separate nervous system centre (Ogawa 1975) with its own neural pathways (Chalmers and Keele 1952), possibly innervating only the glabrous surfaces of the hands and feet (Darrow 1937; Kuno 1956; Ogawa 1975), and quite probably through a noradrenergic sympathetic pathway (Robertshaw 1977; Nakazato et al. 2004). These combined hypotheses have intrigued the current authors for some time, precipitating a series of experiments, three of which are relevant to the current topic (Machado-Moreira and Taylor 2012a, b; Machado-Moreira et al. 2012).

In the first experiment, passive, whole-body heating was used to elicit steady-state sweating in 30 individuals ($0.5 \text{ }^\circ\text{C}$ deep-body temperature elevation above thermoneutral:

Machado-Moreira and Taylor 2012a). Secretion was measured from 38 sites (ventilated capsules), with an emphasis upon glabrous and non-glabrous surfaces. Following this priming of sweat secretion, cognitive challenges and a painful stimulus (palmar pressure) were used to evoke psychological sweating. These stimuli always elevated sweating, with $>70 \%$ of sites revealing significant increases, but with no change in body temperatures. Sweating from both glabrous and non-glabrous skin increased significantly, with no consistent differences between skin types. Furthermore, these whole-body trends were equally apparent at the hands and feet (Fig. 5), and appeared to refute the possibility of independent control mechanisms for thermal and psychological sweating from these surfaces.

Since most research on psychological sweating was undertaken in thermoneutral conditions, and since thermal loading potentiates sudomotor function, it was necessary to verify these observations without first priming the sweat glands (Machado-Moreira and Taylor 2012b). Eccrine sweating was therefore evaluated when thermoneutral individuals were challenged to perform 10 min of mental arithmetic ($26 \text{ }^\circ\text{C}$). Sudomotor function was first quantified using ventilated sweat capsules. Very low, but significant secretion was observed not only from the palm, the volar surfaces of third finger and the sole, but also from the dorsal aspects of the finger and foot (Fig. 6), with only the dorsal

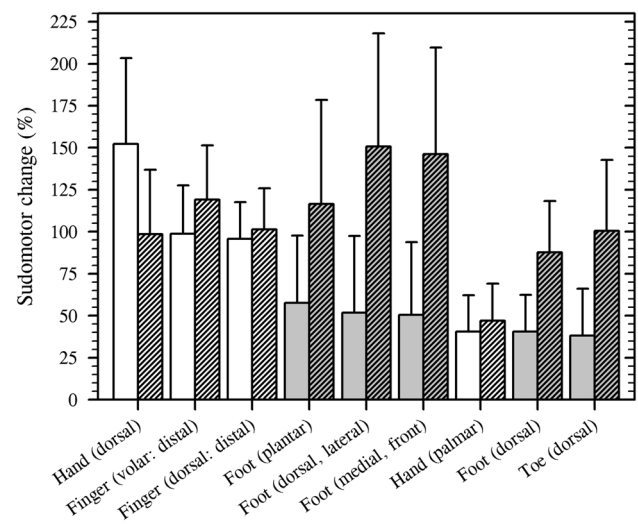


Fig. 5 Relative changes in sweat secretion (ventilated capsules) from the glabrous (volar) and non-glabrous (dorsal) skin surfaces of the hands and feet (shaded bars) following the superimposition of cognitive (open bars) and painful stimulations (hatched bars) upon steady-state, thermal sweating. These stimuli were applied after passive heating (climatic chamber: $36 \text{ }^\circ\text{C}$, 60% relative humidity; water-perfusion suit: $40\text{--}46 \text{ }^\circ\text{C}$) had elicited a deep-body temperature elevation of $\sim 0.5 \text{ }^\circ\text{C}$ and fully primed thermal sweating. Data are mean changes relative to the pre-stimulus thermal sweating (with standard errors of the means), and were extracted from Machado-Moreira and Taylor (2012a) and used with permission

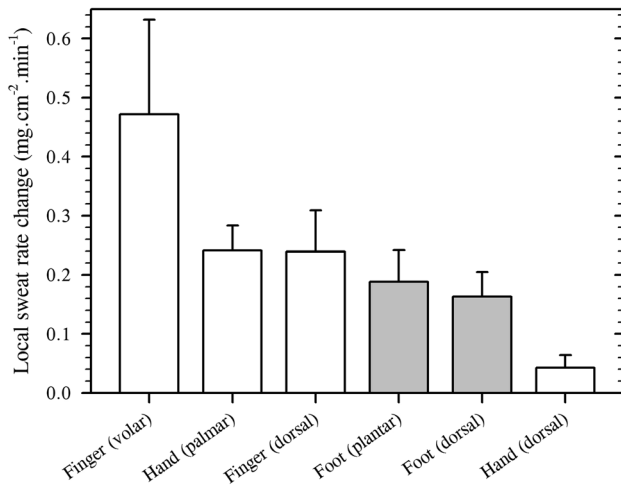


Fig. 6 Psychological sweating (ventilated capsules) from the glabrous (volar) and non-glabrous (dorsal) surfaces of the hands and feet (*shaded bars*) during mental arithmetic (10 min) performed under thermoneutral conditions (26 °C, 50 % relative humidity). Data are mean changes in sweating (peak minus baseline secretion with standard errors of the means), extracted from Machado-Moreira and Taylor (2012b) and used with permission

hand failing to yield significant sweat. In addition, changes in skin conductance were measured at the volar and dorsal aspects of the first and second fingers. This technique was used because the reabsorption of primary sweat can prevent low-intensity (subliminal) secretion from reaching the skin surface, thus remaining undetected via sweat capsule methods. Indeed, psychogenic sweat can remain within the duct for 150–200 s before being fully absorbed (Ohmi et al. 2009), but it can easily be detected from changes in skin conductance (Thomas and Korr 1957). Both the glabrous and non-glabrous surfaces of the fingers were found to produce significant primary sweat. Collectively, these observations demonstrated that psychological sweating is ubiquitous, further contesting the hypothesis that it might be restricted to the glabrous skin surfaces of the hands and feet.

In the most recent project from this series, the hypothesis was tested that psychological sweating was not mediated via noradrenergic neural pathways (Machado-Moreira et al. 2012). Subjects were exposed to mental arithmetic, palmar pain and isometric handgrip stimulations under each of three different conditions, applied in series and within one trial: thermoneutral rest (27–28 °C), passive whole-body heating (water-perfusion garment and foot bath) and a systemic atropine infusion (0.04 mg kg⁻¹) with deep-body temperature still elevated, but now clamped (Cotter and Taylor 2005). Sweating responses were measured using ventilated capsules on the dorsal and volar surfaces of one hand (plus forehead, dorsal forearm and calf), and from changes in skin conductance at the same hand sites

(plus forehead and dorsal forearm). When thermoneutral, these non-thermal treatments elicited significant discharged sweat only from the palm, but following passive heating, significant secretions were also induced from the dorsal and volar sites, verifying previous observations (Machado-Moreira and Taylor 2012a). When the atropine blockade was established and sweating was completely suppressed, the non-thermal stimuli were repeated, with no site producing either primary or discharged sweat. These data demonstrated that sweating during these thermal, psychological and static exercise stimulations was exclusively cholinergically mediated. Whilst eccrine sweat glands can respond to catecholamines (Robertshaw 1977; Nakazato et al. 2004), these observations were not consistent with the existence of functionally relevant noradrenergic pathways to the glands of the glabrous hand surfaces.

Palmar and plantar hyperhidrosis

Primary hyperhidrosis is a pathological state in which discharged sweating exceeds that required for the maintenance of normal skin function or that which might normally be observed during thermal and non-thermal stimulations (Kuno 1956; Quinton 1983; Vorkamp et al. 2010). It can be a whole-body phenomenon, but is more frequently observed at the palms, soles and axillae. Epidemiological evidence indicates that perhaps 1 % of the population suffers from this condition (Adar et al. 1977; Vorkamp et al. 2010), with about one-fifth of these people being affected only at the palms (Strutton et al. 2004). Hyperhidrosis usually occurs early during adolescence (Edmondson et al. 1992), with most patients being young women (Quraishi and Giddings 1993). In some individuals, palmar and plantar sweating can be so excessive that it can handicap the performance of tasks for which hand grip may be essential. A range of treatments exist from topical medication and the administration of cholinergic antagonists, through to injections of botulinum toxin to block sudomotor neurotransmitter release (Vorkamp et al. 2010). In more severe cases, surgical interventions may be used (Kux 1978; Edmondson et al. 1992; Rieger et al. 2011).

Thermal biophysics

When a warm object is moved from one thermal steady state to a colder state, its energy content changes, with the outermost layer of molecules losing thermal energy to the environment, forming a cooler shell. A series of thermal layers soon form, with heat continuously moving away from the centre until thermal equilibration occurs. Between adjacent layers, thermal gradients are formed, and each remains until heat transfer ceases (Burton and Bazett 1936;

Table 6 The biophysical attributes and heat exchanges of one hand and one foot from an average, resting man (79.1 kg, 1.72 m) and women (66.2 kg, 1.60 m)

Attributes	Hand		Foot	
	Male	Female	Male	Female
Basal blood flow (mL min ⁻¹) ^{a, b}	24.4	20.0	24.2	19.8
Minimal blood flow (mL min ⁻¹) ^c	1.46	1.20	1.72	1.41
Minimal blood volume (mL) ^{a, c}	3.4	2.8	1.7	1.4
Maximal blood flow (mL min ⁻¹) ^c	109.5	89.8	154.8	126.9
Maximal blood volume (mL) ^{a, c}	110.0	90.0	155.0	127.0
Average specific heat (kJ kg ⁻¹ °C ⁻¹): all tissues ^d	1.201	0.699	2.635	1.835
Radiation and convection (W): cold air (15 °C) ^e	-17.9	-14.2	-29.0	-23.0
Radiation and convection (W): neutral air (27 °C) ^e	-6.6	-8.3	-10.6	-13.4
Radiation and convection (W): hot air (45 °C) ^e	19.2	15.7	31.2	25.4
Evaporation (W): rest (air 36 °C) ^f	-14.8		-22.4	
Evaporation (W): exercise (air 36 °C) ^f	-66.5		-45.8	

Authors' compilation using data obtained from 49 countries (height) and seven countries (body mass)

^a Derived using appendage volumes from Table 1 and the following blood flows

^b Derived using appendage volumes and basal volume-specific blood flows: hand = 6.7 mL 100 mL⁻¹ min⁻¹; foot = 2.8 mL 100 mL⁻¹ min⁻¹ (Caldwell et al. 2014)

^c Minimal blood flow = 0.4 (hand: mid-range value from Forster et al. 1946) and 0.2 mL 100 mL⁻¹ min⁻¹ (foot: Kunkel and Stead 1938), maximal blood flow = 30 (hand: Roddie et al. 1957a) and 18 mL 100 mL⁻¹ min⁻¹ (foot: Allwood and Burry 1954)

^d Weighted average derived from tissue-related mass and specific heat: blood = 3.610 kJ kg⁻¹ °C⁻¹ (González-Alonso et al. 2000), bone = 1.256 kJ kg⁻¹ °C⁻¹ (Karmani 2006), muscle = 3.590 kJ kg⁻¹ °C⁻¹ (González-Alonso et al. 2000), skin = 3.600 kJ kg⁻¹ °C⁻¹ (Henriques and Moritz 1947), other tissues = 2.302 kJ kg⁻¹ °C⁻¹ (Henriques and Moritz 1947)

^e Radiative plus convective heat loss (W) = 6.45 × appendage surface area × 1/total insulation × (ambient - skin temperature): assumes naked skin (surface insulation 0.13 m²K W⁻¹) and uses skin temperatures from Webb (1992) with a -0.5 °C offset for women (Cunningham et al. 1978)

^f Area-weighted evaporation using sweat rates from Figs. 3 and 4, assuming 100 % evaporation with heat loss of 2.43 kJ mL⁻¹

Golden and Hervey 1977). The energy exchanges during this dynamic phase are determined by the physical properties of the object and its environment, and these first principles apply to the hands and feet. However, these appendages also produce heat, and they secrete sweat and are variably perfused.

In thermally comfortable individuals, temperature gradients favouring heat loss exist along and below the surfaces of both appendages (Pennes 1948; Werner and Reents

1980; Webb 1992). These result from local metabolism and heat transfers among adjacent tissues, including its convective delivery in the blood. Since the hands and feet have a relatively limited capacity for heat production, then local tissue temperatures are principally altered through vasomotor and sudomotor changes, and the corresponding dry and evaporative heat transfers. Tables 1 and 6 summarise the biophysical characteristics of the hands and feet that support heat conservation and dissipation, allowing one to predict heat exchange across different thermal environments. Readers are directed to hand and foot models that may supplement this information (Lotens 1992; Kuklane et al. 2000). In cool-cold conditions, skin temperatures track changes in cutaneous blood flow quite well, but this relationship becomes weaker under thermoneutral states and is almost non-existent in the heat (Fetcher et al. 1949).

Powerful vasoconstriction reduces blood flows to 0.2–0.4 mL 100 mL⁻¹ min⁻¹ (foot-hand), theoretically delivering <0.1 W of heat to each appendages for a 1 °C thermal gradient. Conversely, maximal segmental flows of 18–30 mL 100 mL⁻¹ min⁻¹ (foot-hand) increase heat mass flow to 8.5 and 6.0 W (respectively) for the same thermal gradient, elevating dry and evaporative heat losses. At the hand, maximal blood flows are typically 4.5-fold greater than in the thermoneutral state, and ~75 times greater than may be expected during maximal vasoconstriction; the corresponding comparisons for the foot are 6.4- and 90-fold larger.

To evaluate the impact of these vascular changes on the dry heat exchange of the hands and feet in air, three environments (15, 27, 45 °C) were modelled using data from Tables 1 and 4, first-principle equations (Goldman and Kampman 2007) and skin temperatures observed for unclothed people in these conditions (Webb 1992). The results of these computations are presented in Table 6.

Whilst the combined radiative and convective transfers of the hands and feet were not high, when normalised to segmental and gender-specific surface areas, these became impressive due to the large surface area to mass ratios of these segments. For instance, at 27 °C, each hand and foot could lose 150–220 W m² (male–female); Chen et al. (1999) reported losses of 50–300 W m⁻² in cold air from the hand. This gender difference is potentially quite important and needs to be explored to help explain differences in thermoeffector function. However, when considered across genders, and in combination with the arteriovenous anastomoses found in these limb segments, these capacities make the hands and feet important sites for heat dissipation, and this attribute has been investigated during water immersion (Wade et al. 1979; Livingstone et al. 1989; Kuklane et al. 1999). Indeed, others have taken advantage of this characteristic to rapidly extract heat from the hands of hyperthermic individuals (Tipton et al. 1993; House et al.

1997, 2003b; House 2003). When both hands were placed into cold water ($\sim 10^\circ\text{C}$), heat extraction approximated 70–85 W, whilst the feet lost 90–95 W.

For heated, resting subjects secreting sweat from the hand at 22 mL h^{-1} (as described above), complete evaporation would dissipate a further 15 W (rest: 336 W m^{-2}) from each hand. Sweat from each foot under identical conditions (33 mL h^{-1}) would remove another 22 W (313 W m^{-2}). During exercise in the heat ($\sim 100\text{ W}$ of external work), the potential contributions from each appendage increase to 67 W (hand: $1,506\text{ W m}^{-2}$) and 46 W (foot: 642 W m^{-2}) using corresponding sweat rates of 99 and 68 mL h^{-1} . Thus, these body segments, and in particular the hands, have a considerable thermolytic potential.

Since the hands and feet have such area-specific heat transfer potentials, then a brief reflection on gloves and socks appears warranted. These garments add insulation, but do not modify local temperature in the absence of either external heating or a significant change in cutaneous circulation (House et al. 2003a). However, since such garments do reduce heat loss and help defend deep-body temperature, then they add effective insulation that can enhance thermal comfort. In states close to thermoneutrality, blood will perfuse both appendages, and the hands and feet will become warmer and more comfortable. Thus, within this zone, hand and footwear can have a significant impact on thermal comfort. For instance, if an individual with cold hands or feet, but normal deep-body temperature, puts on gloves or socks, and rapidly feels a warming of the extremities, then one could assume that person was losing heat just slightly faster than its local delivery to these limb segments. One can also assume that cold discomfort preceded a fall in deep-body temperature. In this case, clothing increased total insulation to match or exceed that required for thermal homeostasis, and the thermoneutral state was rapidly restored. In another example, one often observes people removing hand or footwear without modifying torso insulation. In this instance, the upper limit of thermal comfort was crossed, prompting an effective and learned behavioural response to facilitate a subtle increase in heat removal. However, if the deep-body tissue temperature has fallen sufficiently, adding gloves and socks will have a negligible impact upon local blood flow (Figs. 1, 2), deep-body temperature or thermal comfort.

Concluding remarks

The surface area to mass ratios of the hands and feet are ideally suited to conserving and dissipating heat. This characteristic is supported by counter-current heat exchanges and the arteriovenous anastomoses that permit large local blood flow increase, with maximal hand blood flow rising

to be 4.5 times greater than in the thermoneutral state. At the foot, these flows differ by a factor of 6.4. Thus, the theoretical maximal heat deliveries for the hand and foot are 6.0 and 8.5 W (respectively) for a 1°C thermal gradient. Maximal vaso- and venoconstriction reduces blood flows to levels less than the metabolic requirement, physiologically isolating the extremities to conserve heat, and restricting the heat flow for each segment to $<0.1\text{ W}$. In addition, the production of eccrine sweat from each hand (22 mL h^{-1}) and foot (33 mL h^{-1}) in heated, resting individuals could dissipate a further 15 and 22 W (respectively), assuming 100 % evaporation. Such attributes allow these regions to behave as excellent radiators, insulators and evaporators in resting and unclothed individuals, characteristics that are shared with the large, well-perfused and poorly insulated ears of elephants (Phillips and Heath 1992) and bills of toucans (Tattersall et al. 2009). However, during upright locomotion and tool use, vascular dilatation is much less effective, with load bearing and muscle activation redirecting plantar and palmar venous return to the dorsal surfaces, possibly reducing heat dissipation. In addition, whilst sweat flows are elevated during work in the heat [e.g. 99 (hand) and 68 mL h^{-1} (foot)], the thermolytic potential of these appendages is often prevented by the use of hand and footwear.

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