THE ROLES OF HANDS AND FEET IN TEMPERATURE REGULATION IN HOT AND COLD ENVIRONMENTS.

Nigel A.S. Taylor[1], *Christiano A. Machado-Moreira*[1], *Anne M.J. van den Heuvel*[1],
Joanne N. Caldwell[1], *Elizabeth A. Taylor*[1] *and Michael J. Tipton*[2]

[1]*Thermal Physiology Laboratory, University of Wollongong, Wollongong, Australia*
[2]*Human and Applied Physiology Laboratory, University of Portsmouth, Portsmouth, England*

Contact person: nigel_taylor@uow.edu.au

INTRODUCTION

In this paper, we briefly review the physiological and biophysical characteristics of the hands and feet, and their association with autonomic (physiological) and behavioural temperature regulation, and with thermal injury. A comprehensive review of this topic is not currently available within the literature.

The temperatures of the skin and subcutaneous tissues, particularly those of the hands and feet, vary significantly as air temperatures move away from the thermal comfort zone. Mean skin temperature increases approximately 0.7°C for each 1°C elevation in air temperature, with smaller changes at the hands ($0.46\ ^{o}.^{o}C^{-1}$) and slightly larger changes at the feet ($0.8^{o}.^{o}C^{-1}$: Bedford, 1936). These variations reflect local differences in metabolic rate, convective heat delivery and thermal exchanges with the thermal environment.

NEURAL PATHWAYS

Thermoregulation is achieved by modulating physiological efferent functions (skin blood flow, sweating, shivering) and implementing behavioural strategies, following the central integration of thermal feedback from the deep body and superficial tissues. In all environments, cutaneous thermoreceptors provide the first thermal feedback signals, giving rise to thermal sensations, physiological adjustments and eventually to decisions relating to the pleasantness or comfort that the environment and associated responses evoke.

The principal nerves carrying thermoreceptor feedback from the hand are the radial and median nerves, with the latter having a more important sensory role. This feedback travels to the spinal cord via the 6th, 7th and 8th cervical spinal nerves, and eventually to the hypothalamus. For the foot, the corresponding nerves are the tibial, sural and superficial fibular nerves, which enter the spinal cord via the 1st sacral and 5th lumbar spinal nerves: these nerves also relay efferent signals that control blood flow, sweating and muscular function. The nerves that dictate thermoeffector function of the hand leave the spinal cord at the thoracic segments (T2-T8), while those for the foot leave at the thoracic and lumbar segments (T11-L2).

Most neurones of the sympathetic nervous system are noradrenergic. However, this does not hold for the thermoefferent fibres, which possess at least three different neurotransmitters. For instance, the fibres that innervate most eccrine sweat glands are cholinergic, with perhaps some evidence of noradrenergic control at the glabrous (hairless) surfaces of the hands and feet. Skin blood flow to these glabrous surfaces is determined solely by noradrenergically mediated vasoconstrictor nerves (Kellogg, 2006). In contrast, blood flow to the non-glabrous (hairy) skin regions is mediated by separate noradrenergic vasoconstrictor and active vasodilatory branches of the sympathetic nervous system; the neurotransmitter for the latter pathway awaits identification (Kellogg, 2006).

VASCULAR FUNCTION AND DYSFUNCTION

Blood flow to the hands is provided through the radial and ulnar arteries, and via the deep palmar arch, the superficial palmar branch, the metacarpal arteries and the digital arteries. In the foot, blood enters from behind each of the malleoli (malleolar arteries) and across the upper surface of the foot (dorsalis pedis artery). The positioning of these vessels with respect to the bones of the foot has significant implications for shoe design. Cutaneous capillaries are located just below the epidermis, with hand veins draining into either superficial or deep vessels, the largest of which run along the dorsal hand and foot surfaces. Hands and feet also contain arteriovenous anastomoses, and when these shunts are open, dramatic elevations in skin blood flow can occur. Indeed, these vessels are responsible for the extremities behaving as very efficient heat exchangers (radiators), with thermal homeostasis sometimes being achieved entirely through subtle changes in skin blood flow through the anastomoses of the hands, face and feet (Hales, 1985).

Under thermoneutral conditions, hand blood flow (10 mL.100 $mL^{-1}.min^{-1}$; Roddie, 1983) is typically 3-4 times greater than that of the foot (3 mL.100 $mL^{-1}.min^{-1}$; Colemont and Decoutere, 1981). When normalised to the skin surface area, hand blood flow is 4-5 times greater than the rest of the body, and about twice that of the foot (Taylor *et al*., 2008a). During protracted cold exposures, extremely low local blood flows are observed (hand: 0.15 mL.100 $mL^{-1}.min^{-1}$; foot: 0.2 mL.100 $mL^{-1}.min^{-1}$; Taylor *et al*., 2008a, b), and such flows can be below the metabolic requirements of these tissues. In the heat, maximal hand blood flow approximates 30 mL.100 $mL^{-1}.min^{-1}$, while 18 mL.100 $mL^{-1}.min^{-1}$ appears maximal for the foot (Taylor *et al*., 2008a, b). Finger blood flows have greater minimal (0.2 mL.100 $mL^{-1}.min^{-1}$) to maximal variations (120 mL.100 $mL^{-1}.min^{-1}$) with changes in whole-body thermal state (Nagasaka *et al*., 1987). In addition, blood flow at the middle phalanx is only about 30% of that at the distal phalanx (Wilkins *et al*., 1938).

The single most important determinant of hand and foot blood flow is the thermal status of the body core (Ferris *et al*., 1947), with a 1^{o}C change in mean skin temperature producing a 1.3 fold change (10 mL.100 $mL^{-1}.min^{-1}$) in finger blood flow, and the corresponding change in core temperature resulting in a 2.8-fold change (32 mL.100 $mL^{-1}.min^{-1}$; Wenger *et al*., 1975). Thus, local temperatures can influence blood flow, but this affect is minimal when the body core is either hot or cold, and it is greatest when deep body temperature is within the thermoneutral range.

The blood supply to the hands and feet represents their primary source of heat, and the minimal blood flows seen with deep and superficial tissue cooling, as a result of intense peripheral vasoconstriction, represent a physiological amputation of these appendages. The consequence of this is a loss of both sensation and function, and in particular manual dexterity. Insufficient tissue perfusion and heat loss affect vascular smooth muscle contractility, which can, if core temperature is normal or raised, result in vasodilatation. This cold-induced vasodilatation can protect from, and delay tissue damage. In the absence of tissue warming, extreme or prolonged cooling of the extremities can result is freezing and non-freezing cold injury. The latter condition has recently been associated with a cold-induced defect in vascular smooth muscle contractility caused by a loss of NO-dependent endothelial function (Stephens *et al*., 2009).

BIOPHYSICAL ATTRIBUTES

Relative to the entire body, the surface area to mass ratio for the hand is 4-5 larger, while that for a foot is 2.5-3 larger (males-females). Therefore, these appendages provide an effective route for heat exchange with the environment, as long as thermal energy can be delivered from the body core via convective (mass flow) pathways.

The maximal hand and foot blood flows (30 and 18 mL.100 $mL^{-1}.min^{-1}$) can result in theoretical peak heat transfers from the core to both hands of 12 W or 286 $W.m^{-2}$ for a 1°C core-skin gradient. The corresponding values for both feet are 16 W or 404 $W.m^{-2}$. Thus, while the absolute heat transfer to the hands and feet from the body core is not high, their surface-area normalised transfer, when considered in combination with the huge capacity of the arteriovenous anastomoses to elevate local skin blood flow, makes these appendages very important locations for heat dissipation (Taylor *et al*., 2008a; 2008b).

This heat delivery, and its subsequent dissipation, is advantageous in the heat, as it facilitates central cooling, but, as described above, it can be dangerous in the cold. Furthermore, these data also represent maximal core-periphery transfers, and not that which occurs between the skin and its surrounding environment. By using foot and hand temperatures observed during actual air exposures to 15°, 27° and 45°C (Webb, 1992), the theoretical radiative and convective heat transfers from each hand and foot to the surrounding air may be computed, and these represent respective losses of 16.6 W and 25.5 W (15°C), and 7.7 W and 11.8 W (27°C), or gains of 18.1 W and 27.7 W (45°C). More impressive heat transfer occurs when the vasodilated appendages of heated individuals are placed into cold water (Tipton *et al*., 1993). In this circumstance, heat loss can range from 70-85 W (hands) and 90-95 W (feet: House and Tipton, 2002).

SUDOMOTOR FUNCTION

Sweat glands are widely distributed over the body surface, with a total of two-four million glands capable of producing sweat at peak rates of 10-15 $L.d^{-1}$. Each hand has approximately 160,000 eccrine sweat glands, with greater numbers on the palmar (115,000) than dorsal surface (46,000: Machado-Moreira *et al*., 2008). Similarly, one foot has approximately 155,000 glands, with more on the plantar surface (100,000) than dorsal surface (55,000; Taylor *et al*., 2006).

Both the hands and feet display two general sweat patterns during heating: low secretion at the glabrous surfaces, and moderate secretion from all other surfaces. During passive heating at rest (40 min), where the average whole-body skin temperature was increased from 34.5°C to 35.9°C, and core temperature was elevated to 37.2°C from 36.9°C, the palms and soles displayed the lowest intra-segmental sweat rates (palm: 0.16 $mg.cm^{-2}.min^{-1}$; sole: 0.23 $mg.cm^{-2}.min^{-1}$). Conversely, the dorsal distal phalanges of the fingers (0.62 $mg.cm^{-2}.min^{-1}$) and the distal phalanx of the big toe (0.50 $mg.cm^{-2}.min^{-1}$) displayed the highest sweat rates. Under these experimental conditions, sweating averaged 0.38 $mg.cm^{-2}.min^{-1}$ from the hands (Machado-Moreira *et al*., 2008) and 0.45 $mg.cm^{-2}.min^{-1}$ from the feet (Taylor *et al*., 2006).

When exercising in the heat, sweat gland recruitment occurs almost simultaneously across most body surfaces, including the hands and feet, although the intra-segmental distribution is not uniform. The dorsal surfaces of both appendages display a relatively consistent secretion rate, accounting for approximately 65-70% of total sweat flow from each extremity. Peak hand sweat rates during heavy exercise are: 4.0 mL.h^{-1} (palm); 16.8 mL.h^{-1} (volar fingers); 16.6 mL.h^{-1} (dorsal fingers); and 15.0 mL.h^{-1} (dorsal hand: Machado-Moreira *et al*., 2008). Corresponding sweat production from the foot is: 14.5 mL.h^{-1} (dorsal), 5.4 mL.h^{-1} (medial) 5.0 mL.h^{-1} (lateral), 16.0 mL.h^{-1} (plantar), 2.9 mL.h^{-1} (dorsal toes), and 1.1 mL.h^{-1} (plantar toes; Taylor *et al*., 2006). Therefore, the maximal theoretical evaporative cooling possible from a single hand is about 35.4 W (assuming 100% evaporation), and 27.6W from one foot. Indeed, when normalised to surface area, the potential for evaporative heat loss from the two hands is 110% greater than at the torso, and 200% greater than at both feet, but only half that of the forehead (Taylor *et al*., 2008b).

THERMAL SENSATION AND DISCOMFORT

Thermal sensations arise within the somatosensory cortex. Sensory feedback from the face and hands, and to a lesser extent the feet and toes, is very powerful as these areas provide feedback to a larger volume of the somatosensory cortex (Penfield and Rasmussen, 1952). Discomfort drives behaviour, based upon the pleasantness of a given thermal state, and while this sensation is related to both the core and peripheral temperatures, it is believed that thermal comfort is primarily determined by the thermal state of the core (Hensel, 1981). It is known that a separation exists between local and whole-body discomfort, such that one can have uncomfortable feet while the rest of body remains thermally comfortable. However, the face, hands and feet are associated with significantly greater thermal discomfort with local tissue temperature changes. Indeed, the hands and feet provide very powerful feedback relative to local comfort, but play a minimal role relative to whole-body thermal discomfort (Cotter *et al*., 1996). These high local sensitivities are important to clothing design, but are of less importance to behavioural responses. The head, however, dominates whole-body thermal sensation and discomfort (Cotter and Taylor, 2005), so the thermal status of the face has a more powerful role in dictating thermoregulatory behaviour.

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