Aging impairs heat loss, but when does it matter?

Jill M. Stapleton,[1] Martin P. Poirier,[1] Andreas D. Flouris,[2] Pierre Boulay,[3] Ronald J. Sigal,[4] Janine Malcolm,[5] and Glen P. Kenny[1]

[1]*Human and Environmental Physiology Research Unit, University of Ottawa, Ottawa, Canada;* [2]*FAME Laboratory, Department of Exercise Science, University of Thessaly, Trikala, Greece;* [3]*Faculty of Physical Education and Sports, University of Sherbrooke, Sherbrooke, Canada;* [4]*Departments of Medicine, Cardiac Sciences and Community Health Sciences, Faculties of Medicine and Kinesiology, University of Calgary, Calgary, Canada;* and [5]*Division of Endocrinology and Metabolism, Ottawa Hospital–Riverside Campus, Ottawa, Canada*

Stapleton JM, Poirier MP, Flouris AD, Boulay P, Sigal RJ, Malcolm J, Kenny GP. Aging impairs heat loss, but when does it matter? *J Appl Physiol* 118: 299–309, 2015. First published December 11, 2014; doi:10.1152/japplphysiol.00722.2014.—Aging is associated with an attenuated physiological ability to dissipate heat. However, it remains unclear if age-related impairments in heat dissipation only occur above a certain level of heat stress and whether this response is altered by aerobic fitness. Therefore, we examined changes in whole body evaporative heat loss (H_E) as determined using whole body direct calorimetry in young ($n = 10$; 21 ± 1 yr), untrained middle-aged ($n = 10$; 48 ± 5 yr), and older ($n = 10$; 65 ± 3 yr) males matched for body surface area. We also studied a group of trained middle-aged males ($n = 10$; 49 ± 5 yr) matched for body surface area with all groups and for aerobic fitness with the young group. Participants performed intermittent aerobic exercise (30-min exercise bouts separated by 15-min rest) in the heat (40°C and 15% relative humidity) at progressively greater fixed rates of heat production equal to 300 (Ex1), 400 (Ex2), and 500 (Ex3) W. Results showed that H_E was significantly lower in middle-aged untrained (Ex2: 426 ± 34; and Ex3: 497 ± 17 W) and older (Ex2: 424 ± 38; and Ex3: 485 ± 44 W) compared with young (Ex2: 472 ± 42; and Ex3: 558 ± 51 W) and middle-aged trained (474 ± 21; Ex3: 552 ± 23 W) males at the end of Ex2 and Ex3 ($P < 0.05$). No differences among groups were observed during recovery. We conclude that impairments in H_E in older and middle-aged untrained males occur at exercise-induced heat loads of ≥ 400 W when performed in a hot environment. These impairments in untrained middle-aged males can be minimized through regular aerobic exercise training.

calorimetry; evaporative capacity; sweating; skin blood flow; age; aerobic fitness

AGE-RELATED REDUCTIONS IN whole body and/or local heat loss and/or increased body heat storage during exercise in the heat have been reported in a number of studies (1, 17, 18, 23, 28–30, 40, 41). A recent study (30) reported that older males (63 ± 3 yr) demonstrate a reduced rate of whole body heat loss as early as 10 min after the onset of exercise at fixed rates of metabolic heat production (i.e., 400 W) in the heat [35°C, 20% relative humidity (RH)] relative to their younger counterparts (26 ± 2 yr) (30). Furthermore, in the same study, the ability to dissipate heat in middle-aged males (43 ± 2 yr) was intermediate to that measured in young and older males for the given heat load employed (30). The differences between young and older males were not the result of a change in the mean body temperature at which heat loss responses were activated (i.e.,

the onset threshold) but rather the result of a reduced rate of increase in heat loss (i.e., thermosensitivity) leading to greater amount of heat stored. While this study was the first to examine age-related differences in whole body heat dissipation during exercise as assessed by direct calorimetry, it could not be determined if age-related differences occur at lower exercise intensities (and therefore heat loads) and if the age-related differences would be exacerbated at higher heat loads. This is due to the fact the study employed a single repeated short duration exercise-induced heat load. Moreover, all participants were matched for aerobic fitness [defined by peak oxygen uptake ($\dot{V}_{O_{2peak}}$)]. As a consequence, the effects of aerobic fitness in the context of aging could not be evaluated. Of note, however, no differences in whole body heat loss were observed when young (22 ± 2 yr) and middle-aged (45 ± 4 yr) males, matched for $\dot{V}_{O_{2peak}}$ (~ 52 ml·kg^{-1}·min^{-1}), exercised for 90 min at a rate of metabolic heat production of 290 W (equivalent to $\sim 22\%$ $\dot{V}_{O_{2peak}}$) (24). However, it is unclear if the similar responses were due to the fact that the heat load employed did not exceed the individual's physiological capacity to dissipate heat or if the middle-aged adults had a higher rate of heat dissipation due to the relatively higher aerobic fitness level.

Aerobic fitness level is an important determinant in the health status of individuals of any age, however, advanced aging is associated with a $\sim 7\%$ reduction in $\dot{V}_{O_{2peak}}$ per decade (43). Some studies showed that the level of aerobic fitness, associated with regular endurance-type exercise, can induce partial acclimation and thereby improve thermoregulatory control during exercise (3, 5, 11, 13, 34). While a study by Stapleton et al. (39) found no improvements in heat dissipation following 8 wk of acute exercise training in young adults, the long-term effects (i.e., as a function of increasing age) of regular exercise training may help attenuate the age-related impairment in heat loss (2, 7, 18, 41). On the contrary, two other studies showed that heat loss was reduced in older adults irrespective of aerobic fitness (1, 28). Thus the separate and combined influence of age and aerobic fitness on the maximal capacity to dissipate heat remains to be elucidated.

Thus we used an exercise model consisting of progressive increases in heat load (and therefore thermal drive) in young, middle-aged untrained, and older males to examine the threshold at which age-related impairments in the body's physiological capacity to dissipate heat during exercise exist. Additionally, we examined the effects of aerobic fitness, in the context of aging, on whole body heat loss in a group of middle-aged trained males matched for $\dot{V}_{O_{2peak}}$ with the

Address for reprint requests and other correspondence: G. P. Kenny, 125 Univ. Private, Rm. 367, Montpetit Hall, Ottawa, Ontario, Canada K1N 6N5 (e-mail: gkenny@uottawa.ca).

young males. The rates of metabolic heat production were chosen to ensure that a near uncompensable heat stress condition was achieved during the first exercise bout, progressing to a fully uncompensable condition during the final exercise bout. Based on the disparity of age-related impairments in heat loss among studies, we hypothesized that differences in the capacity to dissipate heat between both middle-aged untrained and older males and their younger counterparts would occur at some heat load threshold, thereafter, the magnitude of difference would be greater with progressive increases in heat load. Additionally, we hypothesized that the heat load in which age-related differences occur would be higher in the middle-aged trained males compared with their middle-aged untrained counterparts.

MATERIALS AND METHODS

Ethical Approval

The experimental protocol was approved by the University of Ottawa Health Sciences and Science Research Ethics Board in accordance with the Declaration of Helsinki. Volunteers provided written informed consent before participating in the study.

Participants

Participant characteristics are presented in Table 1. We conducted a power analysis using 80% power and a significance level of 0.05 to calculate the minimum sample size required based on reported age-related differences in whole body heat loss in young, middle-aged, and older males during exercise in the heat at a moderate heat load (30). Assuming an effect of 30% and standard deviation of 25%, the calculated minimum sample size per group was $n = 6$. Thus 40 males volunteered for the study and were divided into 4 groups of 10 young (21 ± 1 yr), 10 middle-aged trained (49 ± 5 yr), 10 middle-aged untrained (48 ± 5 yr), and 10 older (65 ± 3 yr) males. Participants were matched for height ($P = 0.436$), body mass ($P = 0.895$), and body surface area ($P = 0.762$). We carefully matched our participants for physical characteristics by first recruiting an individual for one of the groups (i.e., young) and then selected a match for each of the other groups (i.e., middle-aged trained/untrained and older). However, there was a significant difference among groups for percent body fat ($P < 0.001$) and $\dot{V}O_{2peak}$ ($P < 0.001$). Specifically, the young males had a lower percent body fat compared with the middle-aged untrained and older males ($P < 0.05$). Moreover, the young and middle-aged trained males had a similar $\dot{V}O_{2peak}$ ($P > 0.05$), which was greater compared with the middle-aged untrained and older males ($P < 0.05$). All participants were healthy and nonsmokers. The Kohl physical activity questionnaire (27) was used to assess the participant's physical activity level (i.e., duration, frequency, and mode) for a period of 3 mo before the start of the experimental test session. The results from the questionnaire revealed that young, middle-aged untrained, and older adults were performing a minimum of 30 min of exercise/day (i.e., walking, running, cycling) for 1–3 day/wk (habitually active), while middle-aged trained males were highly endurance trained ($\geq$30 min

of exercise per/day of running, cycling, or cross country skiing for 4–7 days/wk).

Experimental Design

Each participant completed one preliminary and one experimental session. During the preliminary session, body height, mass, and density, as well as $\dot{V}O_{2peak}$ were determined. Body height was determined using a stadiometer (model 2391; Detecto, Webb City, MO), while body mass was measured using a digital high-performance weighing terminal (model CBU150X; Mettler Toledo, Mississauga, ON, Canada). Body surface area was subsequently calculated from the measurements of body height and mass (8). Body density was measured using the hydrostatic weighing technique and used to calculate body fat percentage (36). $\dot{V}O_{2peak}$ was measured on a recumbent cycle ergometer (Corival; Lode, Groningen, The Netherlands) during a progressive incremental exercise protocol that consisted of a 2-min warm-up at 40 W followed by 20-W increments every min until the participant could no longer maintain a pedaling cadence of at least 60 rpm. For the older males, a 12-lead ECG was monitored continuously throughout the maximal exercise test by a qualified technician to detect any abnormalities in heart activity. If detected, participants were excluded from the study and referred to their physician. No participants were excluded from the study based on this criterion.

The experimental protocol was performed in a whole body direct air calorimeter outside of summer months (September to May only) to ensure that there was no potential confounding effect of acclimatization. An equal number of participants within each group performed the experimental protocol in the morning and in the afternoon. Participants consumed a standardized light meal or snack of dry toast and orange juice before their arrival (a minimum of 2 h before testing) and avoided major thermal stimuli on their way to the laboratory (i.e., running, cycling, etc.). Strenuous activity and alcohol were avoided for 24 h and caffeine for 12 h before testing sessions. To ensure euhydration, participants drank ~250 ml of water before bed in the morning of the experimental trial and within 2 h of the start of the trial. No fluid was ingested for the duration of the experimental protocol.

The calorimeter was regulated to an ambient temperature of 40°C and 15% RH. Since some participants may not have been able to withstand high levels of exercise intensity, and therefore high exercise-induced heat loads (i.e., >600 W), the high ambient temperature (i.e., 40°C) was used to create an additional heat load (i.e., environmental heat load). All participants wore a light pair of athletic shorts and sandals. Following instrumentation, participants rested for a 30-min habituation period on an upright seated cycle ergometer in the calorimeter. Habituation was followed by three bouts of 30-min cycling exercise (Ex) at increasingly greater rates of metabolic heat production (Ex1: 300 W; Ex2: 400 W; and Ex3: 500 W). Each exercise bout was followed by a 15-min recovery (Rec) period (Rec1, Rec2, and Rec3) in the calorimeter. The rates of metabolic heat production employed were equivalent to ~25 and ~33% $\dot{V}O_{2peak}$ for Ex1, ~35 and ~47% $\dot{V}O_{2peak}$ for Ex2 and ~44 and ~60% $\dot{V}O_{2peak}$ for Ex3 for young/middle-aged trained and older/middle-aged untrained, respectively.

Table 1. *Participant characteristics*

	Age, yr	Height, cm	Mass, kg	BSA, m²	$\dot{V}O_{2peak}$, ml·kg⁻¹·min⁻¹	Body fat, %
Y	21 ± 1	179 ± 6	79 ± 9	1.98 ± 0.12	50.0 ± 3.7	13.4 ± 3.3
MAT	49 ± 5*	181 ± 5	82 ± 8	2.02 ± 0.11	51.0 ± 6.8	19.1 ± 4.3
MUT	48 ± 5*	179 ± 8	82 ± 12	2.00 ± 0.18	37.3 ± 3.5*†	23.1 ± 6.3*
O	65 ± 3*	176 ± 5	80 ± 7	1.96 ± 0.06	37.9 ± 7.8*†	21.2 ± 5.6*

Values are means ± SD. Y, young; MAT, middle-aged trained; MUT, middle-aged untrained; O, older; BSA, body surface area; $\dot{V}O_{2peak}$, peak oxygen uptake. *Significant difference from young males. †Significant difference from middle-age trained males.

Measurements

Whole body evaporative loss and dry heat exchange as well as change in body heat content were quantified using the modified Snellen direct air calorimeter. A full technical description of the fundamental principles and performance characteristics of the Snellen calorimeter is available elsewhere (33). Data from the direct calorimeter were collected continuously at 8-s intervals during the experimental sessions. Real-time data were displayed and recorded on a personal computer with Lab-VIEW software (version 7.0; National Instruments, Austin, TX). The rate of evaporative heat loss was calculated from the calorimetry data using the following equation: [mass flow $\times$ (humidity$_{out}$ $-$ humidity$_{in}$] $\times$ 2,426)/60, where mass flow is the rate of air mass (kg air/s); (humidity$_{out}$ $-$ humidity$_{in}$) is the difference in absolute humidity (g water/kg air) between the in and out flows of the calorimeter; and 2,426 is the latent heat of vaporization of sweat (J/g sweat). The rate of dry heat loss, from radiation, convection, and conduction was calculated from calorimetry data using the following equation: [mass flow $\times$ (temperature$_{out}$ $-$ temperature$_{in}$) $\times$ 1,005]/60, where mass flow is the rate of air mass (kg air/s); (temperature$_{out}$ $-$ temperature$_{in}$) is the difference in inflow-outflow air temperature (°C) of the calorimeter; and 1,005 is the specific heat of air [J·(kg air·°C)$^{-1}$]. Direct calorimetry measures whole body evaporative loss and dry heat exchange (radiation, conduction, and convection), yielding an accuracy of $\pm$ 2.3 W for the measurement of total heat loss. Indirect calorimetry was used to measure metabolic heat production. Electrochemical gas analyzers located outside of the calorimeter (AMETEK model S-3A/1 and CD 3A; Applied Electrochemistry, Pittsburgh, PA) were used to continuously determine the concentration of expired O_2 and CO_2 during testing sessions. To account for respiratory heat exchange, expired air was recycled back into the calorimeter. The change in body heat content was subsequently calculated by subtracting the total amount of heat production and heat loss over the experimental protocol. The amount of evaporation required to achieve heat balance (E$_{req}$) was defined as the combination of metabolic heat production and dry heat exchange.

Local sweat production was measured using the ventilated capsule technique. A 3.8-cm^2 plastic capsule was attached to three skin sites (upper back, chest, and forearm) with an adhesive ring and topical skin glue (Collodion HV; Mavidon Medical Products, Lake Worth, FL). Compressed dry air was passed through the capsule at a rate of 1.0 l/min. Water content of the effluent air was measured using high precision dew point mirrors (model 473; RH Systems, Albuquerque, NM). Local sweat rate was calculated using the difference in water content between effluent and influent air multiplied by the flow rate and normalized for the skin surface area under the capsule. Laser-Doppler velocimetry was employed to measure skin blood flow (PeriFlux System 5000, main control unit; PF5010 LDPM). A laser-Doppler probe (Perimed Integrating Probe 413, Järfälla, Sweden) was affixed to the forearm's surface in an area that did not seem overly vascular upon visual inspection and provided stable readings at rest. To measure maximal skin blood flow, the heater housing the laser-Doppler probe was heated to 44°C at the end of Rec3 until maximal skin vasodilation was achieved ($\sim$30–40 min) (42).

Esophageal temperature was measured using a thermocouple temperature probe (Mon-a-therm General Purpose Temperature Probe; Mallinckrodt Medical, St. Louis, MO). The esophageal probe was inserted 40 cm past the nostril entrance while the participants sipped water (100–300 ml) through a straw. Mean skin temperature was calculated as the weighted average of four skin temperature measurements: biceps 30%, chest 30%, quadriceps 20%, and front calf 20% (32). Data were collected in 15-s intervals and were displayed and recorded in spreadsheet format using a HP Agilent data acquisition module (model 3497A; Agilent Technologies Canada, Mississauga, ON, Canada) and a personal computer with LabVIEW software (Version 7.0; National Instruments).

Heart rate was monitored, recorded continuously, and stored using a Polar coded WearLink and transmitter, Polar RS400 interface, and Polar ProTrainer 5 software (Polar Electro, Oy, Finland). Preexperimental session urine specific gravity was determined in duplicate using a handheld total solids refractometer (model TS400; Reichter, Depew, NY).

Data and Statistical Analysis

Minute averages for all variables were calculated and used to obtain values for the end of each exercise (Ex) bout and recovery (Rec) period. Baseline values were obtained by averaging the last 5–10 min of data during the 30-min baseline resting period. Mean body temperature was calculated as follows: $0.9 \times$ esophageal temperature $+ 0.1 \times$ mean skin temperature (35). Whole body evaporative heat loss was plotted against the corresponding mean body temperature. The onset threshold and thermosensitivity of whole body evaporative heat loss during each exercise period were determined using the linear portion of each response and analyzed using a segmented regression analysis as described by Cheuvront et al. (6) with aid of a computer algorithm (GraphPad Prism 6.0; GraphPad Software, La Jolla, CA). The onset threshold was determined by plotting evaporative heat loss over time and determining visually the point at which it increased over three consecutive measurements. The corresponding mean body temperature at that time point was selected as the onset threshold. The thermosensitivity was determined as the slope of the relationship between evaporative heat loss and mean body temperature for each exercise period. Time constant (τ, the time it takes to reach 63.2% of the total response) and amplitude (the difference between the evaporative heat loss value at the onset and at the end of each exercise bout) values were calculated for evaporative heat loss at each exercise heat load and recovery period. Whole body sweat production at the end of each Ex heat load and Rec period (in g/min) was calculated as evaporative heat loss (in W) multiplied by 60 s and divided by the latent heat of vaporization of sweat (2,426 J/g of sweat).
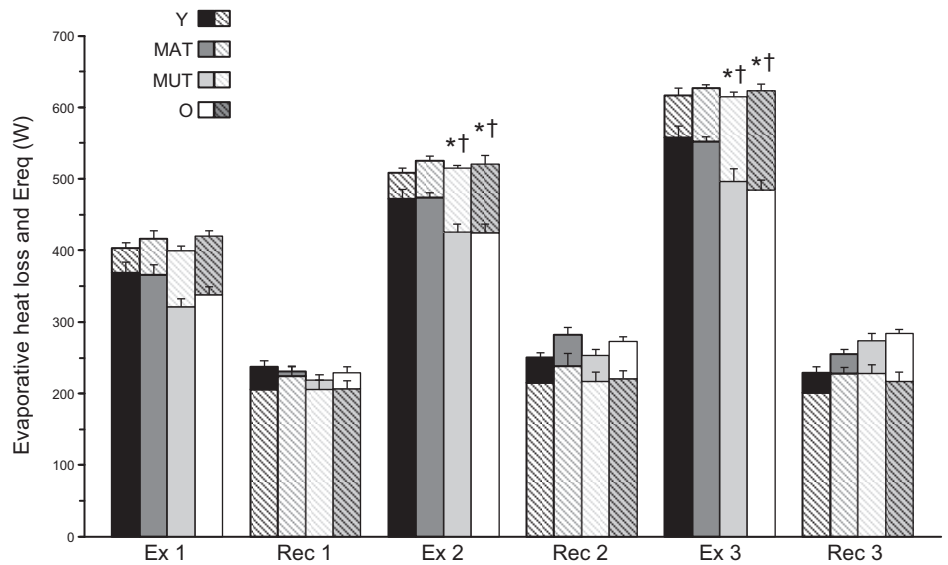
Dependent variables of rates of metabolic heat production, total heat loss, evaporative heat loss, dry heat exchange, and E$_{req}$, as well as esophageal and mean skin temperatures, local sweat rates, skin blood flow, and heart rate responses were analyzed using a two-way ANOVA. The ANOVAs were performed with one factor of group (4 levels: young, middle-aged trained, middle-aged untrained, and older) and repeated factor of exercise time (3 levels: Ex1, Ex2, and Ex3) or recovery time (3 levels: Rec1, Rec2, and Rec3). Additionally, changes in body heat content, physical characteristics, and baseline values were analyzed using a one-way ANOVA to identify differences among groups. When a significant main effect was observed, period- and group-specific post hoc comparisons were carried out using the Newman-Keuls procedure. The level of significance for all analyses was set at $P \leq 0.05$. When $0.05 \leq P \leq 0.10$, the effect size (eta squared, η^2) is reported. Statistical analyses were performed using commercially available statistical software (GraphPad Prism 6.0; GraphPad Software). All values are reported as means $\pm$ SD unless otherwise indicated.

RESULTS

Hydration Status

On the day of the experimental session, all participants were well hydrated according to urine specific gravity, a measure of hydration status, with similar values among groups (young: 1.013 ± 0.010; middle-aged trained: 1.014 ± 0.011; middle-aged untrained: 1.016 ± 0.008; and older: 1.014 ± 0.009; $P = 0.907$). For all groups, baseline urine specific gravity ranged between 1.002 and 1.020, which was below the cut-off value of >1.020 (4).

Fig. 1. Means ± SE values for evaporative heat loss (solid bars) and the required amount of evaporation for heat balance (E_{req}, striped bars) measured over three 30-min exercise bouts (Ex 1, Ex 2, and Ex 3) and three 15-min recovery periods (Rec 1, Rec 2, and Rec 3) in a hot, dry [40°C, 15% relative humidity (RH)] environment. The black bars/stripes represent the young (Y) group, the dark grey bars/stripes represent the middle-aged trained (MAT) group, the light grey bars/stripes represent the middle-aged untrained (MUT) group, and the white bars/grey and black stripes represent the older (O) group. There were no differences in the required amount of evaporation for heat balance between groups. Significance level was set at $P \leq 0.05$. *Significant difference in evaporative heat loss from young. †Significant difference in evaporative heat loss from middle-aged trained.
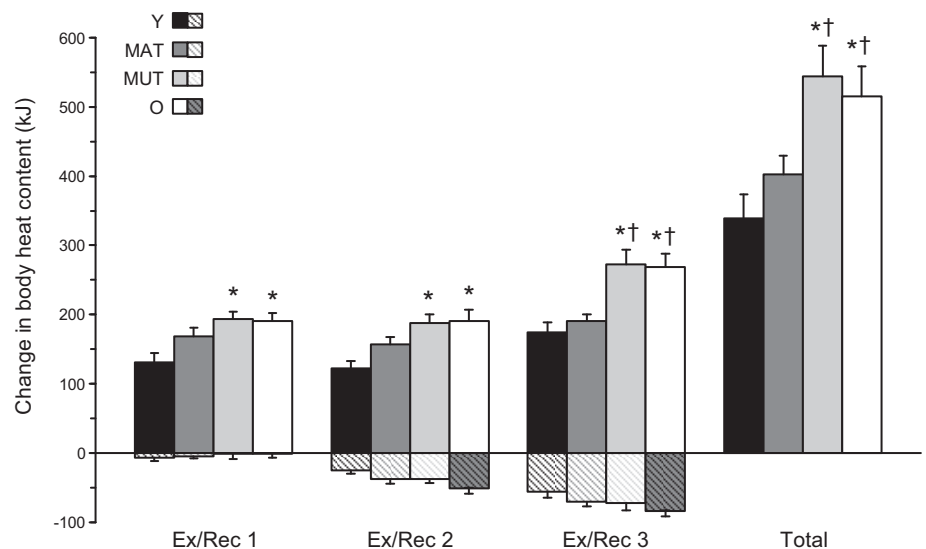
Whole Body Direct Calorimetry

Baseline and exercise. The rate of metabolic heat production at baseline was similar for young (117 ± 19 W), middle-aged trained (123 ± 9 W), middle-aged untrained (112 ± 11 W), and older (112 ± 13 W) males ($P = 0.212$). By experimental design, the rate of metabolic heat production was similar among groups ($P = 0.758$) during each of the exercise periods (average across groups: Ex1 = 305 ± 18; Ex2: 404 ± 18; and Ex3: 504 ± 17 W). The rates of evaporative heat loss and E_{req} during exercise are shown in Fig. 1. The rate of evaporative heat loss at baseline was similar for young (146 ± 42 W), middle-aged trained (150 ± 46 W), middle-aged untrained (132 ± 40 W), and older (125 ± 34 W) males ($P = 0.516$). However, a main effect of group on the rate of evaporative heat loss ($P = 0.002$) was detected during exercise, whereby the rate of evaporative heat loss was greater for the young and middle-aged trained compared with the middle-aged untrained and older males at the end of Ex2 ($P < 0.05$) and Ex3 ($P < 0.05$). Rates of dry heat exchange during baseline were not

different among the young (−77 ± 16 W), middle-aged trained (−83 ± 12 W), middle-aged untrained (−79 ± 11 W), and older (−78 ± 12 W) males ($P = 0.696$). Likewise, there were no differences in dry heat exchange among groups at the end of each exercise bout, an indication of the amount of heat gained by the body from the environmental heat load (average among groups: Ex1 = −105 ± 14; Ex2: −114 ± 17; and Ex3: −117 ± 20 W; $P = 0.384$). As a consequence, the total heat load for each exercise (rate of metabolic heat production and dry heat gain or E_{req}) was similar among groups (Ex1 = 410 ± 28; Ex2: 518 ± 25; and Ex3: 621 ± 25 W; $P = 0.443$). Whole body sweat rate was significantly different among groups during exercise ($P = 0.001$), whereby whole body sweat rate was significantly greater in the young and middle-aged trained groups compared with the older and middle-aged untrained groups at the end of Ex2 ($P < 0.05$) and Ex3 ($P < 0.05$; see Table 3).

The changes in body heat content are presented in Fig. 2. There was a main effect of group on change in body heat content during exercise ($P < 0.001$). The young males had a

Fig. 2. Means ± SE values for changes in body heat content during each exercise/recovery cycle as well as the total change in body heat content over the exercise protocols in a hot, dry (40°C, 15% RH) environment. The solid bars represent changes in body heat content during exercise and the striped bars represent the changes in body heat content during recovery. The black bars/stripes represent the young (Y) group, the dark grey bars/stripes represent the middle-aged trained (MAT) group, the light grey bars/stripes represent the middle-aged untrained (MUT) group, and the white bars/grey and black stripes represent the older (O) group. Significance level was set at $P \leq 0.05$. *Significantly different from young. †Significantly different from middle-aged trained.

lower change in body heat content for all three exercise periods (Ex1–3) compared with the middle-aged untrained (percent difference from young = Ex1: 48%; Ex2: 55%; and Ex3: 57%) and older males (percent difference from young = Ex1: 47%; Ex2: 57%; and Ex3: 54%; $P < 0.05$). Additionally, the middle-aged trained males had a lower change in body heat content for Ex3 ($P < 0.05$) compared with the middle-aged untrained (percent difference from middle-aged trained for Ex3 = 44%) and older (percent difference from middle-aged trained for Ex3 = 41%) males.

Recovery. There was a rapid decline in the rate of metabolic heat production following each exercise bout, which occurred to a similar extent among groups ($P = 0.454$). The rates of evaporative heat loss and E_{req} for recovery are presented in Fig. 1. There was no main effect of group on evaporative heat loss ($P = 0.326$) at the end of the recovery periods. However, there was a main effect of group on the rate of dry heat exchange ($P = 0.046$) such that the young males (-78 ± 8 W) had a lower rate of dry heat exchange compared with both the middle-aged trained (-102 ± 14 W) and untrained males (-97 ± 16 W) at the end of Rec3 ($P < 0.05$). Nevertheless, there was no difference in E_{req} ($P = 0.065$; $\eta^2 = 0.20$) among groups. Moreover, there was no main effect of group on whole body sweat rate ($P = 0.271$) during recovery (see Table 3).

The changes in body heat content during recovery are presented in Fig. 2. The change in body heat content was similar among groups during recovery ($P = 0.255$). However, there was a main effect of group on the residual change in body heat content (Ex plus Rec; $P = 0.001$). As such, the middle-aged untrained and older males had 61 and 53% significantly greater cumulative changes in body heat content respectively, compared with the young adults. Furthermore, the cumulative changes in body heat content were 35 and 28% greater in the middle-aged untrained and older males, respectively, compared with the middle-aged trained males ($P < 0.05$). There were no differences between the young and middle-aged trained groups ($P > 0.05$).

Onset Thresholds and Thermosensitivities, Time Constant, and Amplitude Values for Whole Body Evaporative Heat Loss

Exercise. Mean body temperature onset thresholds, thermosensitivities, time constant, and amplitude values for whole body evaporative heat loss during each exercise bout are presented in Table 2. The mean body temperature onset threshold for whole body evaporative heat loss did not differ among groups ($P = 0.294$). However, a main effect of group on thermosensitivity was observed ($P = 0.001$). For Ex1, the young males had a significantly greater thermosensitivity for the whole body evaporative heat loss response compared with the other three groups ($P < 0.05$). Additionally, during the third exercise bout, the young and middle-aged trained males had a significantly greater thermosensitivity compared with both the middle-aged untrained and older males ($P < 0.05$). Furthermore, there was a significant difference among groups in time constant values for the rate of evaporative heat loss during exercise ($P = 0.045$). This was demonstrated by the young having a shorter time to reach 63.2% of the evaporative heat loss response during the third exercise bout compared with the other three groups. Likewise, the amplitude for evaporative heat loss was different among groups ($P = 0.036$) such that the young and middle-aged trained males had a significantly greater amplitude for Ex3 compared with both the middle-aged untrained and older males.

Recovery. Time constant and amplitude values during recovery for whole body evaporative heat loss during each exercise bout are presented in Table 2. There was a significant difference among groups in time constant values for the rate of evaporative heat loss during recovery ($P < 0.001$). The young had a shorter time to reach 63.2% of the evaporative heat loss response during Rec2 compared with the other three groups and during Rec3 compared with the middle-aged untrained and older males. Similarly, the amplitude for evaporative heat loss

Table 2. *Time constants, amplitudes, onset thresholds, and thermosensitivities of evaporative heat loss for each exercise/recovery bout*

	Ex1	Rec1	Ex2	Rec2	Ex3	Rec3
τ, min						
Y	11.0 ± 10.4	2.99 ± 1.67	6.5 ± 3.1	3.09 ± 0.74	4.8 ± 1.4	2.87 ± 1.03
MAT	16.4 ± 5.4	5.69 ± 4.70	8.0 ± 5.2	5.39 ± 1.22*	7.9 ± 3.1*	3.93 ± 1.08
MUT	21.9 ± 14.1	3.98 ± 1.85	6.9 ± 2.9	5.84 ± 0.91*	7.0 ± 2.6*	5.51 ± 2.10*
O	14.0 ± 6.1	5.09 ± 2.90	8.7 ± 3.2	7.33 ± 2.60*	8.5 ± 2.3*	7.09 ± 4.66*
Amplitude, W						
Y	172 ± 43	119 ± 71	198 ± 52	223 ± 54	268 ± 51	255 ± 53
MAT	175 ± 46	145 ± 52	207 ± 51	185 ± 51	265 ± 69	272 ± 29
MUT	148 ± 56	110 ± 50	179 ± 46	177 ± 28	215 ± 61*†	201 ± 66*†
O	158 ± 28	129 ± 44	180 ± 31	161 ± 48	189 ± 50*†	189 ± 69*†
Onset threshold of evaporative heat loss, °C						
Y	36.63 ± 0.40		36.82 ± 0.37		36.94 ± 0.33	
MAT	36.57 ± 0.21		36.72 ± 0.20		36.83 ± 0.26	
MUT	36.91 ± 0.70		36.88 ± 0.14		37.08 ± 0.21	
O	36.64 ± 0.28		36.88 ± 0.31		36.97 ± 0.31	
Thermosensitivity of evaporative heat loss, W/°C						
Y	1,575 ± 1,160		1,217 ± 559		1,295 ± 629	
MAT	1,022 ± 270*		1,141 ± 536		1,031 ± 352	
MUT	879 ± 415*		833 ± 604		513 ± 238*†	
O	721 ± 318*		694 ± 424		411 ± 263*†	

Values are means ± SD. Ex, exercise; Rec, recovery; τ, time constant. *Significant difference from young males. †Significant difference from middle-age trained group. Mean body temperature was used to calculated the onset threshold and thermosensitivity.

was different among groups ($P = 0.050$). As such, the young had larger amplitude values for Rec2 relative to the older males and the young and middle-aged trained males had larger amplitude compared with the middle-aged untrained and older males for Rec3.

Esophageal and Mean Skin Temperatures

Baseline and exercise. Esophageal and mean skin temperatures are presented in Fig. 3. Esophageal temperatures during baseline were not different among the young ($36.77 \pm 0.40°C$), middle-aged trained ($36.72 \pm 0.22°C$), middle-aged untrained ($36.83 \pm 0.24°C$), and older ($36.83 \pm 0.26°C$) males ($P = 0.787$). However, there was a main effect of group on esophageal temperature during exercise ($P = 0.013$). This was evidenced by the young and middle-aged trained males having lower esophageal temperatures at the end of Ex3 compared with middle-aged untrained and older males ($P < 0.05$). Baseline values for mean skin temperature were not different among the young ($35.33 \pm 0.66°C$), middle-aged trained ($35.26 \pm 0.44°C$), middle-aged untrained ($35.16 \pm 0.37°C$), and older ($35.26 \pm 0.48°C$) males ($P = 0.882$). Likewise, there was no difference among groups for mean skin temperature ($P = 0.765$) during exercise. Similarly, when values were

examined from a change from baseline, a main effect of group on esophageal temperature during exercise ($P = 0.016$) was observed. The young and middle-aged trained males demonstrated smaller changes in esophageal temperatures at the end of Ex3 (young: $0.65°C$; middle aged trained: $0.57°C$) compared with middle-aged untrained ($1.10°C$) and older ($0.95°C$) males ($P < 0.05$). However, there was no difference in the change in mean skin temperature ($P = 0.357$) during exercise among groups.

Recovery. Esophageal and mean skin temperatures at the end of recovery are presented in Fig. 3. There was no main effect of group on esophageal temperature during recovery ($P = 0.061$; $\eta^2 = 0.24$). Likewise, mean skin temperature was not different among groups during recovery ($P = 0.256$). When values were compared from a change in baseline, there remained no differences in esophageal ($P = 0.073$; $\eta^2 = 0.21$) or mean skin temperature ($P = 0.137$) among groups during the recovery period.

Local Heat Loss and Heart Rate Responses

Baseline and exercise. Local sweat rate (chest, back, and forearm), skin blood flow (percentage of maximum), and heart rate values are presented in Table 3. There were no differences
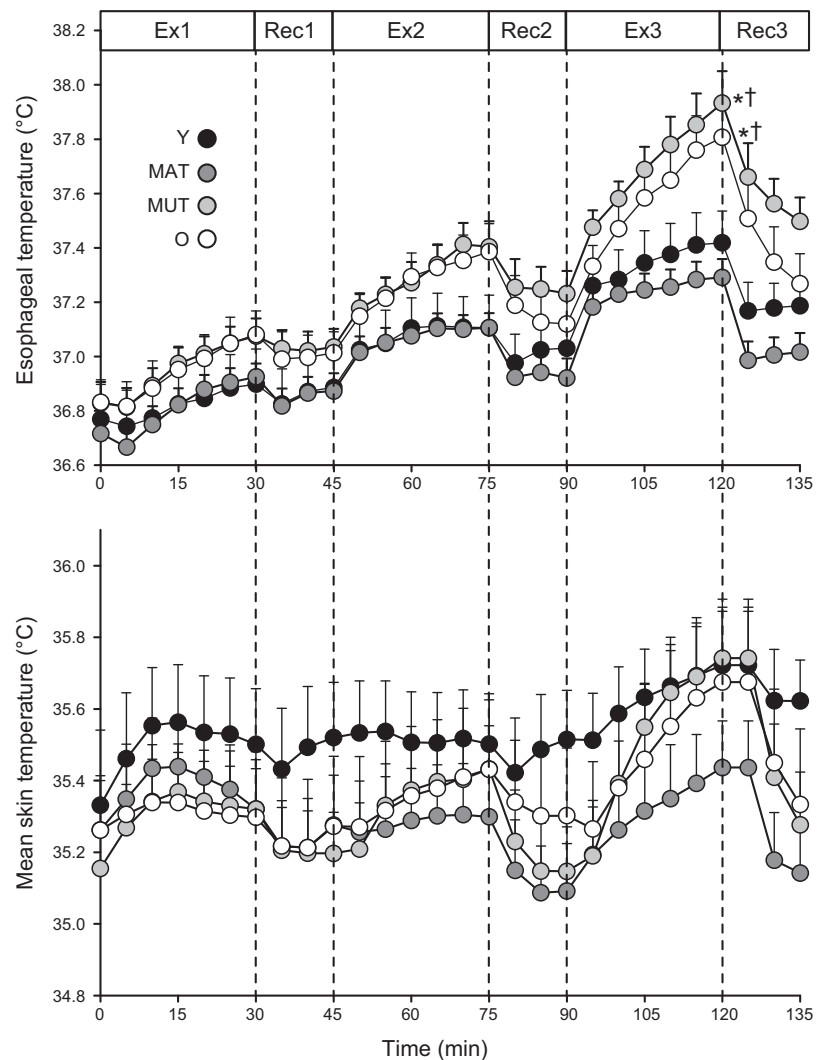

Fig. 3. Means ± SE values for esophageal and mean skin temperatures during each exercise/recovery cycle in a hot, dry (40°C, 15% RH) environment. The black circles represent the young (Y) group, the dark grey circles represent the middle-aged trained (MAT) group, the light grey circles represent the middle-aged untrained (MUT) group, and the white circles represent the older (O) group. Significance level was set at $P \leq 0.05$. Analysis was performed at the end of each exercise/recovery period. *Significantly different from young. †Significantly different from middle-aged trained.

Table 3. *Local heat loss, whole body sweat rate, and heart rate responses during each Ex/Rec cycle*

	Ex1	Rec1	Ex2	Rec2	Ex3	Rec3
LSR–chest, mg·min^{-1}·cm^{-2}						
Y	0.37 ± 0.19	0.18 ± 0.11	0.50 ± 0.20	0.18 ± 0.14	0.66 ± 0.26	0.20 ± 0.16
MAT	0.44 ± 0.15	0.29 ± 0.13	0.60 ± 0.26	0.26 ± 0.09	0.79 ± 0.38	0.34 ± 0.15
MUT	0.37 ± 0.16	0.23 ± 0.12	0.55 ± 0.27	0.29 ± 0.14	0.68 ± 0.31	0.40 ± 0.21
O	0.38 ± 0.19	0.22 ± 0.11	0.51 ± 0.17	0.26 ± 0.12	0.58 ± 0.22	0.39 ± 0.25
LSR–back, mg·min^{-1}·cm^{-2}						
Y	0.44 ± 0.24	0.23 ± 0.11	0.54 ± 0.22	0.22 ± 0.10	0.67 ± 0.22	0.27 ± 0.12
MAT	0.44 ± 0.18	0.28 ± 0.14	0.59 ± 0.22	0.26 ± 0.11	0.80 ± 0.25	0.31 ± 0.11
MUT	0.30 ± 0.14	0.23 ± 0.10	0.48 ± 0.20	0.30 ± 0.15	0.60 ± 0.25	0.36 ± 0.17
O	0.39 ± 0.16	0.28 ± 0.13	0.56 ± 0.17	0.35 ± 0.11	0.67 ± 0.15	0.39 ± 0.13
LSR–arm, mg·min^{-1}·cm^{-2}						
Y	0.36 ± 0.13	0.16 ± 0.07	0.53 ± 0.16	0.20 ± 0.10	0.82 ± 0.14	0.24 ± 0.13
MAT	0.40 ± 0.18	0.23 ± 0.07	0.52 ± 0.08	0.25 ± 0.10	0.77 ± 0.23	0.25 ± 0.12
MUT	0.34 ± 0.14	0.29 ± 0.11	0.53 ± 0.22	0.38 ± 0.12	0.77 ± 0.21	0.41 ± 0.15*†
O	0.43 ± 0.17	0.26 ± 0.10	0.55 ± 0.14	0.30 ± 0.10	0.68 ± 0.16	0.43 ± 0.14*†
WBSR, g/min						
Y	9.1 ± 1.1	5.9 ± 1.1	11.7 ± 1.0	6.2 ± 1.2	13.8 ± 1.3	5.7 ± 0.7
MAT	9.1 ± 1.1	5.7 ± 1.1	11.7 ± 0.5	7.0 ± 1.4	13.7 ± 0.6	6.3 ± 0.6
MUT	8.0 ± 0.9	5.5 ± 1.0	10.5 ± 0.8*†	6.3 ± 1.0	12.3 ± 1.3*†	6.1 ± 2.3
O	8.3 ± 0.9	5.7 ± 0.9	10.5 ± 0.9*†	6.8 ± 0.8	12.0 ± 1.1*†	7.0 ± 1.0
SkBF, %max						
Y	43.2 ± 12.9	33.9 ± 9.5	44.3 ± 12.8	32.8 ± 9.3	49.1 ± 12.7	30.9 ± 9.0
MAT	49.4 ± 9.9	39.7 ± 16.2	54.4 ± 14.0	44.3 ± 16.9	62.2 ± 15.7	41.0 ± 9.8
MUT	44.6 ± 15.7	32.3 ± 14.5	52.5 ± 16.0	31.8 ± 14.6	54.7 ± 14.9	36.9 ± 13.5
O	51.9 ± 12.0	42.4 ± 9.5	55.1 ± 14.1	41.9 ± 8.9	60.2 ± 16.1	40.2 ± 8.5
HR, beats/min						
Y	95 ± 8	81 ± 10	111 ± 11	84 ± 12	131 ± 14	90 ± 7
MAT	85 ± 14	70 ± 15	99 ± 13	74 ± 14	117 ± 18	79 ± 17
MUT	99 ± 11	85 ± 11	119 ± 18†	92 ± 14	143 ± 23†	101 ± 17
O	93 ± 11	76 ± 8	109 ± 17	84 ± 10	135 ± 14	94 ± 14

Values are means ± SD. LSR, local sweat rate. WBSR, whole body sweat rate. SkBF, skin blood flow. HR, heart rate. *Significant difference from young males. †Significant difference from middle-age trained males.

in baseline sweat rates among groups on the chest (young: 0.16 ± 0.13; middle-aged trained: 0.18 ± 0.08; middle-aged untrained: 0.15 ± 0.09; and older: 0.14 ± 0.06 mg·min^{-1}·cm^{-2}; $P = 0.840$), back (young: 0.14 ± 0.09; middle-aged trained: 0.18 ± 0.09; middle-aged untrained: 0.14 ± 0.09; and older: 0.16 ± 0.08 mg·min^{-1}·cm^{-2}; $P = 0.818$), or forearm (young: 0.13 ± 0.08; middle-aged trained: 0.15 ± 0.07; middle-aged untrained: 0.15 ± 0.09; and older: 0.18 ± 0.10 mg·min^{-1}·cm^{-2}; $P = 0.693$). Similarly, sweat rates were similar among groups during exercise at the chest ($P = 0.734$), back ($P = 0.404$), and forearm ($P = 0.903$). Likewise, local skin blood flow was similar among groups at baseline (young: 32.9 ± 10.7; middle-aged trained: 41.3 ± 9.5; middle-aged untrained: 29.6 ± 15.1; and older: 41.0 ± 14.4% of max; $P = 0.129$) and for all three exercise bouts ($P = 0.219$). There was a tendency for heart rate to be different among groups ($P = 0.057$; $\eta^2 = 0.86$) at the end of the exercise bouts such that the middle-aged trained males had a lower heart rate compared with the middle-aged untrained males at the end of Ex2 ($P < 0.05$) and Ex3 ($P < 0.05$).

Recovery. Local sweat rates, skin blood flow, and heart rate values for recovery are presented in Table 3. Sweat rates were similar among groups at the chest ($P = 0.109$) and back ($P = 0.443$) during recovery; however, a main effect of group was measured on local forearm sweating ($P = 0.014$). At the forearm local sweat rate site, sweating was lower for the young and middle-aged trained males compared with middle-aged untrained and older males at the end of Rec3 ($P < 0.05$). In contrast, no differences in local skin blood flow ($P = 0.176$) or

heart rate ($P = 0.060$; $\eta^2 = 0.54$) were measured among groups during each of the recovery periods.

DISCUSSION

The main finding of the present study is that aging alters the physiological capacity to dissipate heat. This was evident by the fact that older males exhibited a reduced whole body evaporative heat loss compared with young males at exercise-induced heat loads as low as 400 W. Furthermore, middle-aged untrained males had a similar level of impairment compared with the older males, matched for aerobic fitness (i.e., V̇O$_{2peak}$). Conversely, we observed that middle-aged trained males maintain a higher rate of heat dissipation than their untrained counterparts, such that the rate of heat dissipation was similar to that measured in young males. As a result, the rate of heat storage was markedly greater in older and middle-aged untrained males compared with young and middle-aged trained males.

Effects of Age on the Physiological Capacity to Dissipate Heat

In the current study, we employed a unique incremental exercise model involving progressive increases in heat load (and therefore E$_{req}$) to determine the threshold at which age-related differences in the body's physiological capacity to dissipate heat occurs. Of note, when we factor in the heat gained from the environment (i.e., dry heat gain), the net heat loads, or E$_{req}$, were ~400 W for Ex1, ~500 W for Ex 2, and

~600 W for Ex 3 (Fig. 1). In the present study, we showed that whole body evaporative heat loss was reduced in both middle-aged untrained and older males compared with young males at the end of the two highest heat loads employed (Fig. 1). Similar findings were reported by previous studies employing an exercise-induced heat load similar to that of Ex2 in our study (i.e., 400 W), albeit lower environmental stress (35°C and 20% RH), and therefore minimal dry heat gain (28, 30). As such, heat loads greater than ~400 W, derived from a combination of metabolic and environmental heat, are sufficient to exceed the physiological capacity to dissipate heat of middle-aged as well as older adults matched for aerobic fitness. In line with our study hypothesis, as the heat load increased, the degree of impairment in whole body evaporative loss was greater in both the middle-aged untrained and older adults. While the young adults were able to increase their rate of whole body evaporative heat loss from Ex1 to Ex 2 by ~28% and Ex2 to Ex3 by ~18%, the older adults had an increase in whole body evaporative heat loss from Ex1 to Ex2 of ~26% and from Ex2 to Ex3 of only ~14%. This translated into 69 and 95 kJ of greater body heat storage at the end of Ex2 and Ex3, respectively, in the older compared with the young adults. Although, a true measure of maximal heat loss capacity would be observed if no increase in the rate of whole body heat loss occurred from Ex2 to Ex3, our observations provide evidence to indicate that both the middle-aged untrained and older adults are approaching near maximal levels of heat dissipation.

Insight into whether impairment in heat loss occurs centrally (neural activity/integration) or peripherally (end organ) can be gleaned from examining the mean body temperature at which heat loss is activated (central) or from the rate of rise in the heat loss response relative to increasing mean body temperature (peripheral) (12, 31). While the mean body temperature onset threshold of evaporative heat loss was not different between each group (Table 2), the thermosensitivity of the evaporative heat loss response was reduced in the middle-aged untrained and older males. These results are consistent with previous studies that have reported that older adults have a reduced rate of heat loss (i.e., sweating) for a given increase in mean body temperature (1, 17, 30), which is indicative of a peripheral modification (31). In our study, we observed the greatest level of impairment during Ex3 where the time constant of the evaporative heat loss response was lower in young (4.8 ± 1.4 min) compared with both middle-aged untrained (7.0 ± 2.6 min) and older (8.5 ± 2.3 min) males (Table 2). The lower thermosensitivities and greater time constants were coupled with reduced amplitude of evaporative heat loss during the third exercise bout. It has been suggested that the attenuated heat loss response in older adults during heat stress is due to a decrease in cholinergic sensitivity and lower sweat gland output, rather than fewer heat-activated sweat glands ultimately resulting in a reduced capacity for heat dissipation in older adults (1, 22). We showed that this may be true for middle-aged untrained males as well. As a consequence of the reduced thermosensitivity and magnitude of evaporative heat loss, the change in body heat content was greater in middle-aged untrained and older males relative to their younger counterparts, respectively, by 48 and 47% for Ex1, 55 and 57% for Ex2, and 57 and 54% for Ex3.

Effects of Aerobic Fitness on Age-Related Impairments in Heat Loss

We observed that the middle-aged trained group had a significantly greater capacity for whole body heat dissipation at the moderate (400 W) and high (500 W) heat load conditions compared with the age-matched untrained group (Fig. 1). The differences in heat loss between the two middle-aged groups were solely due to the level of aerobic fitness, since the middle-aged trained males participated in regular endurance-type exercise training (i.e., running, cycling, cross country skiing), while the untrained males did not. Furthermore, participants were matched for physical characteristics such as body mass, body surface area, and body composition, which are known to influence heat dissipation and therefore body heat storage (13, 34). The increased capacity for heat dissipation in middle-aged trained males was the result of an increased thermosensitivity of the evaporative heat loss response combined with greater amplitude of increase in the rate of evaporative heat loss (Table 2). As such, evaporative heat loss reached significantly greater values for a given mean body temperature in the trained compared with untrained middle-aged counterparts in addition to the higher rate of evaporative heat loss at the last two exercise bouts. This finding is consistent with previous studies showing that endurance-trained adults demonstrate greater thermosensitivity of the sweating and/or skin blood flow response compared with their untrained counterparts (14, 41). It has been proposed by some that this response is in part attributed to partial acclimation caused by regular vigorous exercise training (3, 5, 11, 13, 34). In the present study, the greater rate of heat dissipation measured in the middle-aged trained adults translated into a 20 and 44% reduction in the amount of heat stored in the moderate and high heat load exercise bouts (i.e., Ex2 and Ex3), respectively, relative to the middle-aged untrained group. Future studies should be conducted to assess differences between nontrained adults with a low vs. high $\dot{V}_{O_{2peak}}$ to discern if the level of $\dot{V}_{O_{2peak}}$ per se (likely genetically determined) may influence this response.

Improvements in thermoregulatory capacity due to high levels of aerobic fitness are not always observed. Jay et al. (21) examined two groups of young (19–24 yr) males matched for body mass and surface area during exercise for 60 min at a fixed rate of metabolic heat production (540 W) in a thermoneutral environment. Jay et al. reported no differences in rectal temperature, whole body sweat rate, or local sweat rate (upper back) between the two groups despite the large differences in $\dot{V}_{O_{2peak}}$ (~40 vs. 60 ml·kg^{-1}·min^{-1}). Thus, while aerobic fitness may not be a factor affecting heat loss in young males when exercising at moderate levels of heat production, we showed that maintaining a higher level of aerobic fitness in middle-aged males promotes a greater capacity to dissipate heat. Furthermore, consistent with previous studies, when older untrained are compared with older trained adults during exercise (35–67% $\dot{V}_{O_{2peak}}$), heat loss responses of sweating and skin blood flow are reported to be lower in the older untrained adults (18, 41). However, it is unknown if the results would have been the same if both groups had exercised at the same rate of heat production, thereby providing a similar thermal drive (9). Therefore, further research is required to examine the effect of aerobic fitness with increasing age (i.e., >60 yr).

Whole Body Calorimetry vs. Core Temperature and Local Heat Loss Responses

An interesting finding of the current study is that we only observed a significantly greater increase in esophageal temperature at the end of the third exercise bout (Fig. 3), despite the greater change in body heat content measured at all heat loads in the older and middle-aged untrained males compared with their younger counterparts. Ultimately, direct calorimetry allows us to precisely measure the amount of heat that is stored in the body irrespective of differences in tissue heat distribution that may occur as a result of age-related changes in tissue blood distribution during and following exercise. While changes in esophageal temperature provide us with an indication of where some of the heat is stored, they cannot be used as a reliable measure to quantify whole body heat storage (25). By the same logic, the reverse is correct. The calorimeter can only tell us how much heat is stored in the body but not where it is stored. Of note, the measurement of esophageal temperature is affected by the powerful vascular changes that occur in this region. This effect is clearly observed in our study findings such that, as noted above, we only observed a significantly greater increase in esophageal temperature by the end of the third exercise bout between the middle-aged untrained and older group compared with both the young and middle-aged trained group. In contrast, we observed significant differences in heat storage by Ex1 for the middle-aged untrained and older males relative to the young and middle-aged trained males. From a practical standpoint, measurement of body core temperature using esophageal temperature may underestimate the level of thermal strain experienced by a middle-age untrained and older adult exercising in the heat especially when exercise is of short duration and/or low intensity.

In the present study, age-related differences in whole body evaporative heat loss (and therefore sweat production) were not paralleled by similar differences in local sweat rate at the three skin sites. Previous studies have reported within-group regional differences in sweating during passive heating and/or exercise within groups (10, 19, 20, 37, 38). However, the measurement of whole body evaporative heat loss by direct calorimetry allows us to precisely measure the net consequences of aging per se on whole body sweat production without the confounding effects of regional differences in sweating. While age-related differences in local skin blood flow responses have been observed (15, 16, 23), the pattern of response can differ between skin sites (20, 37, 38). In the present study, we only measured skin blood flow at one site, thus it is plausible that differences might have been observed at other sites. Taken together, our findings demonstrate that caution should be used when employing surrogate measures of body heat storage (i.e., core temperature) and local heat loss responses for the purpose of assessing age-related differences in the body's physiological capacity to dissipate heat, especially at low to moderate heat loads. These thermoregulatory measures can underestimate the extent to which aging may alter the body's physiological capacity to dissipate heat.

Postexercise Response

We observed a rapid reduction in whole body evaporative and local heat loss in all groups at the cessation of exercise despite sustained elevations in esophageal temperature, which is the typical pattern of response postexercise (25, 26). The rapid reductions in heat loss have been attributed to nonthermal factors overriding the thermal control of heat loss during postexercise recovery in young adults (25, 26), thus altering the body's ability to dissipate heat during recovery. In the present study, we observed a lower amplitude of change in evaporative heat loss for the third recovery period in the middle-aged untrained and older males compared with their young and middle-aged trained counterparts (Table 2). Furthermore, it took a longer amount of time to achieve ~63% of the evaporative heat loss response for Rec3 in older males. These findings may imply that the level of influence of nonthermal factors on heat loss postexercise may be reduced in middle-aged untrained and older adults as a result of the greater thermal drive, associated with the progressively greater heat storage during exercise. Moreover, we see that the rates of whole body heat loss are slightly elevated in the middle-aged untrained and older males compared with the young and middle-aged trained males during the third recovery period. It is possible that the greater rates of heat loss during recovery in the middle-aged untrained and older groups are due to some compensatory mechanism to try to offset the greater amounts of heat stored during exercise. Therefore, it brings into question if these differences would become more pronounced had we extended the recovery time period. Despite the few previous studies examining heat loss during the postexercise recovery period in older adults (29, 30, 40), future research is required to examine the potential influence of thermal and nonthermal factors on heat loss responses postexercise as a function of age and aerobic fitness.

Limitations

Due to technical limitations associated with performing measurements of whole body heat loss in a calorimeter (i.e., subject must remain isolated in the calorimeter and access in and out of temperature chamber housing the calorimeter is restricted during the trial), we were unable to measure changes in hydration status during the experimental trial. As a consequence, we were unable to determine the potential effects of age-related differences in fluid distribution on whole body heat dissipation as a function of increases in exercise-induced heat loads. However, by design we employed an incremental exercise model that required that the young, middle-aged, and older adults exercise at the same fixed absolute heat load and therefore requirement for heat loss. This experimental model was used to ensure that any differences in sweating (and therefore fluid loss) would be the result of age-related differences and not due to differences in the requirement for heat loss. Additional research is required to determine how changes in hydration status may influence this pattern of response as a function of increasing heat loads.

Perspectives

Advanced aging is associated with adverse changes to the thermoregulatory system, but when do these alterations matter? The results from this study provide important insight into the level of heat load in which differences in the capacity to dissipate heat occur as a function of age and aerobic fitness. We showed for the first time that the impairment in thermo-

regulatory function in older as well as middle-aged untrained males is heat load dependent. Thus our results can be used by health care providers, exercise specialists, health and safety managers, sporting event organizers (i.e., marathons, soccer tournaments, etc.), and others to better understand the level of heat stress in which dangers associated with exercise in hot conditions occur and decide when it is safe to perform physical activity in the heat. As such, it is critical that the previously mentioned groups reevaluate heat exposure thresholds and adjust these limits to include information based on the age as well as level of aerobic fitness of the individual to reduce the risk of heat-related illness/injury for all adults. However, during a work shift, it is possible that older adults self-pace differently relative to their younger counterparts as a way to mitigate the level of physical/thermal strain they experience. Thus, while older adults, and/or those who are less physically active, might have a reduced capacity to dissipate heat during work in the heat, they may experience similar levels of thermal strain as their younger and/or endurance-trained counterparts when allowed to self-pace. Furthermore, the participants in the present study were relatively healthy. Therefore, older adults with health conditions such as cardiovascular disease, diabetes etc. may be at an even greater risk of heat-related illness and/or injury during work in the heat.

Summary

Our findings demonstrate that age-related impairments in whole body evaporative heat loss in middle-aged untrained and older relative to young males are evident at exercise-induced heat loads as low as 400 W. This impairment in the capacity to dissipate heat is characterized by a reduced thermosensitivity of the evaporative heat loss response as well as a lower level of whole body heat loss achieved during exercise. Ultimately, the inability to dissipate heat to the same extent as younger adults led to a 1.5- to 1.6-fold greater increase in heat storage in the older and middle-aged untrained males, respectively. However, the age-related impairments in the body's physiological capacity to dissipate heat can be minimized through maintaining a high level of aerobic fitness (as defined by $\dot{V}o_{2peak}$).

AUTHOR CONTRIBUTIONS

Author contributions: J.M.S., A.D.F., P.B., R.J.S., J.M., and G.P.K. conception and design of research; J.M.S. and M.P.P. performed experiments; J.M.S. analyzed data; J.M.S., M.P.P., A.D.F., P.B., R.J.S., J.M., and G.P.K. interpreted results of experiments; J.M.S. prepared figures; J.M.S. drafted manuscript; J.M.S., M.P.P., A.D.F., P.B., R.J.S., J.M., and G.P.K. edited and revised manuscript; J.M.S., M.P.P., A.D.F., P.B., R.J.S., J.M., and G.P.K. approved final version of manuscript.

REFERENCES

1. **Anderson RK, Kenney WL.** Effect of age on heat-activated sweat gland density and flow during exercise in dry heat. *J Appl Physiol* 63: 1089–1094, 1987.
2. **Best S, Caillaud C, Thompson M.** The effect of ageing and fitness on thermoregulatory response to high-intensity exercise. *Scand J Med Sci Sports* 22: e29–37, 2012.
3. **Buono MJ, Sjoholm NT.** Effect of physical training on peripheral sweat production. *J Appl Physiol (1985)* 65: 811–814, 1988.
4. **Casa DJ, Armstrong LE, Hillman SK, Montain SJ, Reiff RV, Rich BS, Roberts WO, Stone JA.** National athletic trainers' association position statement: fluid replacement for athletes. *J Athl Train* 35: 212–224, 2000.
5. **Cheung SS, McLellan TM.** Heat acclimation, aerobic fitness, and hydration effects on tolerance during uncompensable heat stress. *J Appl Physiol (1985)* 84: 1731–1739, 1998.
6. **Cheuvront SN, Bearden SE, Kenefick RW, Ely BR, Degroot DW, Sawka MN, Montain SJ.** A simple and valid method to determine thermoregulatory sweating threshold and sensitivity. *J Appl Physiol* 107: 69–75, 2009.
7. **de Paula Viveiros J, Amorim FT, Alves MN, Passos RL, Meyer F.** Run performance of middle-aged and young adult runners in the heat. *Int J Sports Med* 33: 211–217, 2012.
8. **DuBois D, DuBois EF.** A formula to estimate the approximate surface area if height and weight be known. *Nutrition* 5: 303–311, 1989.
9. **Gagnon D, Jay O, Kenny GP.** The evaporative requirement for heat balance determines whole-body sweat rate during exercise under conditions permitting full evaporation. *J Physiol* 591: 2925–2935, 2013.
10. **Gagnon D, Kenny GP.** Sex differences in thermoeffector responses during exercise at fixed requirements for heat loss. *J Appl Physiol (1985)* 113: 746–757, 2012.
11. **Gisolfi C, Robinson S.** Relations between physical training, acclimatization, and heat tolerance. *J Appl Physiol* 26: 530–534, 1969.
12. **Gisolfi CV, Wenger CB.** Temperature regulation during exercise: old concepts, new ideas. *Exerc Sport Sci Rev* 12: 339–372, 1984.
13. **Havenith G, van Middendorp H.** The relative influence of physical fitness, acclimatization state, anthropometric measures and gender on individual reactions to heat stress. *Eur J Appl Physiol Occup Physiol* 61: 419–427, 1990.
14. **Henane R, Flandrois R, Charbonnier JP.** Increase in sweating sensitivity by endurance conditioning in man. *J Appl Physiol Respir Environ Exercise Physiol* 43: 822–828, 1977.
15. **Holowatz LA, Houghton BL, Wong BJ, Wilkins BW, Harding AW, Kenney WL, Minson CT.** Nitric oxide and attenuated reflex cutaneous vasodilation in aged skin. *Am J Physiol Heart Circ Physiol* 284: H1662–H1667, 2003.
16. **Holowatz LA, Thompson CS, Minson CT, Kenney WL.** Mechanisms of acetylcholine-mediated vasodilatation in young and aged human skin. *J Physiol* 563: 965–973, 2005.
17. **Inbar O, Morris N, Epstein Y, Gass G.** Comparison of thermoregulatory responses to exercise in dry heat among prepubertal boys, young adults and older males. *Exp Physiol* 89: 691–700, 2004.
18. **Inoue Y, Havenith G, Kenney WL, Loomis JL, Buskirk ER.** Exercise- and methylcholine-induced sweating responses in older and younger men: effect of heat acclimation and aerobic fitness. *Int J Biometeorol* 42: 210–216, 1999.
19. **Inoue Y, Nakao M, Araki T, Murakami H.** Regional differences in the sweating responses of older and younger men. *J Appl Physiol* 71: 2453–2459, 1991.
20. **Inoue Y, Shibasaki M.** Regional differences in age-related decrements of the cutaneous vascular and sweating responses to passive heating. *Eur J Appl Physiol Occup Physiol* 74: 78–84, 1996.
21. **Jay O, Bain AR, Deren TM, Sacheli M, Cramer MN.** Large differences in peak oxygen uptake do not independently alter changes in core tem-

perature and sweating during exercise. *Am J Physiol Regul Integr Comp Physiol* 301: R832–R841, 2011.

22. **Kenney WL, Fowler SR.** Methylcholine-activated eccrine sweat gland density and output as a function of age. *J Appl Physiol* 65: 1082–1086, 1988.

23. **Kenney WL, Morgan AL, Farquhar WB, Brooks EM, Pierzga JM, Derr JA.** Decreased active vasodilator sensitivity in aged skin. *Am J Physiol Heart Circ Physiol* 272: H1609–H1614, 1997.

24. **Kenny GP, Gagnon D, Dorman LE, Hardcastle SG, Jay O.** Heat balance and cumulative heat storage during exercise performed in the heat in physically active younger and middle-aged men. *Eur J Appl Physiol* 109: 81–92, 2010.

25. **Kenny GP, Jay O.** Thermometry, calorimetry, and mean body temperature during heat stress. *Compr Physiol* 3: 1689–1719, 2013.

26. **Kenny GP, Jay O, Journeay WS.** Disturbance of thermal homeostasis following dynamic exercise. *Appl Physiol Nutr Metab* 32: 818–831, 2007.

27. **Kohl HW, Blair SN, Paffenbarger RS Jr, Macera CA, Kronenfeld JJ.** A mail survey of physical activity habits as related to measured physical fitness. *Am J Epidemiol* 127: 1228–1239, 1988.

28. **Larose J, Boulay P, Sigal RJ, Wright HE, Kenny GP.** Age-related decrements in heat dissipation during physical activity occur as early as the age of 40. *PLoS One* 8: e83148, 2013.

29. **Larose J, Boulay P, Wright-Beatty HE, Sigal RJ, Hardcastle S, Kenny GP.** Age-related differences in heat loss capacity occur under both dry and humid heat stress conditions. *J Appl Physiol (1985)* 117: 69–79, 2014.

30. **Larose J, Wright HE, Stapleton J, Sigal RJ, Boulay P, Hardcastle S, Kenny GP.** Whole body heat loss is reduced in older males during short bouts of intermittent exercise. *Am J Physiol Regul Integr Comp Physiol* 305: R619–R629, 2013.

31. **Nadel ER, Mitchell JW, Saltin B, Stolwijk JA.** Peripheral modifications to the central drive for sweating. *J Appl Physiol* 31: 828–833, 1971.

32. **Ramanathan NL.** A new weighting system for mean surface temperature of the human body. *J Appl Physiol* 19: 531–533, 1964.

33. **Reardon FD, Leppik KE, Wegmann R, Webb P, Ducharme MB, Kenny GP.** The Snellen human calorimeter revisited, re-engineered and upgraded: design and performance characteristics. *Med Biol Eng Comput* 44: 721–728, 2006.

34. **Selkirk GA, McLellan TM.** Influence of aerobic fitness and body fatness on tolerance to uncompensable heat stress. *J Appl Physiol (1985)* 91: 2055–2063, 2001.

35. **Shibasaki M, Wilson TE, Crandall CG.** Neural control and mechanisms of eccrine sweating during heat stress and exercise. *J Appl Physiol* 100: 1692–1701, 2006.

36. **Siri WE.** Gross composition of the body. In: *Advances in Biological and Medical Physics*, edited by Lawrence JH, Tobias CA. New York: Academic, 1956, p. 239–280.

37. **Smith CJ, Alexander LM, Kenney WL.** Nonuniform, age-related decrements in regional sweating and skin blood flow. *Am J Physiol Regul Integr Comp Physiol* 305: R877–R885, 2013.

38. **Smith CJ, Kenney WL, Alexander LM.** Regional relation between skin blood flow and sweating to passive heating and local administration of acetylcholine in young, healthy humans. *Am J Physiol Regul Integr Comp Physiol* 304: R566–R573, 2013.

39. **Stapleton J, Gagnon D, Kenny GP.** Short-term exercise training does not improve whole-body heat loss when rate of metabolic heat production is considered. *Eur J Appl Physiol* 109: 437–446, 2010.

40. **Stapleton JM, Fujii N, Carter M, Kenny GP.** Diminished nitric oxide-dependent sweating in older males during intermittent exercise in the heat. *Exp Physiol* 99: 921–932, 2014.

41. **Tankersley CG, Smolander J, Kenney WL, Fortney SM.** Sweating and skin blood flow during exercise: effects of age and maximal oxygen uptake. *J Appl Physiol* 71: 236–242, 1991.

42. **Taylor WF, Johnson JM, O'Leary D, Park MK.** Effect of high local temperature on reflex cutaneous vasodilation. *J Appl Physiol Respir Environ Exercise Physiol* 57: 191–196, 1984.

43. **Wilson TM, Tanaka H.** Meta-analysis of the age-associated decline in maximal aerobic capacity in men: relation to training status. *Am J Physiol Heart Circ Physiol* 278: H829–H834, 2000.