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ORIGINAL ARTICLE

Maximum rate of sweat ions reabsorption during exercise with regional differences, sex, and exercise training

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Abstract
Purpose It is recently reported that determining sweat rate (SR) threshold for increasing galvanic skin conductance (GSC) would represent a maximum rate of sweat ion reabsorption in sweat glands. We evaluate the maximum rate of sweat ion reabsorption over skin regions, sex, and long-term exercise training by using the threshold analysis in the present study.
Methods Ten males (2 untrained, 4 sprinters, and 4 distance runners) and 12 females (5 untrained, 4 sprinters, and 3 distance runners) conducted graded cycling exercise for 45 min at low, middle, and high exercise intensities (heart rate 100–110, 120–130, and 140–150 beats/min, respectively) for 10, 15, and 20 min, respectively, at 30 °C and 50% relative humidity. Comparisons were made between males and females and among untrained individuals, distance runners, and sprinters on the back and forearm.
Results SR threshold for increasing GSC on back was significantly higher than that of forearm ($P < 0.05$) without any sex differences (back 0.70 ± 0.08 and 0.61 ± 0.04, forearm 0.40 ± 0.05 and 0.45 ± 0.06 mg/cm^2/min for males and females, respectively). Distance runners and sprinters showed higher SR threshold for increasing GSC than that of untrained subjects on back ($P < 0.05$) but not on forearm (back 0.45 ± 0.06, 0.83 ± 0.06, and 0.70 ± 0.04, forearm 0.33 ± 0.04, 0.49 ± 0.02, and 0.39 ± 0.07 mg/cm^2/min for untrained subjects, distance runners, and sprinters, respectively).
Conclusion These results suggest that the maximum sweat ion reabsorption rate on the back is higher than that of forearm without sex differences. Furthermore, exercise training in distance runners and sprinters improves the maximum sweat ion reabsorption rate on the back.

Keywords Sweat sodium · Dehydration · Sports nutrition · Thermoregulation · Hyperthermia

Abbreviations

ANOVA	Analysis of variance
GSC	Galvanic skin conductance
HR	Heart rate
$\dot{V}O_{2max}$	Maximal oxygen uptake
T_b	Mean body temperature
$\bar{T}_{sk}$	Mean skin temperature
RPE	Rating of perceived exertion
T_{re}	Rectal temperature
T_{sk}	Skin temperature
SEM	Standard error of the mean
SR	Sweat rate

Introduction

It is well recognized that sweat ion (e.g. sodium) concentration during exercise is influenced by many factors (e.g. skin regions, sex, and exercise trainings) (Inoue

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et al. 1998; Buono et al. 2007; Allan and Wilson 1971; Meyer et al. 1992, 2007). Sweat is produced in the proximal duct of eccrine sweat gland which is isotonic relative to plasma (Sato et al. 1989; Saga 2002; Quinton 2007). When sweat rate (SR) is low, approximately 85% of sodium is reabsorbed in the distal duct (Buono et al. 2008). Once the sweat ions secretion rate increases more than the maximum rate of its absorption, the sweat ions concentration increases linearly to the rate of sweating (Buono et al. 2008; Shamsuddin et al. 2005b). Therefore, the break point (threshold) for increasing sweat ions concentration to changes in SR may reflect the maximum sweat ion reabsorption rate in eccrine sweat gland (Shamsuddin et al. 2005a, b). Identification of the maximum rate of sweat ions reabsorption in sweat glands is important to investigate physiological reason(s) of variations in sweat ions concentration during exercise. However, despite the well known variations in sweat sodium concentration associated with above mentioned factors, it is unknown whether these factors indeed influence the maximum rate of sweat ions reabsorption in sweat glands.

It is reported that an increase rate of sweat sodium concentration to the changes in SR on the extremities during exercise is higher than that of the torso (Inoue et al. 1998). This implies greater sweat sodium reabsorption in torso sweat glands than the extremities. In addition, sweat sodium concentrations during exercise would be similar between males and females when SR is taken into account (van den Heuvel et al. 2007), which may imply similar sweat sodium reabsorption rate in males and females. Finally, it is well known that heat acclimation improves sweat sodium reabsorption capacity evidenced by a rightward shift of SR-sweat sodium concentration relationship after acclimation (Buono et al. 2007; Allan and Wilson 1971). However, influence of long-term exercise training (comparisons of trained and untrained individuals) on sweat ion concentration is controversial such that trained individuals show lower sweat chloride concentrations than untrained individuals during exercise (Araki et al. 1981) while sweat sodium concentrations are not different between these groups when SR is take into account (Hamouti et al. 2011). It is also unknown whether a difference of exercise trainings (e.g. endurance or non-endurance) would affect the maximum rate of sweat ion reabsorption while endurance runners show higher sweating response during passive heating relative to untrained counterparts but not in sprinters (Amano et al. 2013). Given that higher sweat secretary ability would be associated with higher sweat sodium reabsorption (Sato and Dobson 1970), it is assumed that habitual endurance training would improve the maximum rate of sweat ions reabsorption.

We recently reported an appearance of SR threshold for increasing galvanic skin conductance (GSC) based on continuous measurement of both local SR and GSC that reflects the maximum rate of sweat ion reabsorption in sweat glands (Amano et al. 2016). The purpose of the present study was to evaluate the maximum rate of sweat ion reabsorption in sweat glands over the multifaceted factors associated with skin regions, sex, and exercise trainings by using SR threshold for increasing GSC. We hypothesized that the SR threshold for increasing GSC as an index of maximum rate of sweat ion reabsorption would be higher on back than that of forearm without sex differences. We further hypothesized that the SR threshold for increasing GSC would be higher in distance runners than that of sprinters and untrained counterparts.

Materials and methods

Ethical approval

This study was approved by the ethics committee for human investigation of Osaka International University (Moriguchi, Japan) in compliance with the Declaration of Helsinki. Verbal and written informed consent was obtained from all volunteers.

Participants

Ten young males and 12 young females volunteered for the present study. Participants include untrained to trained athletes who engaged in daily athletic training (male: 2 untrained, 4 sprinters, and 4 distance runners; female: 5 untrained, 4 sprinters, and 3 distance runners). All participants were healthy non-smokers. Physical characteristics are separately described into males and females (Table 1) and into untrained individuals, distance runners, and sprinters (Table 2), respectively. All females participated in the experiment during the mid-follicular phase (6–9 days after the onset of menstruation).

Table 1 Physical characteristics of the male and female participants

	Males ($n = 10$)	Females ($n = 12$)
Age (years)	20.0 ± 0.3*	21.3 ± 0.3
Height (cm)	170 ± 2*	159 ± 2
Weight (kg)	61.6 ± 1.8	51.2 ± 1.2
Body surface area (m^2)	1.71 ± 0.03*	1.51 ± 0.02
%Body fat (%)	11.5 ± 1.6*	21.8 ± 1.7
Estimated $\dot{V}O_{2max}$ (ml/kg/min)	47.8 ± 3.2	46.1 ± 2.9

The values given are the mean ± SEM

* Significantly different from female ($P < 0.05$)

Table 2 Physical characteristics of the subjects classified into untrained subjects, distance runners, and sprinters

	Untrained ($n = 7$)	Distance runners ($n = 8$)	Sprinters ($n = 7$)
Age (years)	21.4 ± 0.3	21.3 ± 0.3	20.4 ± 0.4
Height (cm)	160 ± 3	164 ± 3	168 ± 3
Weight (kg)	54.5 ± 2.7	54.3 ± 1.9	59.9 ± 3.2
Body surface area (m^2)	1.55 ± 0.05	1.58 ± 0.04	1.68 ± 0.05
%Body fat (%)	24.3 ± 2.3	12.8 ± 2.7*	14.8 ± 1.7*
Estimated $\dot{V}O_{2max}$ (ml/kg/min)	38.0 ± 2.2	59.1 ± 1.4*,#	43.3 ± 1.2

The values given are the mean ± SEM

* Significantly different from the untrained ($P < 0.05$)

Significantly different from sprinters ($P < 0.05$)

Graded cycling exercise

The appearance of sweating threshold for increasing GSC is clearer during gradual increase in SR rather than rapid increases. Therefore, to induce gradual increases in SR, we used a graded cycling exercise for assessing the SR threshold for increasing GSC in the present study. Upon arrival to the laboratory, participants changed into shorts (and sports bra for female) and measured body weight, height, and %body fat (Inner Scan BC-600; Tanita, Tokyo, Japan). Subsequently, rectal and skin thermistors, sweat capsules, and electrodes were applied to subjects in temperate room conditions. Thereafter, participants moved into an environmental chamber (FLC-38S3; Fuji Ika Sangyo, Chiba, Japan) maintained at an ambient temperature of 25 °C and relative humidity of 50% with minimal air movement. Following 3 min baseline recording in the chamber, participants cycled at low, middle, and high exercise intensities for 10, 15, and 20 min each, respectively. The workload was adjusted based on the heart rate (HR) at approximately 100–110, 120–130, and 140–150 beats/min for low, middle, and high exercise intensities, respectively. To increase the heat load, the ambient temperature was elevated to 30 °C with maintaining the relative humidity of 50% at the initiation of exercise. We determined this protocol based on our pilot testing to induce gradual increase in local SR.

Estimation of maximal oxygen uptake ($\dot{V}O_{2max}$)

On a different day to the graded exercise test, maximal oxygen uptake was estimated in a submaximal step-load cycling exercise test. Participants completed 4–5 submaximal workloads at 55 rpm whilst measuring HR for 5 min during each bout. Maximal oxygen uptake was estimated based on HR and workload using an equation of American College of Sports Medicine (ACSM 1995).

Measurements

HR was measured by using a chest-strap HR monitor (RS800CX; Polar Electro Oy, Kempele, Finland) during the entire protocol. Rectal temperature (T_{re}) probe (LT-ST08-11; Gram corporation, Saitama, Japan) was self inserted 10 cm past the anal sphincter. Skin temperature (T_{sk}) was measured at three skin sites using thermistors (LT-ST08-12; Gram Corporation, Saitama, Japan) attached with surgical tape. T_{re} and T_{sk} were recorded every 1 min using a data logger (LT-8; Gram Corporation, Saitama, Japan). Mean skin temperature ($\bar{T}_{sk}$) was calculated using a formula modified from Roberts et al. (1977): back 43%, forearm 25%, and thigh 32%.

Local SR was measured continuously on back (left scapula) and forearm (ventral centre of left arm) using a ventilated plastic capsule (4.15 cm^2) that was affixed at each site using glue (collodion). Dry nitrogen gas was passed through each capsule over the skin surface at a rate of 1.0 L/min. The humidity and temperature from the effluent air were measured using a capacitance hygrometer (HMT333; Vaisala, Helsinki, Finland). Two Ag/AgCl electrodes (Vitrode J, Nihon Kohden, Tokyo, Japan) were attached on the back (right scapula) and forearm (ventral centre of right arm) separated by 3 cm, respectively, and GSC was measured using an amplifier (GSR100C; Biopac, Goleta, CA, USA). It has been reported that SR on the bilateral forearm and upper back are similar during exercise (Kenefick et al. 2012; Ueda and Inoue 2013), assuming that the contralateral measurements of SR and GSC are comparable in the present study. Local SR and GSC were recorded at 1 Hz using a data logger (MP150; Biopac, Goleta, CA, USA). Rating of perceived exertion (RPE) was recorded every 5 min during exercise (Borg 1982).

Data and statistical analyses

For the comparisons of sex, we analysed the data set separated into males and females while it was separated into untrained subjects, sprinters, and distance runners for the comparisons of exercise trainings. Baseline data were averaged during 3 min resting period prior to the initiation of exercise. Local SR and GSC were averaged every 1 min during exercise. Figure 1 shows typical changes in GSC (ΔGSC) on forearm and back as a function of each local SR, respectively, during graded cycling exercise in a subject. Firstly, ΔGSC shows an abrupt increase prior to the increases in local SR (phase A in Fig. 1), which may reflect a production of precursor sweat in distal sweat gland (Machado-Moreira and Taylor 2012; Thomas and Korr 1957; Darrow 1964). Subsequently, local SR started to increase while the increase in ΔGSC is small or absent (phase B in Fig. 1), which may reflect a higher sodium reabsorption rate in the sweat gland than the increased rate of sweating (Amano et al. 2016; Shamsuddin et al. 2005b). Finally, after the onset of the abrupt increase in ΔGSC, ΔGSC linearly increases as a function of SR (phase C in Fig. 1), which may suggest an exceeded sodium reabsorption rate over the increase rate of sweating (Buono et al. 2008; Shamsuddin et al. 2005b; Bulmer and Forwell 1956; Amano et al. 2016). To identify SR threshold for increasing ΔGSC, we used phase B and C for a linear regression analysis (Cheuvront et al. 2009).

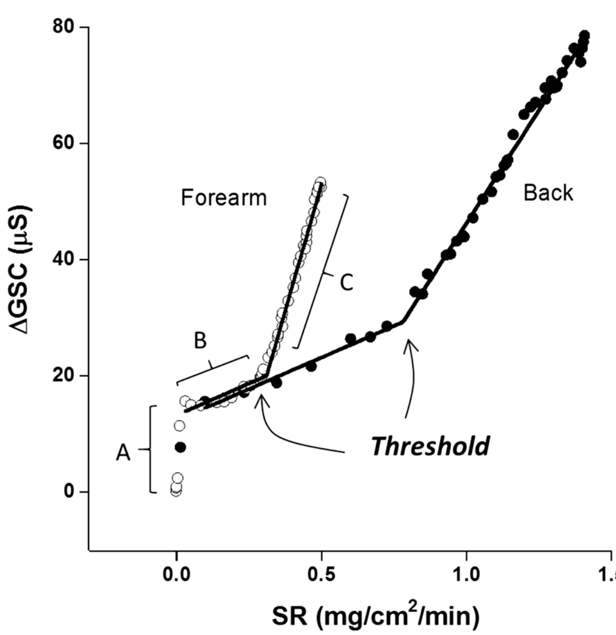


Fig. 1 Typical changes in galvanic skin conductance (ΔGSC) to increasing sweat rate (SR) on back and forearm in one participant. Each phases may indicate a production of precursor sweat in proximal sweat gland (*A*), higher sweat ion reabsorption rate than the sweat production (*B*), and lower sweat ion reabsorption rate than the sweat production (*C*), respectively (see text in details). SR thresholds for increasing ΔGSC was determined based on the intersection of regression analysis from phase *B* and *C* (Amano et al. 2016)

Anthropometric variables (age, height, weight, body surface area, %body fat, and estimated $\dot{V}O_{2max}$) were compared between males and females using unpaired Student's *t* test and among untrained subjects, sprinters, and distance runners using one-way ANOVA. Three-way ANOVA was used to compare SR between forearm and back in males and females (skin regions × sex × time) during exercise from the final 5 min of each exercise intensities (5–10, 20–25, and 40–45 min of the graded exercise bout for low, middle, and high exercise intensities). Two-way repeated measured ANOVA (sex × time or exercise training × time) was used to compare physiological variables between males and females or among untrained subjects, sprinters, and distance runners. Two-way repeated measured ANOVA was also used to identify the influence of sex or training status and skin regions on SR thresholds for increasing GSC (sex × skin regions or exercise training × skin regions). Post hoc analysis was conducted using Bonferroni's test. Linear regression analysis was conducted in the relationship between SR threshold for increasing GSC and SR at the end of exercise. Statistical significance was set at $P \leq 0.05$. The values are represented as the mean ± SEM. All statistical analyses were performed using SigmaPlot (version 12.5, Systat Software, CA, USA).

Results

Regional and sex comparisons

Anthropometric characteristics

Males were significantly younger than females (Table 1). Males were generally larger than females such that they were significantly higher in height, greater in body weight, and larger in body surface area (Table 1). On the other hand, %body fat was significantly higher in females than that of males. Estimated $\dot{V}O_{2max}$ was similar between the sexes (Table 1).

Physiological measurements during graded exercise

HR, T_{re}, back T_{sk}, thigh T_{sk}, $\bar{T}_{sk}$, T_b, RPE, SR on forearm and back, and ΔGSC on forearm and back were not significantly different between males and females during exercise (Table 3). Significant main effect of sex was observed in T_{sk} on the forearm which showed higher temperature in females than that of males ($P < 0.05$, Table 3). Significant main effect of skin regions were observed in T_{sk} such that the back T_{sk} was higher than that of forearm and thigh during

Table 3 Exercise intensities and physiological parameters during graded exercise organised by sex

	Baseline	Low	Middle	High
Exercise intensity* (W)				
M	–	70 ± 3	95 ± 5	119 ± 7
F	–	60 ± 2	80 ± 4	98 ± 4
HR (beats/min)				
M	76 ± 5	119 ± 5	131 ± 4	158 ± 2
F	77 ± 4	120 ± 4	136 ± 4	159 ± 3
T_{re} (°C)				
M	37.18 ± 0.08	37.23 ± 0.08	37.44 ± 0.07	37.85 ± 0.06
F	37.25 ± 0.09	37.33 ± 0.09	37.53 ± 0.08	37.98 ± 0.07
T_{sk} forearm* (°C)				
M	32.20 ± 0.25	32.88 ± 0.28	33.55 ± 0.42	34.13 ± 0.33
F	32.22 ± 0.30	33.29 ± 0.27	34.30 ± 0.21	34.79 ± 023
T_{sk} back# (°C)				
M	33.82 ± 0.12	34.47 ± 0.14	35.39 ± 0.15	35.49 ± 0.17
F	33.80 ± 0.15	34.37 ± 0.16	35.14 ± 0.16	35.26 ± 0.15
T_{sk} thigh (°C)				
M	32.35 ± 0.23	33.54 ± 0.31	34.39 ± 0.34	33.97 ± 0.41
F	31.79 ± 0.20	33.19 ± 0.30	34.47 ± 0.29	34.45 ± 0.30
$\bar{T}_{sk}$ (°C)				
M	32.94 ± 0.16	33.78 ± 0.19	34.61 ± 0.21	34.66 ± 0.15
F	32.74 ± 0.15	33.69 ± 0.19	34.69 ± 0.17	34.88 ± 0.17
T_b (°C)				
M	36.33 ± 0.08	36.54 ± 0.09	36.87 ± 0.07	37.21 ± 0.07
F	36.35 ± 0.09	36.60 ± 0.10	36.96 ± 0.09	37.36 ± 0.07
RPE				
M	–	11 ± 1	13 ± 1	15 ± 0
F	–	10 ± 1	12 ± 1	14 ± 1
SR back# (mg/cm^2/min)				
M	0.01 ± 0.01	0.52 ± 0.10	0.87 ± 0.11	1.05 ± 0.12
F	0.00 ± 0.00	0.47 ± 0.07	0.82 ± 0.07	1.03 ± 0.07
SR forearm (mg/cm^2/min)				
M	0.00 ± 0.00	0.25 ± 0.05	0.53 ± 0.07	0.74 ± 0.10
F	0.00 ± 0.00	0.22 ± 0.04	0.45 ± 0.04	0.61 ± 0.04
ΔGSC back# (μS)				
M	0.0 ± 0.0	21.6 ± 2.5	59.7 ± 6.6	84.2 ± 7.1
F	0.0 ± 0.0	23.0 ± 3.7	57.0 ± 7.0	86.6 ± 9.0
ΔGSC forearm (μS)				
M	0.0 ± 0.0	11.8 ± 2.2	25.4 ± 5.1	40.0 ± 5.3
F	0.0 ± 0.0	14.0 ± 1.6	27.9 ± 3.1	48.1 ± 6.0

The values given are the mean ± SEM. Values are averaged during the final 5 min bouts of low, middle, and high exercise intensities

M males, *F* females

* Significant main effect of sex ($P < 0.05$)

Significant main effect of skin regions ($P < 0.05$)

exercise in both males and females ($P < 0.05$, Table 3). Significant main effect of skin regions were observed in SR and ΔGSC that showed significantly higher SR and ΔGSC on the back compared with the forearm ($P < 0.05$, Table 3).

SR threshold for increasing GSC

Changes in GSC to increasing local SR on the back and forearm during exercise were shown in Fig. 2. Back showed significantly higher SR thresholds for increasing ΔGSC such that significant main effect of skin regions was observed (Fig. 3). No significant main effect of sex or an interaction were observed on the SR thresholds for increasing ΔGSC on the back (0.70 ± 0.08 and 0.61 ± 0.04 mg/cm^2/min for males and females, respectively) or the forearm (0.40 ± 0.05 and 0.45 ± 0.06 mg/cm^2/min, respectively) (Fig. 3).

Comparisons among untrained subjects, sprinters, and distance runners

Anthropometric characteristics

Untrained subjects, sprinters, and distance runners showed similar anthropometric characteristics in age, height, weight, and body surface area (Table 2). Percentage of body fat was higher in untrained subjects than that of distance runners and sprinters (Table 2). Estimated $\dot{V}O_{2max}$ in distance runners was significantly higher than that of sprinters and untrained subjects (Table 2).

Physiological measurements during graded exercise

Significant main effect of groups was observed in HR which shows significantly lower HR in distance runners and sprinters than that of untrained participants at rest and during exercise ($P \leq 0.05$, Table 4). T_{re} during exercise were similar among the groups while it was significantly lower in distance runners than that of sprinters at rest. Significant main effect of group was observed in T_{sk} on the thigh which shows higher T_{sk} in sprinters compared with other groups ($P < 0.05$) while forearm and back T_{sk} were not significantly different among the groups ($P > 0.05$, Table 4). Main effect of group was observed in $\bar{T}_{sk}$ such that $\bar{T}_{sk}$ in sprinters were significantly higher than untrained ($P < 0.05$, Table 4). Significantly higher T_b in sprinters compared to the untrained group and distance runners were observed at baseline and low exercise intensities ($P < 0.05$, Table 4). SR on the back during exercise was significantly different in the order of distance runners, sprinters and untrained

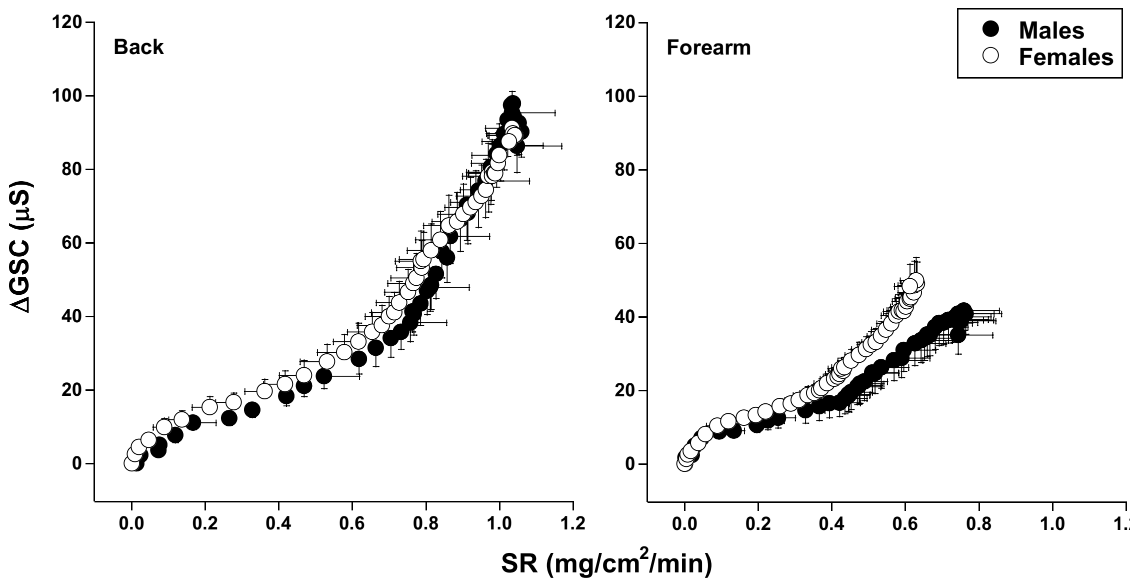


Fig. 2 Changes in galvanic skin conductance (ΔGSC) to increasing sweat rate (SR) on back and forearm during graded exercise in males and females

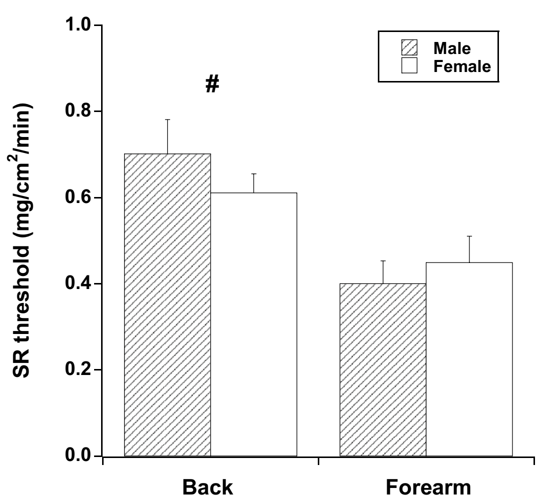


Fig. 3 Sweat rate (SR) thresholds for an increasing ΔGSC on back and forearm in males and females. #Significant main effect of skin regions ($P < 0.05$)

participants ($P < 0.05$). SR on the forearm was significantly higher in distance runners compared with sprinters and the untrained, while these were similar between untrained and sprinters. ΔGSC on the back and forearm were not significantly different among the groups ($P > 0.05$).

SR threshold for increasing ΔGSC

A significant interaction was observed that showed significantly higher SR thresholds for increasing ΔGSC on back in distance runners and sprinters compared with the untrained group while these were not significantly different between sprinters and distance runners (0.45 ± 0.06, 0.83 ± 0.06, and 0.70 ± 0.04 mg/cm^2/min for untrained, distance runners, and sprinters, respectively, $P < 0.05$, Figs. 4, 5). The SR threshold for increasing ΔGSC on the forearm was not significantly different among the groups (0.33 ± 0.04, 0.49 ± 0.02, and 0.39 ± 0.07 mg/cm^2/min for untrained, distance runners, and sprinters, respectively, Fig. 5). When SR thresholds for an increasing ΔGSC on the back and forearm in male and females were plotted against SR at the end of exercise, a significant linear relationship was observed ($P < 0.01$, $R = 0.87$, Fig. 6).

Discussion

We evaluated the maximum sweat ion reabsorption rate in eccrine sweat glands across skin regions, sex, and exercise training status by identifying SR threshold for increasing ΔGSC during exercise in the present study. Firstly, SR thresholds for increasing ΔGSC was higher on the back than that of the forearm. Secondly, irrespective of the skin regions, there were no sex differences in the SR threshold for increasing ΔGSC. Finally, the SR threshold for increasing ΔGSC on back in distance runners and sprinters were significantly higher than that of untrained subjects while these differences was not observed on the forearm. These results suggest that the maximum rate of sweat ion reabsorption of the eccrine sweat glands is higher on the back than that of forearm without sex differences. Furthermore, the maximum rate of sweat ion reabsorption on the back is

Table 4 Exercise intensities and physiological parameters during graded exercise organised by training status

	Baseline	Low	Middle	High
Exercise intensity (W)				
UT	–	54 ± 2	72 ± 2	89 ± 4
D	–	73 ± 3*	100 ± 4*	125 ± 5*
S	–	67 ± 4*	90 ± 6*	108 ± 8
HR** (beats/min)				
UT	84 ± 6	134 ± 6	141 ± 6	165 ± 4
D	65 ± 4	110 ± 3	127 ± 3	154 ± 2
S	80 ± 4	116 ± 2	134 ± 3	157 ± 3
T_{re} (°C)				
UT	37.14 ± 0.10	37.19 ± 0.11	37.44 ± 0.11	37.87 ± 0.12
D	37.08 ± 0.09#	37.14 ± 0.09	37.35 ± 0.08	37.87 ± 0.08
S	37.41 ± 0.07	37.48 ± 0.07	37.65 ± 0.07	38.00 ± 0.05
T_{sk} forearm (°C)				
UT	31.93 ± 0.32	32.54 ± 0.30	33.28 ± 0.36	34.44 ± 0.32
D	32.27 ± 0.51	32.65 ± 0.31	33.84 ± 0.44	34.17 ± 0.26
S	32.42 ± 0.17	33.22 ± 0.25	34.29 ± 0.37	34.59 ± 0.44
T_{sk} back (°C)				
UT	33.71 ± 0.18	34.23 ± 0.18	35.15 ± 0.17	35.39 ± 0.21
D	33.60 ± 0.12	33.99 ± 0.22	35.25 ± 0.22	35.39 ± 0.26
S	34.08 ± 0.14	34.43 ± 0.13	35.08 ± 0.15	35.24 ± 0.17
T_{sk} thigh** (°C)				
UT	31.44 ± 0.17	32.02 ± 0.20	33.50 ± 0.25	34.11 ± 0.26
D	31.88 ± 0.24	32.64 ± 0.34	34.43 ± 0.34	33.85 ± 0.46
S	32.71 ± 0.19	33.51 ± 0.17	34.98 ± 0.29	34.91 ± 0.31
$\bar{T}_{sk}$** (°C)				
UT	32.49 ± 0.19	33.39 ± 0.23	34.37 ± 0.16	34.77 ± 0.14
D	32.72 ± 0.12	33.59 ± 0.22	34.63 ± 0.27	34.58 ± 0.16
S	33.22 ± 0.14	34.16 ± 0.16	34.91 ± 0.22	34.95 ± 0.24
T_b (°C)				
UT	36.21 ± 0.11#	36.43 ± 0.12#	36.83 ± 0.11	37.25 ± 0.11
D	36.21 ± 0.08#	36.43 ± 0.09#	36.81 ± 0.09	37.21 ± 0.08
S	36.57 ± 0.06	36.82 ± 0.07	37.10 ± 0.08	37.39 ± 0.08
RPE				
UT	–	10 ± 1	12 ± 1	14 ± 0
D	–	9 ± 1	12 ± 1	15 ± 1
S	–	11 ± 1	13 ± 0	15 ± 1
SR back ($mg/cm^2/min$)				
UT	0.00 ± 0.00	0.23 ± 0.04	0.58 ± 0.07	0.77 ± 0.10
D	0.02 ± 0.01	0.73 ± 0.08*	1.10 ± 0.08*,#	1.32 ± 0.08*,#
S	0.00 ± 0.00	0.52 ± 0.06*	0.84 ± 0.06*	0.99 ± 0.08*
SR forearm ($mg/cm^2/min$)				
UT	0.00 ± 0.00	0.12 ± 0.02	0.39 ± 0.03	0.57 ± 0.04
D	0.00 ± 0.00	0.34 ± 0.05*	0.63 ± 0.04*,#	0.87 ± 0.07*,#
S	0.00 ± 0.00	0.24 ± 0.05	0.46 ± 0.08	0.59 ± 0.09
ΔGSC back (μS)				
UT	0.0 ± 0.0	16.6 ± 2.6	46.8 ± 6.7	83.8 ± 12.2
D	0.0 ± 0.0	30.4 ± 4.5	75.1 ± 7.5	106.5 ± 10.6
S	0.0 ± 0.0	20.4 ± 3.1	53.3 ± 7.5	77.0 ± 7.9
ΔGSC forearm (μS)				
UT	0.0 ± 0.0	10.0 ± 1.5	22.4 ± 4.5	34.9 ± 5.8
D	0.0 ± 0.0	16.0 ± 3.4	32.6 ± 5.6	57.4 ± 7.8
S	0.0 ± 0.0	13.1 ± 1.1	25.5 ± 4.3	39.6 ± 5.2

The values given are the mean ± SEM. Values are averaged during the final 5 min bouts of low, middle, and high exercise intensities

UT untrained subjects, *D* distance runners, *S* sprinters

* Significantly different from the untrained ($P < 0.05$)

Significantly different from sprinters ($P < 0.05$)

** Significant main effect of groups ($P < 0.05$)

improved in both sprinters and distance runners relative to that of untrained individuals.

Methodology

We recently reported an appearance of SR threshold for an increasing ΔGSC during passive heat stress and this threshold moved rightward after short-term heat acclimation (Amano et al. 2016). These findings were in good agreement with observations in previous literatures that reported a possible appearance of SR threshold for increasing sweat ion concentrations at around 0.2–0.5 $mg/cm^2/min$ (Buono et al. 2008; Shamsuddin et al. 2005b) and a rightward shift of this relationship after heat acclimation (Buono et al. 2007; Allan and Wilson 1971). Given that GSC would be affected by the presence of sweat and its electrolytes and is closely related to the changes in sweat NaCl concentrations ($R = 0.95$) (Amano et al. 2016), we suggested that the simultaneous measurements of GSC and local SR would be useful, simple, and an easy method to compare physiological sweat ion reabsorption capacity of sweat glands.

Regional differences

It is well known that sweat sodium concentration is dependent on the SR (Sato et al. 1989). Therefore, the sweat ion concentrations should be evaluated relative to the changes in SR. By using this comparison, Inoue et al. (1998) reported significantly higher slopes for increasing sweat sodium concentration on forearm and thigh than of the chest and back, suggesting that the rate of sweat sodium reabsorption, and thus possible capacity for reabsorbing sweat sodium, was higher in torso than that of the extremities (Inoue et al. 1998). Our results support the findings of Inoue et al. (1998) such that the maximum rate of sweat ion reabsorption on back might be higher than that of forearm. On the other hand, Sato and Dobson (1970) reported opposite regional differences in sweat sodium concentration to the changes in

SR during thermal and exercise stimulus. They calculated an intersection of *x* axis in the relationship between sweat sodium concentration (*y* axis) and SR (*x* axis) where the intersection indicates a maximum sodium reabsorption in the sweat gland duct (Sato and Dobson 1970). This method is a similar concept to the present study. The exact reasons for the discrepancy between the present and Sato's studies is unknown. Contrary to our present study, the SR on the forearm was slightly higher than that of back in the study of Sato and Dobson (1970) while this was not significant. Given that higher sweat secretary activity links higher sweat sodium reabsorption (Sato and Dobson 1970), the sweat sodium reabsorption rate would be higher in the forearm than that of the chest in their study. Typically, the back is fundamentally reported to have higher SR than the extremities (Smith and Havenith 2011; Taylor and Machado-Moreira 2013) as we have observed in the present study.

Sex differences

As we hypothesized, there were no significant differences in the SR threshold for an increasing ΔGSC between males and females, suggesting that the maximum rate of sweat ion reabsorption is similar between males and females. Previous studies have reported lower sweat sodium concentrations in females than males during exercise (Meyer et al. 1992, 2007), however these studies did not evaluate the differences of SR between the groups which is generally lower in females (Inoue et al. 2014; Ichinose-Kuwahara et al. 2010; Gagnon et al. 2013a; Gagnon and Kenny 2012a, b). Indeed, when the differences in the SR between sexes are considered, the sweat sodium concentration and SR relationship becomes similar between males and females (van den Heuvel et al. 2007). Taken together, it is assumed that the different sweat sodium concentrations during exercise between males and females (Meyer et al. 1992, 2007) is due to the differences in SR between the groups rather than the differences in the maximum reabsorbing rate of sweat ions in eccrine sweat glands. However, we did not observe sex-dependent differences in SR during exercise (Table 3). Thus, it is unknown whether we would have similar results if we had recruited male and female participants with different levels of sweating during exercise.

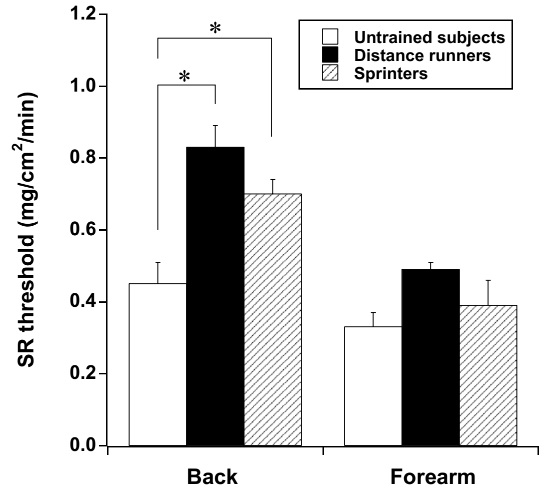
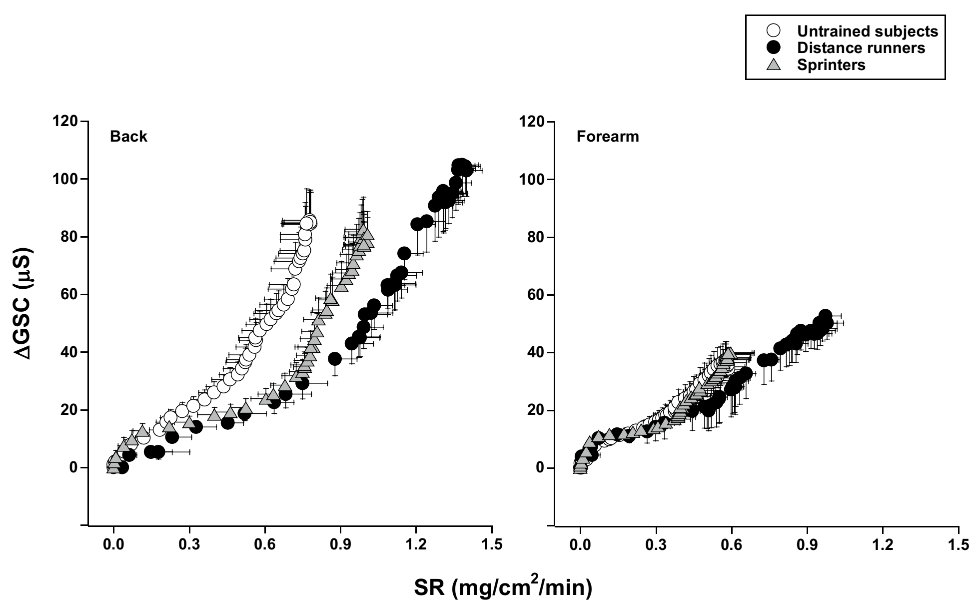


Fig. 5 Sweat rate (SR) thresholds for an increasing ΔGSC on back and forearm in untrained subjects, sprinters, and distance runners. *Significant differences between the groups ($P < 0.05$)

Comparisons among untrained subjects, distance runners, and sprinters

A recent study did not demonstrate a reduced sweat sodium secretion or enhanced sodium reabsorption in

Fig. 4 Changes in galvanic skin conductance (ΔGSC) to increasing sweat rate (SR) on back and forearm during graded exercise in untrained subjects, sprinters, and distance runners



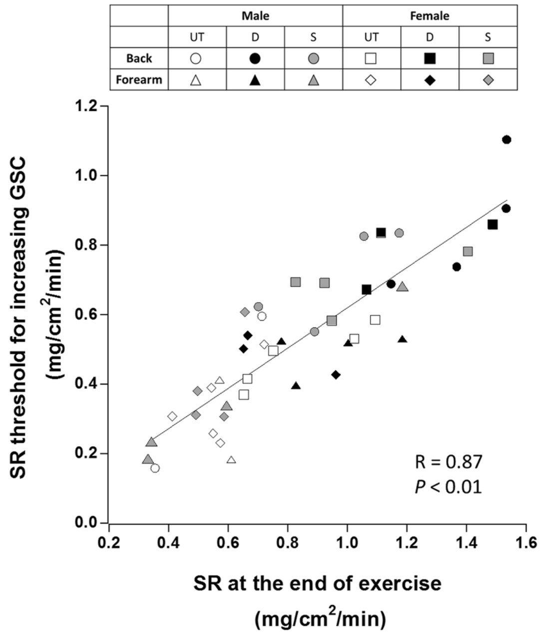


Fig. 6 Sweat rate (SR) thresholds for an increasing ΔGSC on back and forearm in male and females plotted against SR at the end of exercise. *D* distance runners, *S* sprinters, *UT* untrained

endurance-trained athletes compared with untrained counterparts (Hamouti et al. 2011). On the other hand, it is well demonstrated that short-term heat acclimation improves sweat sodium reabsorption capacity (Buono et al. 2007; Allan and Wilson 1971; Amano et al. 2016; Inoue et al. 1999). Given that the maximum sodium reabsorption rate would link to the ability of sweat secretion (Sato and Dobson 1970), a discrepancy exists in the result of endurance-trained athletes since long-term exercise training improves sweating function more than that of short-term heat acclimation (Henane et al. 1977). One possible explanation for this discrepancy is that the speed to pass the sweat through the duct would be too quick to reabsorb sweat ions in endurance athletes (Hamouti et al. 2011). Whether or not it is true, importantly, identification of SR threshold for increasing GSC is not influenced by the amount of sweat (speed of sweat to pass the duct) since this threshold appears at low levels of sweating (slow passage of sweat through the duct). Therefore, based on our findings in the present study, it is suggested that the long-term exercise trainings can improve sweat sodium reabsorption capacity as seen in response to short-term heat acclimation.

Another interesting point in the present study is that we investigated SR threshold for an increasing ΔGSC in non-endurance-trained athletes. This is important since many sports activities, and thus daily exercise trainings, are not simple endurance exercises. We had previously reported that the sweating response during a passive heat stress was not improved in sprinters relative to untrained counterparts who had trained for many years as did the sprinters in the present study (Amano et al. 2013). Therefore, knowledge based on long-term exercise training in endurance-trained athletes could not always apply to non-endurance-trained athletes for the adaptation of sweating function. Interestingly, our results suggest that the SR threshold for an increasing ΔGSC was significantly higher in sprinters than that of untrained individuals, suggesting that the maximum rate of sweat ion reabsorption of sweat glands was improved in sprinters in the present study. Associated with this, local SR on the back was significantly higher in sprinters than in untrained individuals, supporting a link between the ability of sweat production and sweat ion reabsorption (Sato and Dobson 1970) although this difference may be, at least in part, affected by the different heat production between the groups (Kenny and Jay 2013; Jay et al. 2011; Gagnon et al. 2013b). On the other hand, although the SR on the back and forearm during exercise was significantly higher in distance runners than that of sprinters, SR threshold for an increasing ΔGSC was not significantly different between the groups (Fig. 5). We assume that long-term endurance training may not induce further improvements in the maximum rate of sweat sodium concentration relative to the training in sprinters.

Compiled analysis over skin regions, sex, and exercise trainings

We found significant linear relationship between SR threshold for an increasing ΔGSC and SR at the end of exercise (Fig. 6). This implies that, irrespective of regional differences, sex, and exercise trainings, sweat glands that can produce larger sweat volume may have greater capacity of sweat ions reabsorption. Given that Sato and Dobson (1970) had already suggested similar relationship associated with regional differences, we extend their notion including sex and training differences in the present study. The possible functional relationship between sweat secretary and reabsorption abilities would be physiologically important since a high capacity of sweat secretion and ions reabsorption would contribute to more effective thermoregulation with preventing excessive sodium loss during exercise. We observed a coefficient of determination (R^2) of 0.75 in the relationship between SR threshold for increasing ΔGSC and SR at the end of exercise (Fig. 6), suggesting that approximately 75% of the SR threshold for ΔGSC could be explained by the level of SR achieved during exercise. This is practically important since we may be able to estimate sweat glands ion reabsorption capacity simply from the level of sweating during exercise while further studies are required to clarify this possibility.

We could not reveal any underlying mechanisms that would affect the maximum rate of sweat ions reabsorption in the present study. It has been suggested that the number of activated sweat glands (Sato and Dobson 1970), sweat gland output per a gland (Sato and Dobson 1970), hormones (e.g. aldosterone, vasopressin) (Kirby and Convertino 1986; Brown et al. 2011), and cystic fibrosis transmembrane conductance regulator (Brown et al. 2011; Eichner 2008; Del Coso et al. 2015) would potentially affect sweat ions concentration during exercise. Research is now needed to understand the underlying mechanisms of maximum rate of sweat ions reabsorption.

Considerations

We observed significant differences in T_{sk} such that higher temperature was observed on the back than forearm (Table 3). In addition, forearm T_{sk} was significantly higher in females compared with males (Table 3). It has been reported that a higher T_{sk} would promote sweat ions reabsorption (Shamsuddin et al. 2005a), however, we could not reveal the precise influence of T_{sk} on the SR threshold for increasing ΔGSC in the present study.

Limitations

As mentioned, the absolute exercise intensities, and thus heat production during exercise, were not the same among individuals in the present study. While it is suggested that the different heat production and requirements for evaporative heat loss affect whole body sweat production during exercise (Gagnon et al. 2013b; Jay et al. 2011), its influence on sweat ions concentration is unknown. However, we assume that the analysis of SR threshold for increasing ΔGSC may not be influenced by heat production per se in the present study since we plotted GSC against the levels of sweating.

In summary, based on an analysis of SR threshold for an increasing GSC during exercise, we demonstrated greater maximum rate of sweat ions reabsorption of sweat glands on back than forearm without sex differences. In addition, daily exercise trainings in distance runners and sprinters improve the maximum rate of sweat ion reabsorption on back.

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Author contribution Conception and design of research was undertaken by TA, MH, KK, and YI, data collection and analyses was undertaken by TA, MH, KK, and YI, the manuscript was drafted by TA, NG, HU, NK, and YI, and all authors (TA, MH, KK, NG, HU, NK, and YI) contributed to data interpretation, editing and revision of manuscript, and approved the final version.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interest.

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