Experimental Physiology

Variations in regional sweat composition in normal human males

Mark J. Patterson*, Stuart D. R. Galloway† and Myra A. Nimmo

Scottish School of Sport Studies, University of Strathclyde, Glasgow G13 1PP and †Department of Sport Studies, University of Stirling, Stirling FK9 4LA, UK

(Manuscript received 11 May 2000; accepted 25 August 2000)

This project aimed to quantify the regional distribution of sweat composition over the skin surface and to determine whether sweat constituent concentrations collected from regional sites can estimate whole-body concentrations. Ten males cycled for 90 min in a 20 °C (50% relative humidity) environment at 45% peak aerobic power. Sweat was collected from eleven skin regions and the whole body, using a wash-down technique. Strong relationships were evident between the regional and whole-body sweat [Na^+] and [Cl^-], such that the thigh and calf exhibited greater correlation coefficients than area-weighted means derived from four and eight skin regions. Therefore, in this particular protocol the whole-body sweat [Na^+] and [Cl^-] could be predicted from regional sweat collections. Relationships between sweat constituents were evident for sweat [Na^+] and pH, and sweat [K^+] and [lactate] when data were pooled between skin regions and subjects. To our knowledge this is the first investigation to report a positive relationship between sweat [K^+] and [lactate]. The exact mechanism responsible for the positive relationship between sweat [K^+] and [lactate] is uncertain although it is speculated to occur at the secretory coil. *Experimental Physiology* (2000) **85.6**, 869–875.

It is well recognised that sweat rate is not uniform over the skin surface (Weiner, 1945; Hertzman *et al*. 1953; Park & Tamura, 1992; Cotter *et al*. 1995). Similarly, Sato & Dobson (1970) reported variations in sweat Na^+ excretion rates between the skin regions of the forehead, back and forearm. However, the sweat Na^+ concentration ([Na^+]) at other skin regions and the variation in concentrations of other sweat constituents such as Cl^- ([Cl^-]), lactate ([lactate]), HCO_3^- ([HCO_3^-]) and pH over the body skin surface has received little attention. Most investigators collect sweat from a single skin region, usually the back or forearm (Itoh *et al*. 1952; Fellman *et al*. 1983; Sato & Sato, 1990; Falk *et al*. 1991; Boisvert *et al*. 1993; Yosipovitch *et al*. 1994), and do not evaluate relationships between sweat constituents. A relationship has been reported between sweat [Na^+] and pH in isolated sweat glands (Kaiser *et al*. 1974), such that the greater the sweat [Na^+] the greater the sweat pH. Regressing sweat constituents against each other assists the assessment of potential secretory and re-absorptive processes, which are ultimately responsible for the composition of the excreted sweat. Furthermore, while it is clear that sweat rate affects the sweat [Na^+], [Cl^-], [lactate], [HCO_3^-] and pH within a single gland or at a particular skin region (Sato & Dobson, 1970; Alan & Wilson, 1971; Kaiser *et al*. 1974; Falk *et al*. 1991; Yosipovitch *et al*. 1994), it is uncertain whether differences in gland structure, between skin regions (Sato & Dobson, 1970), may affect relationships between sweat rate and sweat constituent concentrations.

The determination of sweat composition is also important for providing estimates of changes in extracellular fluid and nutritional replacement. However, the determination of whole-body sweat electrolyte losses is usually desired during the measurement of other physiological parameters such as plasma constituent concentrations, skin and core temperatures, heart rate and respiratory function. The measurement of these parameters increases the risk of contamination and may compromise the derivation of sweat constituent losses from a whole-body wash-down technique. Reliable relationships between regional and wash-down sweat constituent concentrations may permit the estimation of whole-body sweat constituent losses without employing a whole-body wash-down technique. Previously a multiple linear regression was employed to estimate whole-body sweat urea loss from regional sweat collections (Lemon *et al*. 1986). However, a multiple linear regression yields both positive and negative coefficients, and thus physiologically does not represent the actual excretion response over the skin surface. It is hypothesised that area-weighted coefficients may provide a more appropriate estimate of the mean whole-body sweat constituent concentrations.

The current investigation was designed to assess the regional variations in sweat composition over the skin surface induced by an endogenous heat load. Comparisons of regional and whole-body sweat constituent concentrations permitted the determination of the most representative skin regions, which

Publication of *The Physiological Society*

* Corresponding author: mark.patterson@strath.ac.uk

can accurately estimate the whole-body values. Furthermore, the determination of various sweat constituent concentrations at different skin regions allowed the assessment of potential differences in sweat gland excretory function between skin regions.

METHODS

Subjects

Ten males (age 22.1 ± 4.6 years; mass 76.4 ± 6.9 kg; peak oxygen consumption 4.50 ± 0.85 l min^{-1}; mean ± S.D.) volunteered to participate in this investigation. All procedures were performed according to the Declaration of Helsinki and were approved by the University of Strathclyde ethics committee. Subjects provided written informed consent.

Experimental protocol

Subjects cycled on a friction-braked ergometer (model 684, Monark, Sweden) for 90 min at 20 °C (50 % relative humidity). The work rate was set at 45.5 ± 1.0 % peak aerobic power (167 ± 18.1 W). A whole-body wash-down technique was employed, which has been previously described by Shirreffs & Maughan (1997). Briefly, subjects showered with soap and water after which they rinsed with 4 l deionised water. At completion of the 90 min cycling in a large plastic bag, subjects again rinsed their skin with 4 l deionised water, with a further litre used to rinse the bike, silage bag and frame. The volume of fluid added to the large plastic bag via this rinsing process was corrected for water remaining on the subjects after exiting. Pilot trials confirmed that the cleaning process, performed prior to each experimental trial, resulted in all equipment (ergometer, plastic bag and frame, towel and shorts) being free of electrolytes.

Whole-body sweat loss was determined by change in body mass (±2 g; Sartorius, Germany), uncorrected for respiratory water loss and loss resulting from CO_2–O_2 exchange. Regional sweat collections were obtained from the forehead (middle of the forehead), chest (superior to the nipple and ∼5 cm lateral from the sternum), scapula (over the spine of the scapula and ∼7 cm lateral from the vertebral column), abdomen (∼5 cm lateral from the sternum), lower back (∼5 cm lateral from the vertebral column), upper arm (mid-dorsal), forearm (mid-dorsal), hand (dorsal), thigh (mid-ventral), calf (medial–ventral) and foot (ventral). Sweat patches consisted of parafilm being attached to the skin with a wound dressing (Opsite, Smith & Nephew), as described by Brisson *et al*. (1991). Boysen *et al*. (1984) employed a similar technique for regional sweat collections and found it to be free of epidermal contamination for the measurements of Na^+, K^+, glucose and lactate. The area of sweat collection was 8 cm^2 for the forehead and 24 cm^2 for all other sites. Sweat was aspirated at the end of the 90 min trial from the regional patches in a uniform order. Regional sweat rates were determined gravimetrically (± 0.01 g; A&D Instruments, UK) by the change in mass of the aspirating syringe. From the regional sweat collections mean whole-body values were calculated using surface area-weighted equations. The mean of eight sites was calculated using the following equation (from *Evaluation of Thermal Strain by Physiological Measurements* (ISO 9886: 1992 [E]), International Organisation for Standardization, Geneva, Switzerland, 1992):

Mean whole-body concentration = 7 % forehead + 17.5 % chest + 17.5 % scapula + 7 % upper arm + 7 % forearm + 5 % hand + 19 % thigh + 20 % calf.

The coefficients used in the four-site equation were proportionally modified from the eight-site equation, resulting in:

Mean whole-body concentration = 28.2 % chest + 28.2 % scapula + 11.3 % forearm + 32.3 % thigh.

Sample analysis

Sweat [Na^+] and [K^+] were determined by flame photometry (Sherwood, UK), while [Cl^-] was assessed using the thiocyanate technique (Proc. 461, Sigma Diagnostics, USA). Sweat lactate was assessed by the fluorometric technique described by Maughan (1982). Sweat pH was determined with a micro-combination pH probe (Microelectrodes Inc, USA) after bubbling a 50 μl sample with 5 % CO_2, while sweat [HCO_3^-] was derived from the equation described by Siggaard-Anderson *et al*. (1988). Sweat was equilibrated with 5 % CO_2, being similar to that of the interstitial fluid, since equilibration with the lower CO_2 partial pressure of the room air will elevate pH.

Statistical analysis

Regression analyses were performed to relate local regional sweat collections, and derived mean concentrations, to whole-body sweat constituent concentrations. Relationships were also assessed between sweat rate and sweat constituents using regression analysis, with data being pooled between skin regions and subjects. At times large between-subject variability affected these relationships, therefore separate within-subject analyses were implemented. α was set at 0.05.

RESULTS

Whole-body *versus* regional sites

Large variations were evident within and between skin regions for both sweat rate and sweat constituent concentrations (Table 1). The regional and mean derived sweat rate and sweat constituents were generally greater than the whole-body values (Table 1). Technical problems prevented the collection of sweat from the hand patch in two subjects and the foot patch in one subject. Therefore, data referring to the sweat rate and constituent concentrations from the hand and foot represent eight and nine subjects, respectively.

Strong correlations were evident between the regional, and mean, and the whole-body sweat [Na^+] and [Cl^-] (Table 2). Some of the individual skin regions exhibited stonger relationships with the whole-body sweat [Na^+] and [Cl^-] than the derived mean values (Table 2). Conversely, the regional and mean sweat [lactate] and [K^+] were not related to the whole-body levels.

The gradient and intercept coefficients for the regression relationships between the regional skin regions and the whole-body sweat [Na^+] and [Cl^-] are presented in Table 3. The gradient coefficient for the foot was close to 1.000 and the intercept coefficient was low, therefore it could be assumed that the sweat [Na^+] and [Cl^-] of the foot most closely represents the absolute levels of the whole body. The thigh skin region was the next best single representation of the whole-body sweat [Na^+] and [Cl^-].

Between skin region analysis

Poor relationships were exhibited between sweat rate and sweat [Na^+] and [Cl^-] when data were pooled between subjects and

Table 1. Regional, mean and whole-body sweat rate and sweat constituent concentrations

	Sweat rate (mg cm^{-2} min^{-1})	[Na^+] (mmol l^{-1})	[K^+] (mmol l^{-1})	[Cl^-] (mmol l^{-1})	Lactate (mmol l^{-1})	pH	[HCO_3^-] (mmol l^{-1})
Forehead	2.39 ± 1.24	56.7 ± 28.9	4.52 ± 1.56	53.8 ± 28.6	6.50 ± 2.06	6.16 ± 0.71	2.50 ± 1.79
Chest	1.21 ± 0.54	47.6 ± 25.7	3.79 ± 1.17	43.6 ± 27.0	7.24 ± 2.48	5.81 ± 0.68	1.32 ± 1.67
Scapula	0.95 ± 0.46	41.1 ± 24.8	3.49 ± 1.23	38.1 ± 24.1	7.65 ± 1.49	5.82 ± 0.81	1.80 ± 2.51
Lower back	0.85 ± 0.41	26.2 ± 19.4	3.11 ± 1.55	22.6 ± 20.5	8.13 ± 3.57	5.28 ± 0.65	0.58 ± 1.05
Abdomen	0.65 ± 0.27	28.5 ± 17.5	4.46 ± 1.55	23.2 ± 19.4	9.81 ± 3.31	5.48 ± 0.77	1.04 ± 1.96
Upper arm	0.52 ± 0.25	39.8 ± 25.8	5.74 ± 1.22	35.0 ± 25.7	9.68 ± 2.14	5.61 ± 0.83	1.46 ± 2.28
Forearm	0.75 ± 0.40	42.2 ± 25.8	5.93 ± 1.30	36.1 ± 26.4	10.52 ± 1.89	5.88 ± 0.89	2.38 ± 3.29
Hand ($n = 8$)	0.91 ± 0.76	34.4 ± 18.4	5.65 ± 1.85	25.9 ± 20.4	11.02 ± 2.86	5.68 ± 0.75	1.07 ± 1.64
Thigh	0.66 ± 0.29	27.0 ± 16.4	4.37 ± 1.68	22.0 ± 16.9	8.52 ± 2.95	5.19 ± 0.62	0.39 ± 0.76
Calf	0.76 ± 0.27	31.5 ± 22.1	4.88 ± 0.77	25.7 ± 22.8	9.43 ± 2.16	5.36 ± 0.76	0.73 ± 1.13
Foot ($n = 9$)	0.56 ± 0.23	24.3 ± 13.1	6.83 ± 1.99	18.1 ± 13.6	12.99 ± 2.39	5.21 ± 0.72	0.52 ± 1.09
Whole body	0.72 ± 0.13	24.1 ± 15.0	3.25 ± 0.62	18.6 ± 15.9	5.87 ± 0.66		
Mean 8	0.96 ± 0.34	38.3 ± 20.8	4.48 ± 0.58	33.5 ± 21.7	8.45 ± 1.83		
Mean 4	0.94 ± 0.37	38.6 ± 20.9	4.13 ± 0.76	22.5 ± 17.7	8.14 ± 2.00		

Values are means ± S.D. ; $n = 10$ unless otherwise stated. Whole-body concentration: Mean 8, mean of eight sites; Mean 4, mean of four sites (see equations in Methods)

skin regions (Table 4). To reduce between-subject variability separate regressions were also carried out for each subject. Four subjects exhibited a positive significant relationship between sweat rate and sweat [Na^+] ($r = 0.60$ to 0.71; $P < 0.05$), although this was insignificant in the other subjects, resulting in a poor overall correlation of 0.30 (Table 4). As anticipated a strong relationship was apparent between [Na^+] and [Cl^-] (Table 4). Sweat [lactate] exhibited the strongest relationship with sweat rate (Table 4), with five subjects exhibiting a significant negative relationship when individual regressions were performed ($r = 0.58$–0.87; $P < 0.05$). However, the moderate correlation coefficient resulted in sweat rate only accounting for 28 % of the sweat [lactate]. A strong positive relationship existed between sweat [lactate] and sweat [K^+] (Fig. 1), although both of these constituents were not related to any other sweat constituent (Table 4). Nine of the ten subjects exhibited a significant positive relationship between sweat lactate and [K^+] when individual regressions were performed ($r = 0.73$–0.94; $P < 0.05$).

Sweat [Na^+] and pH were positively related (Fig. 2). A similar correlation coefficient was evident for the relationship between sweat [Na^+] and sweat [HCO_3^-] (Table 4). The sweat [H^+] and [HCO_3^-] did not exhibit a relationship with sweat rate (Table 4).

Table 2. Correlation coefficients for analysis between regional and whole-body sweat constituent concentrations

Whole body *vs.*	[Na^+]	[Cl^-]	[K^+]	Lactate
Forehead	0.41	0.52	0.23	0.30
Chest	0.74*	0.87*	0.40	0.07
Scapula	0.82*	0.93*	0.07	0.02
Lower back	0.88*	0.89*	0.35	0.45
Abdomen	0.64*	0.85*	0.25	0.06
Upper arm	0.82*	0.93*	0.15	0.69*
Forearm	0.88*	0.97*	0.05	0.49
Hand	0.68	0.94*	0.55	0.23
Thigh	0.89*	0.96*	0.32	0.05
Calf	0.93*	0.98*	0.39	0.07
Foot	0.88*	0.93*	0.06	0.12
Mean 8	0.88*	0.97*	0.28	0.29
Mean 4	0.88*	0.95*	0.38	0.04

*Significant relationship with whole-body concentration ($P < 0.05$).

Table 3. Linear regression coefficients for the relationships between the regional and whole-body sweat [Na^+] and [Cl^-]

	[Na^+]		[Cl^-]	
	a	*b*	*a*	*b*
Forehead	0.213	12.023	0.290	3.037
Chest	0.433	3.434	0.511	−3.697
Scapula	0.494	3.728	0.616	−4.855
Lower back	0.715	5.844	0.698	2.884
Abdomen	0.551	8.417	0.699	2.321
Upper arm	0.474	5.243	0.575	−1.588
Forearm	0.510	2.584	0.585	−2.588
Hand	0.565	7.515	0.771	0.504
Thigh	0.811	2.191	0.908	−1.382
Calf	0.629	4.256	0.687	0.912
Foot	1.010	1.120	1.088	0.605
Mean 8	0.632	−0.108	0.706	−4.995
Mean 4	0.629	−0.150	0.793	−0.006

a, gradient of the regression equation; *b*, intercept of the regression equation.

Table 4. Overall correlation coefficients from pooled sweat data of all subjects and skin regions

	SR	$[Na^+]$	$[K^+]$	$[Cl^-]$	$[H^+]$	$[HCO_3^-]$	pH	Lactate
SR		0.24	–0.41	0.33	–0.28	0.24	0.35	–0.53
$[Na^+]$	0.24		0.14	0.96	–0.63	0.65	0.79	0.04
$[K^+]$	–0.41	0.14		0.01	0.12	0.02	–0.04	0.78
$[Cl^-]$	0.33	0.96	0.01		–0.64	0.68	0.81	–0.07
$[H^+]$	–0.28	–0.63	0.12	–0.64		–0.46	–0.84	0.24
$[HCO_3^-]$	0.24	0.65	0.02	0.68	–0.46		0.80	–0.07
pH	0.35	0.79	–0.04	0.81	–0.84	0.80		–0.19
Lactate	–0.53	0.04	0.78	–0.07	0.24	–0.07	–0.19	

SR, sweat rate.

DISCUSSION

Whole body *versus* regional sites

The derived whole-body sweat rate, from the regional collections, overestimated the whole-body mass loss. It was postulated that sweat rate could have been suppressed at the collection regions due to hidromeiosis (Gonzalez *et al.* 1974; Candas *et al.* 1980), since sweat pooled on the skin over the 90 min exercise period. However, the suppression of sweat evaporation at the regional collection sites may have elevated the local skin temperature, and considering that local skin temperature affects sweat rate (Nadel *et al.* 1971), it is likely that the greater regional sweat rates were a function of elevated local skin temperatures.

The regional sweat $[Na^+]$ and $[Cl^-]$ were much greater than the whole-body values (Table 1). This discrepancy is most probably related to the greater regional sweat rates, since sweat $[Na^+]$ and $[Cl^-]$ are related to sweat rate within a skin region, within a subject (Sato & Dobson, 1970; Alan & Wilson, 1971). While the absolute sweat $[Na^+]$ and $[Cl^-]$ were not comparable between the regional and whole-body values, the two measurement techniques were closely related (Table 2). This good agreement was probably due to the large between-subject variability, such that if a subject excreted a low sweat $[Na^+]$ from the whole-body the same response was observed at most of the regional collections. Considering that many skin regions possessed strong relationships with whole-body concentration of constituents it was not surprising that the mean of eight skin regions was no better than the mean of four skin regions in the prediction of whole-body constituent concentrations. Therefore, it would seem that the sweat loss of $[Na^+]$ and $[Cl^-]$ from the whole-body can be accurately predicted from regional sweat collections, and that the inclusion of more than four skin regions did not appreciably increase the predictive power of whole-body sweat constituent concentrations. It could also be considered that a single site, such as the forearm, thigh or calf, could be used to estimate the whole-body concentrations, due to the high correlation coefficients. Furthermore, the regression equation coefficients (Table 3) imply that the absolute sweat $[Na^+]$ and $[Cl^-]$

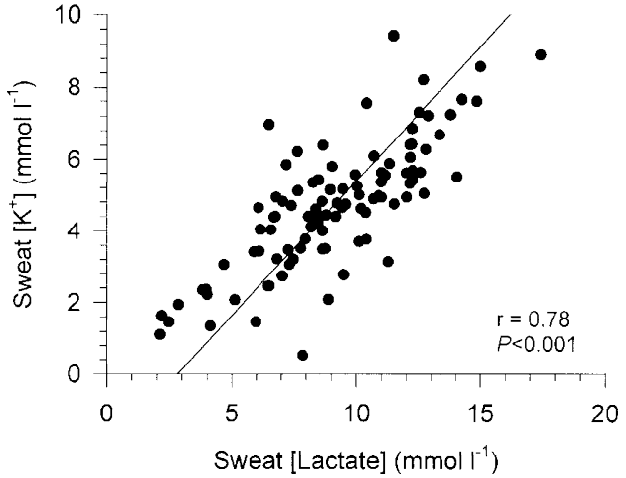

Figure 1
Relationship between sweat [lactate] and sweat $[K^+]$. Data represent eleven skin regions for ten subjects.

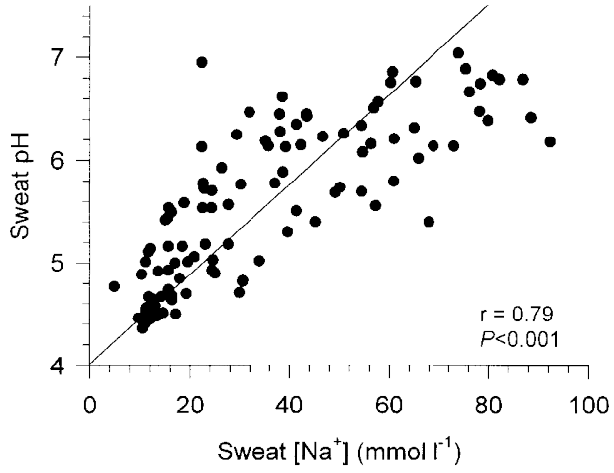

Figure 2
Relationship between sweat $[Na^+]$ and sweat pH. Data represent eleven skin regions for ten subjects.

observed at the foot and thigh were the closest to the whole-body values.

Whole-body sweat [Na^+] and [Cl^-] could be accurately predicted from an area-weighted mean of four skin regions, at the particular sweat rates that occurred in the current investigation. However, it is uncertain whether regional sites can accurately predict whole-body sweat constituent concentrations at higher sweat rates induced by alterations in exercise intensity and environmental conditions.

The regional sweat [lactate] was poorly correlated with the whole-body sweat concentration (Table 2). It is uncertain why these poor relationships were observed and whether either of the collection techniques was responsible. Large variations were evident between subjects and between skin regions from the regional collections (Table 1), yet little variation existed between subjects for the whole-body wash-down data. Therefore, it could be postulated that the wash-down technique was the source of error and not the regional collection technique. Most investigators have used regional sweat collections to measure sweat lactate (Fellmann *et al*. 1983; Boysen *et al*. 1984; Falk *et al*. 1991), rather than a whole-body wash-down, although van Heyningen *et al*. (1952) assessed both arm and whole-body [lactate] during exercise in the heat, and a similar weak relationship can be derived from their raw data ($r = 0.38$).

It is difficult to speculate on the cause of the poor correlation between regional and whole-body sweat [K^+], considering the close relationships exhibited for [Na^+] and [Cl^-]. It might be suggested that the regional collection technique was responsible for the poor relationship. However, as with lactate, between-subject and regional variations were quite large, yet little variation was evident between individuals with respect to the whole-body data. Therefore, it would seem that the wash-down technique might be inadequate for the assessment of whole-body sweat [K^+] and [lactate]. However, the reason for the poor relationships between the regional sites and the whole body is uncertain and requires further investigation.

Between skin region analysis

Many previous investigators have highlighted the relationship between sweat rate and sweat [Na^+], [Cl^-], pH and [HCO_3^-] (Sato & Dobson, 1970; Alan & Wilson, 1971; Kaiser *et al*. 1974; Bijman & Quinton, 1987). However, in the current investigation these sweat constituents were poorly related to sweat rate. These previous investigators determined the relationships within a single gland or within a skin region for a single subject. The poor correlation coefficients observed in the current investigation could be attributed to variations in the reabsorptive capacity, relating to the density of channels and pumps, both between subjects and between skin regions within a subject. However, when between-subject variability was alleviated, by determining these relationships within a subject between the 11 skin regions, poor correlation coefficients were still evident for the majority of the subjects. Therefore, this would imply that not only was there large variability between subjects but also within a subject between skin regions. Furthermore, differences in the active sweat gland density between skin regions may contribute to the poor relationships between sweat rate and sweat constituent concentrations in the current investigation. For example, if the sweat glands of two skin regions had similar secretory and reabsorptive capacities but one region had twice the gland density, then the sweat constituent concentrations would be similar between skin regions although the sweat rate, per square centimetre, would be twofold greater at the region with the greater density. Further investigations are necessary to determine the possible differences in secretory and reabsorptive capacities between sweat glands at various regions over the skin surface.

The sweat [Na^+] and [Cl^-] exhibited strong relationships with the acid–base status of the sweat. It has been assumed that Na^+ is passively transported across the apical membrane into the cell, due to low cytoplasmic [Na^+], which is supported by the basolateral Na^+–K^+-ATPase pump (Quinton & Reddy, 1989). Transport of Cl^- across the apical membrane is passive due to the high Cl^- conductance, although at low luminal [Cl^-] a Cl^-–HCO_3^- exchanger may be involved (Quinton & Reddy, 1989). Therefore, as the sweat reaches the distal duct, and sweat [Cl^-] is lowered, the Cl^-–HCO_3^- exchange is potentially needed to continue Cl^- reabsorption, with an H^+-ATPase pump possibly causing a favourable gradient for HCO_3^- secretion into lumen. The existence of a H^+-ATPase pump has been reported at the epithelial cells of the rat salivary gland and (Roussa & Thevenod, 1998) and more recently at the apical membrane of the duct epithelia (Bovell *et al*. 2000). The combination of H^+ and HCO_3^- would result in CO_2 being reabsorbed into the cell and reformation of HCO_3^- after combining with the cytoplasmic carbonic anhydrase. Therefore, H^+-ATPase pump activity may influence the sweat pH, [HCO_3^-] and [Cl^-] and be subsequently responsible for the relationship between sweat [Cl^-] and pH, and potentially the sweat [Na^+] and pH relationship. Alternatively a Na^+–H^+ exchanger could contribute to the relationship between sweat [Na^+] and pH (Kaiser *et al*. 1974; Bijman, 1987; Quinton, 1987; Sato, 1993). However, sweat [HCO_3^-] and pH are unchanged while [Na^+] and [Cl^-] are much greater in cystic fibrosis patients (Bijman & Quinton, 1987), which may imply that a H^+-ATPase pump is more likely to be responsible for these relationships between sweat [Na^+] and [Cl^-], and the acid–base status of the sweat.

A novel finding of the current investigation was the strong relationship between sweat [lactate] and sweat [K^+]. Considering that neither of these sweat constituents was related to any other sweat constituent, it would seem that a causal relationship possibly exists. It is uncertain whether the mechanism responsible for the sweat [lactate] and [K^+] relationship occurred at the epithelial cells of the secretory coil or reabsorptive duct of the sweat gland. To attribute causal effects for this relationship it first needs to be considered whether both secretory and duct cells can modify the sweat [K^+]. Novak *et al*. (1992) indicated that K^+ could be excreted into the duct, although Reddy & Quinton (1991) observed no evidence for K^+ conductance at the apical

membrane of the epithelial cells at the sweat duct. In the current investigation, sweat [K^+] varied from hypo- to hypertonic levels across the different skin regions (Table 1); consequently, it is difficult to comprehend that both ductal secretion and reabsorption are responsible for the final sweat [K^+]. Therefore, the secretory coil is most probably responsible for the sweat [K^+] and thus the relationship between sweat [K^+] and [lactate]. If lactate was reabsorbed at the duct then the relationship between sweat [K^+] and [lactate] would seem to be coincidental rather than causative. Whereas if the relationship were causative, it would imply that lactate is not transported at the reabsorptive duct.

It is generally assumed that the final sweat [lactate] is attributable to the oxygen-independent metabolism within the cells of the sweat gland (Sato & Dobson, 1971, 1973). Greater Na^+–K^+-ATPase pump activity, which is located at the basolateral membrane (Saga & Sato, 1988), could have elevated metabolism within the secretory glands of the coil and consequently elevated both sweat [lactate] and [K^+]. Greater K^+ influx would probably increase K^+ efflux at both the apical and basolateral membranes. While we currently observed a relationship between sweat [lactate] and [K^+], Bijman & Quinton (1987) reported an unaltered sweat [lactate] and elevated sweat [K^+] in cystic fibrosis patients compared to control subjects. Therefore in this particular population it would seem that sweat [lactate] and [K^+] are not related. The mechanism responsible for this relationship in the current investigation and the location within the sweat gland at which the process occurs are factors which are uncertain and warrant further investigation.

Conclusions

In conclusion, four regional sweat collections, and some single skin regions, could accurately predict the whole-body sweat [Na^+] and [Cl^-]. The inclusion of an additional four skin regions did not improve the strength of the relationship between the estimated and measured whole-body sweat [Na^+] and [Cl^-]. Relationships were also apparent between sweat [Na^+] and [Cl^-], and the acid–base status of the sweat, such that as the sweat [Na^+] and [Cl^-] were reduced so were the sweat pH and [HCO_3^-]. A novel observation was the positive relationship between sweat [lactate] and [K^+]. Due to the holistic nature of this investigation mechanisms can only be speculated.

Allan, J. R. & Wilson, C. G. (1971). Influence of acclimatization on sweat sodium concentration. *Journal of Applied Physiology* **30**, 708–712.

Bijman, J. (1987). Transport processes in the eccrine sweat gland. *Kidney International* **32**, S109–S112.

Bijman, J. & Quinton, P. M. (1987). Lactate and bicarbonate uptake in the sweat duct of cystic fibrosis and normal subjects. *Pediatric Research* **21**, 79–82.

Boisvert, P., Brisson, G. R. & Péronnet, F. (1993). Effect of plasma prolactin on sweat rate and sweat composition during exercise in man. *American Journal of Physiology* **264**, F816–820.

Bovell, D. L., Clunes, M. T., Roussa, E., Burry, J. & Elder, H. Y. (2000). Vacuolar-type H^+-ATPase distribution in unstimulated and acetylcholine-activated isolated human eccrine sweat glands. *Histochemical Journal* **32**, 409–413.

Boysen, T. C., Yanagawa, S., Sato, F. & Sato, K. (1984). A modified anaerobic method of sweat collection. *Journal of Applied Physiology* **56**, 1302–1307.

Brisson, G. R., Boisvert, P., Péronnet, F., Perrault, H., Boisvert, D. & Laford, J. S. (1991). A simple and disposable sweat collector. *European Journal of Applied Physiology* **63**, 269–272.

Candas, V., Libert, J. P. & Vogt, J. J. (1980). Effect of hidromeiosis on sweat drippage during acclimation to humid heat. *European Journal of Applied Physiology* **44**, 123–133.

Cotter, J. D., Patterson, M. J. & Taylor, N. A. S. (1995). The topography of eccrine sweating in humans during exercise. *European Journal of Applied Physiology* **71**, 549–554.

Falk, B., Bar-Or, O., MacDougall, J. D., McGillis, L., Calvert, R. & Meyer, F. (1991). Sweat lactate in exercising children and adolescents of varying physical maturity. *Journal of Applied Physiology* **71**, 1735–1740.

Fellmann, N., Grizard, G. & Coudert, J. (1983). Human frontal sweat rate and lactate concentration during heat exposure and exercise. *Journal of Applied Physiology* **54**, 355–360.

Gonzalez, R. R., Pandolf, K. B. & Gagge, A. P. (1974). Heat acclimation and decline in sweating during humidity transients. *Journal of Applied Physiology* **36**, 419–425.

van Heyningen, R. & Weiner, J. S. (1952). A comparison of arm-bag sweat and body sweat. *Journal of Physiology* **116**, 395–403.

Hertzman, A. B., Randall, W. C., Peiss, C. N. & Seckendorf, R. (1953). Regional rates of evaporation from the skin at various environmental temperatures. *Journal of Applied Physiology* **5**, 153–161.

Itoh, S., Fujishiro, I., Suchi, T. & Shimokata, K. (1952). The secretion of sugar and its intermediate substances in sweat and saliva. *Japanese Journal of Physiology* **3**, 10–17.

Kaiser, D., Songo-Williams, R. & Drack, E. (1974). Hydrogen ion and electrolyte excretion of the single human sweat gland. *Pflügers Archiv* **349**, 63–72.

Lemon, P. W., Yarasheski, K. E. & Dolny, D. G. (1986). Validity/reliability of sweat analysis by whole-body washdown *vs.* regional collections. *Journal of Applied Physiology* **61**, 1967–1971.

Maughan, R. J. (1982). A simple, rapid method for determination of glucose, lactate, pyruvate, alanine, 3-hydroxybutyrate and acetoacetate on a single 20-μl blood sample. *Clinica Chimica Acta* **122**, 231–240.

Nadel, E. R., Bullard, R. W. & Stolwijk, J. A. J. (1971). Importance of skin temperature in the regulation of sweating. *Journal of Applied Physiology* **31**, 80–87.

Novak, I., Pedersen, P. S. & Larsen, E. H. (1992). Chloride and potassium conductances of cultured human sweat ducts. *Pflügers Archiv* **422**, 151–158.

Park, S. A. & Tamura, T. (1992). Distribution of evaporative rate on human body surface. *Annals of Physiological Anthropology* **11**, 593–609.

Quinton, P. M. (1987). Physiology of sweat secretion. *Kidney International* **32**, S102–S108.

Quinton, P. M. & Reddy, M. M. (1989). Cl^- conductance and acid secretion in the human sweat duct. *Annals of the New York Academy of Sciences* **574**, 438–446.

Quinton, P. M. & Reddy, M. M. (1994). Regulation of absorption by phosphorylation of CFTR. *Japanese Journal of Physiology* **44**, S207–S213.

REDDY, M. M. & QUINTON, P. M. (1991). Intracellular potassium activity and the role of potassium in the transepithelial salt transport in the human reabsorptive sweat duct. *Journal of Membrane Biology* **119**, 199–210.

ROUSSA, E. & THEVENOD, F. (1998). Distribution of V-ATPase in rat salivary glands. *European Journal of Morphology* **36**, suppl., 147–152.

SAGA, K. & SATO, K. (1988). Ultrastructural localization of ouabain-sensitivity, K-dependent p-nitrophenyl phosphatase activity in monkey eccrine sweat gland. *Journal of Histochemistry and Cytochemistry* **36**, 1023–1030.

SATO, K. (1993). The mechanisms of eccrine sweat secretion. In *Perspectives in Exercise Science and Sports Medicine*, vol. 6, *Exercise, Heat, and Thermoregulation*, ed. GISOLFI, C. V., LAMB, D. R. & NADEL, E. R., pp. 85–118. Cooper, Carmel, IN, USA.

SATO, K. & DOBSON, R. L. (1970). Regional and individual variations in the function of the human eccrine sweat gland. *Journal of Investigative Dermatology* **54**, 443–449.

SATO, K. & DOBSON, R. L. (1971). Glucose metabolism of the isolated eccrine sweat gland. I. The effect of metholyl, epinephrine and ouabain. *Journal of Investigative Dermatology* **56**, 272–280.

SATO, K. & DOBSON, R. L. (1973). Glucose metabolism of the isolated eccrine sweat gland. II. The relation between glucose metabolism and sodium transport. *Journal of Clinical Investigation* **52**, 2166–2174.

SATO, K. & SATO, F. (1990). Na^+, K^+, H^+, Cl^-, and Ca^{2+} concentrations in cystic fibrosis eccrine sweat *in vivo* and *in vitro*. *Journal of Laboratory and Clinical Medicine* **115**, 504–511.

SHIRREFFS, S. M. & MAUGHAN, R. J. (1997). Whole body sweat collection in humans: an improved method with preliminary data on electrolyte content. *Journal of Applied Physiology* **82**, 336–341.

SIGGAARD-ANDERSON, O., WIMBERLEY, P. D., FOGH-ANDERSON, N. & GØTHGEN, I. H. (1988). Measured and derived quantities with modern pH and blood gas equipment: Calculation algorithms with 54 equations. *Scandinavian Journal of Clinical and Laboratory Investigation* **48** (Suppl. 189), 7–15.

WEINER, J. S. (1945). The regional distribution of sweating. *Journal of Physiology* **104**, 32–40.

YOSIPOVITCH, G., REIS, J., TUR, E., BLAU, H., HARELL, D., MODUCHOWICZ, G. & BONER, G. (1994). Sweat electrolytes in patients with advanced renal failure. *Journal of Laboratory and Clinical Medicine* **124**, 808–812.

Acknowledgements

This research was funded by Unilever Research. We thank Douglas Bovell for his comments in the preparation of this manuscript.