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Whole body heat loss is reduced in older males during short bouts of intermittent exercise

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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. First published July 24, 2013; doi:10.1152/ajpregu.00157.2013.—Studies in young adults show that a greater proportion of heat is gained shortly following the start of exercise and that temporal changes in whole body heat loss during intermittent exercise have a pronounced effect on body heat storage. The consequences of short-duration intermittent exercise on heat storage with aging are unclear. We compared evaporative heat loss (H_E) and changes in body heat content (ΔH_b) between young (20–30 yr), middle-aged (40–45 yr), and older males (60–70 yr) of similar body mass and surface area, during successive exercise (4 × 15 min) and recovery periods (4 × 15 min) at a fixed rate of heat production (400 W) and under fixed environmental conditions (35°C/20% relative humidity). H_E was lower in older males vs. young males during each exercise (Ex1: 283 ± 10 vs. 332 ± 11 kJ, Ex2: 334 ± 10 vs. 379 ± 5 kJ, Ex3: 347 ± 11 vs. 392 ± 5 kJ, and Ex4: 347 ± 10 vs. 387 ± 5 kJ, all $P < 0.02$), whereas H_E in middle-aged males was intermediate to that measured in young and older adults (Ex1: 314 ± 13, Ex2: 355 ± 13, Ex3: 371 ± 13, and Ex4: 365 ± 8 kJ). H_E was not significantly different between groups during the recovery periods. The net effect over 2 h was a greater ΔH_b in older (267 ± 33 kJ; $P = 0.016$) and middle-aged adults (245 ± 16 kJ; $P = 0.073$) relative to younger counterparts (164 ± 20 kJ). As a result of a reduced capacity to dissipate heat during exercise, which was not compensated by a sufficiently greater rate of heat loss during recovery, both older and middle-aged males had a progressively greater rate of heat storage compared with young males over 2 h of intermittent exercise.

evaporative heat loss; aging; calorimetry; thermal transients

A NUMBER OF STUDIES HAVE EXAMINED age-related differences in thermoregulatory control during prolonged exercise (range 30–90 min) in the heat [range: 30–49°C/20–60% relative humidity (RH)] (4, 11–13, 20, 23, 26, 29, 33, 34). Some studies reported no differences in thermoregulatory function (4, 20, 23, 29, 33), whereas others found significant age-related impairments in heat loss capacity (e.g., reduced local sweating rate/onset/sensitivity and/or greater increments in core and skin temperatures) (11–13, 26, 34). It is possible that these discrepancies reflect that in some studies, older adults were able to achieve heat balance, while in other studies, heat load exceeded their physiological maximal sweating capacity; hence, differences in local sweat rate and/or core temperature were evident. What these studies did not examine, however, is whether age-related impairments in heat loss capacity occur during exercise of short duration (i.e., 15 min) when the rate of heat storage has been shown to be the greatest (21).

At the onset of exercise, the rate of metabolic heat production increases immediately and is not initially offset by an increase in the rate of heat loss, thus, giving rise to a pronounced increase in body heat storage in the first 15 min of exercise (21, 35). If as previously suggested (11, 12), older adults have a delayed onset and/or reduced responsiveness of local sweating response, older individuals would likely store more heat during this period of thermal imbalance than young adults. A greater rate of heat storage during short exercise bouts could have a deleterious effect over time, particularly when multiple successive exercise/recovery cycles are performed. Heat balance during thermal transients caused by successive exercise/recovery cycles is well documented in young adults (21). For example, Kenny et al. (21) demonstrated greater heat storage during a first exercise bout, although this was reduced with subsequent exercises as a result of an enhanced rate of whole body heat loss when the body is already warm and core temperature is elevated (i.e., priming effect). On the other hand, their ability to dissipate heat was compromised during postexercise recovery, and this was sustained during successive recovery periods, despite a progressively greater thermal drive for heat dissipation. Conversely, two previous studies involving intermittent exercise suggested that middle-aged males (39–53 yr) had a tendency to sweat less during the exercise bouts but more during the recovery periods compared with younger counterparts (19–31 yr) (12, 26). This sweating response during recovery is consistent with observations made in other conditions that alter heat loss capacity (e.g., sympathectomy procedure, grafted skin) (3, 9) and may be indicative of a compensatory mechanism. Nonetheless, most laboratories are not equipped with the technology (i.e., direct calorimetry) to detect minute changes in whole body total heat loss and, therefore, heat storage during exercise of short duration and during thermal transients. Thus, the consequences of short-duration intermittent exercise on heat storage as a function of age, particularly in adults over the age of 60, remains unclear.

The purpose of this study was to examine the consequences of heat storage during short exercise bouts, as well as the temporal changes in whole body heat loss during intermittent exercise, on body heat storage over 2 h in

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young, middle-aged, and older adults. We hypothesized that for the experimental conditions used (35°C/20% RH), middle-aged and older males would store more heat during successive short exercise bouts than young males. During the recovery periods, middle-aged and older males would have an elevated rate of heat loss; however, this would not be sufficient to offset the greater amount of heat gained during exercise. As a result, both older age groups are expected to have a greater cumulative increase in body heat content compared with the younger group. In addition to advancing our understanding of age-related differences associated with the physiological mechanisms governing heat loss during intermittent exercise, this exercise modality provides some practical insights relevant for many work- and leisure-related activities.

MATERIALS AND METHODS

Participants and Ethical Approval

Healthy and physically active males were recruited for this study. Eleven young (25.8 ± 1.9 yr), middle-aged (43.2 ± 2.3 yr), and older males (63.4 ± 3.3 yr) with similar height, weight, and body surface area volunteered to participate in the study. Males reporting a history of cardiovascular, metabolic, and respiratory disease, or taking medications related to these conditions, were excluded from participating in the study. The current experimental protocol was approved by the University of Ottawa Health Sciences and Science Research Ethics Board. Written informed consent was obtained from all volunteers prior to their participation in the study.

Experimental Design

Prior to the experimental session, body density and maximal oxygen uptake ($\dot{V}O_{2\,max}$) were measured. $\dot{V}O_{2\,max}$ was measured during a progressive cycle ergometer protocol, which consisted of a 2-min warm-up at 40 W followed by 20-W increments every minute until the participant could no longer maintain a pedaling cadence of at least 60 rpm. Continuous electrocardiographic monitoring was used on males aged 50 or older during the maximal exercise test. Body density was measured using the hydrostatic weighing technique, and body fat percentage was calculated using the Siri equation (32). Body surface area was calculated from the measurements of weight and height, according to DuBois and DuBois (5).

Participants performed one experimental session at approximately the same time of day in a warm/dry (35°C/ 20% RH) environment. Participants arrived at the laboratory in the morning after eating a light meal and were asked to refrain from consuming alcohol and caffeine for 24 h prior to experimentation and to avoid major thermal stimuli on their way to the laboratory. Participants were also encouraged to be well hydrated, as no fluids were administered during the experimental session. Following instrumentation, participants entered the whole body calorimeter and rested in an upright seated position for a 30-min baseline period, while a steady-state baseline condition was achieved. Participants then performed four 15-min bouts of cycling at a constant rate of metabolic heat production equal to ~400 W separated by 15-min inactive periods with the exception of the final recovery period, which was 60 min in duration.

For the experimentation, clothing was standardized to running shorts and sandals. We did not conduct any form of heat acclimatization program prior to experimental testing to ensure similar heat acclimatization across participants. Experimental sessions were held throughout the year. The majority of young and middle-aged males were tested during the fall/winter season (October-March), whereas a greater proportion of older males were tested during spring/summer season (April-August). We also inquired about exercise and daily activity patterns of study participants during recruitment. None of our subjects were extremely active or competitive endurance athletes. All participants reported similar activity levels, including occasional exercise (jogging, elliptical, bicycle, and swimming) and leisure sport activities (hockey, cross-country skiing, soccer, martial arts, and golf).

Measurements

Whole body direct calorimetry. Whole body direct calorimetry is the gold standard to accurately measure the rates of whole body evaporative heat loss and dry heat exchange, as well as the change in body heat content (18). The modified Snellen direct air calorimeter was used to measure whole body evaporative heat loss (H_E) and dry heat exchange (H_D) (*R*, radiant heat exchange; $+C$, convective heat exchange; $+K$: conductive heat exchange) with an accuracy of ± 2.3 W for the measurement of total heat loss (H_L). A full peer-reviewed technical description of the performance and calibration characteristics of the Snellen whole body calorimeter is available (30). 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 LabVIEW software (version 7.0, National Instruments, Austin, TX). The rate of evaporative heat loss was calculated from the calorimetry data using the following equation:

$$H_E = \frac{(\text{Massflow} \times (\text{Humidity}_{\text{out}} - \text{Humidity}_{\text{in}}) \times 2{,}426)}{60}$$

where mass flow is the rate of air mass (kg air/s); ($\text{Humidity}_{\text{out}} - \text{Humidity}_{\text{in}}$) is the difference in absolute humidity (g water/kg air) between the inflow and outflow 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:

$$R + C + K = \frac{(\text{Massflow} \times (\text{Temperature}_{\text{out}} - \text{Temperature}_{\text{in}}) \times 1{,}005)}{60}$$

where mass flow is the rate of air mass (kg air/s); ($\text{Temperature}_{\text{out}} - \text{Temperature}_{\text{in}}$) is the difference in outflow-inflow air temperature (°C) of the calorimeter; and 1,005 is the specific heat of air [J·(kg air·°C)$^{-1}$]. A 6-liter fluted mixing box housed within the calorimeter was utilized to measure metabolic energy expenditure (*M*). Expired gas was analyzed for oxygen (O_2) and carbon dioxide (CO_2) concentrations using electrochemical gas analyzers (AMETEK models S-3A/1 and CD 3A, respectively; Applied Electrochemistry, Pittsburg, PA) located outside the calorimeter chamber. Expired air was recycled back into the calorimeter chamber to account for respiratory dry and evaporative heat loss. Prior to each session, gas mixtures of 4% CO_2, 17% O_2, and balance nitrogen were used to calibrate the gas analyzers, and a 3-liter syringe was used to calibrate the turbine ventilometer. The data derived from direct and indirect calorimetry were, thereafter, used to calculate the change in body heat content (in kilojoules).

Local Heat Loss Responses and Heart Rate

The ventilated capsule technique was utilized to measure local sweat rate. Sweat production on the upper back was measured from a 3.8 cm^2 plastic capsule attached to the skin with adhesive rings and topical skin glue (Collodion HV, Mavidon Medical Products, Lake Worth, FL). Anhydrous compressed air was passed through each capsule at a rate of 1 l/min. Water content of the effluent air was measured using high-precision dew point mirrors (model 473; RH Systems, Albuquerque, NM). Subsequently, local sweat rate was determined by calculating 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.

Forearm skin blood flow was estimated using laser-Doppler velocimetry (PeriFlux System 5000; Perimed, Stockholm, Sweden) at the left midanterior forearm. The laser-Doppler flow probe (model PR 401 Angled Probe; Perimed) was fixed with an adhesive ring and surgical tape to the ventral forearm in a site determined to be free of superficial veins that demonstrated high flux values and pulsatile activity prior to the start of the experiment. Local skin temperature was raised to 44°C using a heating element (model PF 5020 Temperature Unit; Perimed) housing the laser-Doppler flow probe at the 15-min mark of the final 60-min recovery period and remained on until the end the experiment (i.e., 45 min), at which point, participants had attained a plateau in skin blood flow. Skin blood flow data are presented as a percentage of maximum flux values.

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).

Core and Skin Temperatures

Rectal temperature was measured by inserting a thermocouple probe (Mon-a-therm General Purpose Temperature Probe, Mallinckrodt Medical, St. Louis, MO) to a minimum of 12 cm past the anal sphincter. An ingestible capsule thermometer (Vital Sense ingestible capsule thermometer; Mini Mitter, Bend, OR) was used to estimate internal body temperature within the lower gut. Skin temperature was measured at four sites using 0.3-mm diameter T-type thermocouples (Concept Engineering, Old Saybrook, CT) attached to the skin with surgical tape. Mean skin temperature was subsequently calculated using four skin temperatures weighted to the following regional proportions: upper back, 30%; chest, 30%; quadriceps, 20%; and back calf, 20%. Temperature data were collected using a HP Agilent data acquisition module (model no. 3497A) at a sampling rate of 15 s and simultaneously displayed and recorded in spreadsheet format on a personal computer with LabVIEW software (version 7.0; National Instruments).

Data Analysis

For statistical purposes, minute averages were calculated for all variables. The rate of increase and decay in whole body evaporative heat loss during exercise and recovery, respectively, were characterized by determining the time constant (τ) of the response using an exponential, one-phase association nonlinear regression analysis (GraphPad Software, La Jolla, CA). The onset threshold of whole body evaporative heat loss during each exercise bout was determined by plotting evaporative heat loss over time and determining visually the point at which it increased. The corresponding mean body temperature (calculated as 0.9 × rectal temperature + 0.1 × mean skin temperature) (31) at that time point was taken as the onset threshold.

Statistical Analysis

Thermoregulatory responses during the exercise (Ex) and recovery periods (R) were analyzed separately. The primary outcome measures included those obtained by direct carlorimetry: metabolic heat production (*M-W*); required evaporation for heat balance (E_{req}), H_L, H_E, H_D; and changes in body heat content. Secondary outcome measurements included onset thresholds, time constants, local sweat rate, skin blood flow (SkBF), and heart rate, as well as rectal (T_{rec}), visceral pill (T_{pill}) and mean skin (T_{sk}) temperatures. The differences between age groups for each variable were analyzed using a two-way repeated-measures ANOVA with the repeated factors of exercise period (four levels: Ex1, Ex2, Ex3, and Ex4) or recovery period (four levels: R1, R2, R3, and R4), as well as a nonrepeated factor of age (levels: young, middle-aged, and older). The values for Ex1, Ex2, Ex3, and Ex4 were obtained at the end of each 15-min exercise period by averaging the last minute of exercise. Similarly, the values for R1, R2, and R3 were obtained by averaging the last minute of each 15-min recovery period, whereas the value for R4 is obtained at the 15-min mark of the final 60-min recovery period. This statistical procedure was repeated to analyze the relative changes from baseline in local sweat rate, core, and skin temperatures during exercise and recovery. We conducted a separate analysis to determine whether differences in H_E between young, middle-aged, and older males occurred at 5, 10, and 15 min of exercise for each exercise period using one-way ANOVAs. Repeated-measures ANOVAs were conducted separately for young, middle-aged, and older males for post hoc comparisons when a significant main effect of time was observed. Physical characteristics, baseline values for all variables, and the cumulative change in body heat content were analyzed using one-way ANOVA. For all comparisons, an α-level of 0.05 was considered statistically significant; this was adjusted during multiple comparisons to limit the rate of type 1 error to 5% during Holm-Bonferroni adjustments. The statistical software package SPSS 18 (SPSS, Chicago, IL) was used for all analyses.

RESULTS

Participant Characteristics

Participant characteristics are presented in Table 1. There were no significant differences between groups for height, weight, and body surface area. Age groups significantly differed in percentage of body fat ($P < 0.001$), $\dot{V}O_{2\,max}$ ($P = 0.002$), and by study design, age ($P < 0.001$). Body fat percentage was significantly greater in older ($P < 0.001$) and middle-aged males ($P = 0.019$) compared with the young males. $\dot{V}O_{2\,max}$ was significantly lower in older males compared with both middle-aged ($P = 0.015$) and young males ($P = 0.003$).

Whole Body Direct Calorimetry

Exercise. The required amount of evaporative heat loss to achieve heat balance (E_{req}) is defined as the sum of metabolic ± environmental heat load (i.e., $M\text{-}W \pm H_D$). E_{req} did not significantly change throughout the exercise bouts and was not different between groups. In young males, E_{req} was equal to 427 ± 6 (Ex1), 427 ± 3 (Ex2), 430 ± 4 (Ex3), and 437 ± 5 W (Ex4). In middle-aged males, E_{req} was 430 ± 8 (Ex1), 439 ± 7 (Ex2), 431 ± 6 (Ex3), and 434 ± 7 W (Ex4). Finally, E_{req} for older males was equal to 437 ± 9 (Ex1), 441 ± 11 (Ex2), 444 ± 10 (Ex3), and 440 ± 12 W (Ex4). By study design, the rate of *M-W* (i.e., 400 W) was the same between groups throughout exercise.

The mean rates of evaporative heat loss (H_E) and dry heat exchange (H_D) throughout the experimental protocol are given in Fig. 1. The increase in total heat loss during exercise was mainly due to an increase in the rate of evaporative heat loss. H_E significantly increased with successive exercise bouts ($P < 0.001$). H_E was greater during Ex2 compared with Ex1 in all three groups (all $P \leq 0.001$) and also during Ex3 compared with Ex2 in older adults ($P = 0.051$). A significant difference in H_E was also observed between groups ($P = 0.005$). H_E was significantly lower in older males compared with young males at 10 and 15 min during each exercise bout (all $P < 0.05$). There were no significant differences in H_E between young and middle-aged, as well as between middle-aged and older males. The rate of dry heat exchange was not significantly different during repeated exercise bouts or between age groups.

Table 1. *Participant characteristics*

	N	Age, yr	Height, m	Weight, kg	A_D, m^2	Body fat, %	HR_{max}, bpm[a]	$\dot{V}O_{2max}$, ml $O_2\cdot kg^{-1}\cdot min^{-1}$
Young	11	26 ± 2 (23–29)	1.8 ± 0.1 (1.7–2.0)	84.3 ± 6.2 (75.5–95.5)	2.0 ± 0.1 (1.9–2.3)	16.9 ± 5.0 (9.0–25.0)	177 ± 13 (156–196)	43.4 ± 6.7 (35.3–58.0)
Middle-Aged	11	43 ± 2†‡ (39–47)	1.8 ± 0.1 (1.7–1.9)	85.5 ± 7.4 (73.9–100.9)	2.0 ± 0.1 (1.9–2.2)	23.3 ± 3.2‡ (19.0–29.0)	173 ± 9 (157–185)	41.8 ± 6.1 (31.5–51.5)
Older	11	63 ± 3* (59–70)	1.8 ± 0.1 (1.7–1.9)	87.7 ± 10.2 (71.8–106.4)	2.1 ± 0.1 (1.9–2.3)	28.3 ± 6.1* (16.0–36.0)	156 ± 9*† (144–174)	33.8 ± 5.7*† (24.1–43.2)

Values are expressed as means with the minimum and maximal value for each group shown in parentheses. A_D, body surface area; HR_{max}, maximal heat rate; bpm, beats per minute; $\dot{V}O_{2max}$, maximal oxygen uptake. [a]Reduced sample size in older males (n = 10). *Significant difference between young and older males. †Significant difference between middle-aged and older males. ‡Significant difference between young and middle-aged males. Significance level was accepted at $P \leq 0.05$.

The change in body heat content significantly increased with successive exercise periods ($P < 0.001$). In all three groups, the change in body heat content was greater during Ex1 than Ex2 (all $P < 0.001$) but similar between Ex2, Ex3, and Ex4. The change in body heat content during exercise was also significantly different between groups ($P = 0.001$). Older adults stored significantly more heat than young adults during Ex1 ($P = 0.002$), Ex2 ($P = 0.007$), Ex3 ($P = 0.007$), and Ex4 ($P = 0.009$). The amount of heat stored during each exercise in middle-aged males was intermediate to that of young and older males (Fig. 2).

Recovery. Immediately after each exercise period, M-W returned close to preexercise values. The postexercise changes in total heat loss again were largely influenced by the rapid attenuation in H_E. H_E was significantly different during the recovery periods ($P < 0.001$). In young, middle-aged, and older males, H_E was significantly elevated at the end of R1 compared with baseline (all $P < 0.02$) but was similar between R1, R2, R3, and R4. H_E was not significantly different between groups during the recovery periods. Dry heat exchange did not significantly change with successive recovery periods and was not significantly different between age groups.

The change in body heat content was significantly less with successive recovery periods ($P < 0.001$). All three age groups had a greater negative change in body heat content during R2 compared with R1 (all $P < 0.03$). No differences were observed between R2, R3, and R4. The change in body heat content during the recovery was not significantly different between age groups.

Cumulative change in body heat content. The cumulative change in body heat content was significantly different between age groups (older: 267 ± 33; middle-aged: 245 ± 16; young: 164 ± 20 kJ, $P = 0.013$). Older males stored significantly more heat overall compared with young males ($P = 0.016$). The difference between middle-aged and young males was just short of statistical significance ($P = 0.073$), and there was no difference between middle-aged and older males.

Time Constants and Onset Thresholds

Exercise. We examined the time constant (τ) of the exponential increase in H_E during exercise, defined as the evaporative heat loss value representing 63.2% of the total amplitude reached during each exercise bout. The amplitude for H_E was calculated as the difference between the evaporative heat loss value at the onset and at the end of each exercise bout. The time required for H_E to reach 63.2% of its total amplitude significantly changed with repeated exercise bouts ($P < 0.001$) (Table 2). In young and middle-aged males, τ was significantly lower during Ex2 relative to Ex1 (all $P < 0.05$). Although not statistically significant, τ was also reduced during Ex2 compared with Ex1 in older males. The difference in τ during the exercise periods was just short of being significantly different between groups ($P = 0.084$). The total amplitude for H_E did not significantly change with successive exercises; however, there was a significant group difference ($P = 0.001$). Young males had a significantly greater total amplitude for H_E than older males during each exercise bout. The onset threshold of whole body evaporative heat loss was not significantly different between groups during each exercise bout (Table 3).

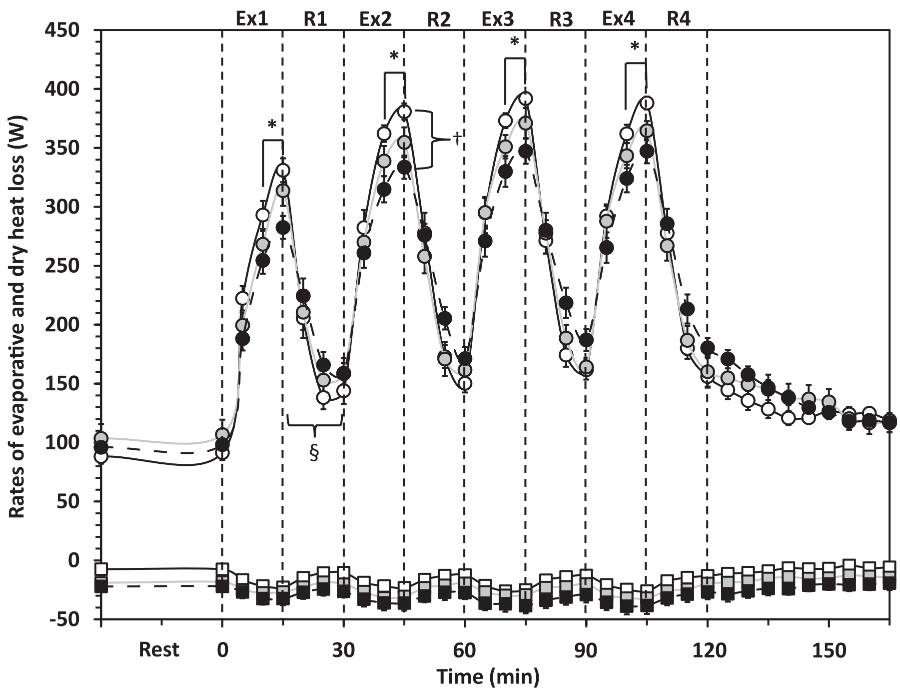

Fig. 1. Values are presented as means ± SE. Rate of evaporative heat loss (H_E) (circles) and dry heat exchange (H_D) (squares) in young (white), middle-aged (gray) and older (black) males during intermittent exercise at 35°C/20% RH. H_E was analyzed at 5-min intervals during the exercise periods. *Significant difference between young and older males at 10- and 15-min of exercise. †Significant difference in H_E compared with the previous exercise bout. §Significant difference in H_E compared with the previous recovery period. Significance level was accepted at $P \leq 0.05$.

Recovery. The time constant of the exponential decay in H_E did not change with repeated rest periods. There was, however, a significant difference between age groups ($P < 0.001$). Older males had a significantly greater τ during R1 and R2 relative to young and middle-aged males and also during R3 compared with young males. The total amplitude of change in H_E between the end of each exercise and the start of the next exercise bout was significantly affected by recovery bouts ($P < 0.001$). Older males had a lower amplitude of decay in H_E compared with young males during each recovery period (all $P < 0.05$) and during R3 compared with middle-aged males ($P = 0.008$).

Local Heat Loss Responses and Heart Rate

Local sweat rates, skin blood flow, and heart rate responses are presented in Table 3.

Exercise. Two young and middle-aged males, as well as one older male, were excluded from the analysis of local sweat rate due to failure of the ventilated capsule to remain attached to the participant during the experiment. The data presented are, therefore, from 9 young, 9 middle-aged, and 10 older males. Local sweat rate increased during successive exercise periods ($P < 0.001$). In young males, local sweat rate was significantly greater during Ex2 compared with Ex1 ($P = 0.009$). In middle-

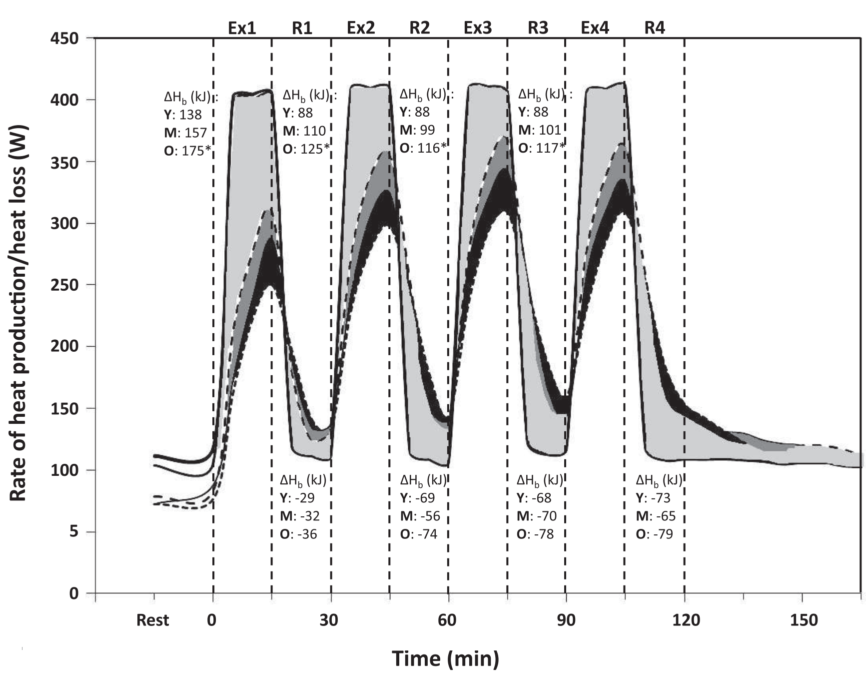

Fig. 2. Mean rates of heat production and whole body total heat loss for young (Y), middle-aged (M), and older (O) males during four successive exercise (Ex1, Ex2, Ex3, Ex4)/recovery (R1, R2, R3, R4) cycles. Changes in body heat content (ΔH_b) are presented as shaded areas and numerically for each exercise and recovery period. Light gray area shows ΔH_b in young males; dark gray area shows the additional amount of heat stored (exercise) or lost (recovery) by middle-aged males compared with young males; and black area denotes the additional amount of heat stored (exercise) or lost (recovery) by older males relative to young and middle-aged males. *Significant differences in ΔH_b compared with young males.

Table 2. *Mean time constants and amplitude of evaporative heat loss response to intermittent exercise and recovery periods*

	Young			Middle-Aged			Older		
	τ, min	Amplitude, W	R^2	τ, min	Amplitude, W	R^2	τ, min	Amplitude, W	R^2
Ex1	5.8 ± 0.4	238 ± 14	0.95	6.9 ± 0.4	207 ± 13	0.94	6.6 ± 0.5	177 ± 13*	0.95
R1	3.8 ± 0.4	192 ± 12	0.93	4.6 ± 0.5	167 ± 14	0.91	6.7 ± 0.5*§	131 ± 10*	0.88
Ex2	4.3 ± 0.4†	235 ± 12	0.97	5.4 ± 0.5†	198 ± 15	0.94	5.3 ± 0.4	181 ± 10*	0.97
R2	5.2 ± 0.5	228 ± 11‡	0.92	5.1 ± 0.5	197 ± 16	0.91	6.8 ± 0.2*§	182 ± 11*‡	0.92
Ex3	4.5 ± 0.4†	237 ± 9	0.95	4.6 ± 0.3†	211 ± 16	0.97	5.2 ± 0.4	175 ± 11*	0.97
R3	4.8 ± 0.3	230 ± 10‡	0.91	5.6 ± 0.4	222 ± 14‡	0.89	6.6 ± 0.3*	164 ± 12*‡§	0.92
Ex4	4.6 ± 0.3	224 ± 9	0.98	4.1 ± 0.4†	198 ± 11	0.96	5.9 ± 0.4	164 ± 10*	0.97
R4	4.9 ± 0.4	229 ± 10	0.94	5.5 ± 0.4	207 ± 16‡	0.94	6.3 ± 0.4	169 ± 6*‡	0.92

Values are expressed as means ± SE. The values represent the time constant (τ) of the exponential increase (Ex1, Ex2, Ex3, Ex4) and decay (R1, R2, R3, R4) in evaporative heat loss for young, middle-aged, and older males. During exercise, amplitude is the difference between evaporative heat loss at the start and end of each exercise bout. During recovery, amplitude is the difference in evaporative heat loss between the end of exercise and start of the next bout. *Significantly different compared to young males. †Significantly different compared to Ex 1. ‡Significantly different compared to R1. §Significantly different compared to middle-aged males.

aged males, local sweat rate was greater during Ex2 vs. Ex1 (P = 0.010), Ex3 vs. Ex2 (P = 0.016), and Ex4 vs. Ex3 (P = 0.021). In older males, there was a tendency for local sweat rate to be greater during Ex2 compared with Ex1 (P = 0.089). Absolute sweat rate or sweat rate expressed as a relative change from baseline value did not significantly differ between groups.

One middle-aged participant was excluded from the analysis of SkBF due to a technical error during the experimental session. Data from 11 young and older males, as well as 10 middle-aged males are presented as a percentage of each participant's maximal skin blood flow measured in perfusion units. SkBF changed significantly with repeated exercises (P = 0.036). While remaining fairly consistent throughout Ex1, Ex2, and Ex3, SkBF was reduced during Ex4 in each group. SkBF was not significantly different between groups.

Heart rate responses are presented as absolute values and as a percentage of maximal heart rate to account for differences between age groups in maximal heart rate achieved during the maximal exercise test (P = 0.053). When absolute heart rate responses were analyzed, heart rate did not significantly increase from one exercise bout to the next and was not different between groups. When analyzed as a percentage of maximum heart rate, again, the main effect for exercise bout was not significant, but there was a significant effect of group (P = 0.014). The older males exercised at a greater percentage of their maximum heart rate relative to younger males during Ex1 (P = 0.043), Ex3 (P = 0.014), and Ex4 (P = 0.025), whereas group differences during Ex2 were short of statistical significance (P = 0.072). The differences between older and middle-aged males were also significant during Ex1 (P = 0.052), Ex2

Table 3. *Thermoregulatory and heart rate responses during each exercise/recovery cycle and onset thresholds of evaporative heat loss*

	Baseline	Ex1	R1	Ex2	R2	Ex3	R3	Ex4	R4
Heart rate, bpm									
Y	82 ± 5	105 ± 7	87 ± 6	107 ± 6	84 ± 6	106 ± 6	88 ± 6	107 ± 7	80 ± 5
MA	71 ± 4	103 ± 4	74 ± 5	104 ± 4	74 ± 4	104 ± 4	74 ± 4	106 ± 4	75 ± 4
O	74 ± 3	109 ± 6	80 ± 4	108 ± 5	81 ± 4	110 ± 4	82 ± 4	111 ± 4	80 ± 4
Heart rate, $\%HR_{max}$									
Y	46.5 ± 2.6	59.2 ± 3.1	47.6 ± 3.0	60.6 ± 3.0	47.4 ± 3.1	59.5 ± 3.2	49.8 ± 3.1	60.2 ± 3.6	45.1 ± 2.2
MA	40.8±.1.8	59.6 ± 1.9	42.8 ± 2.5	59.8 ± 2.0	42.8 ± 2.3	60.2 ± 1.8	42.6 ± 2.2	61.3 ± 2.0	43.1 ± 2.4
O	47.6 ± 1.4	69.7 ± 3.2*†	51.1 ± 2.2	69.1 ± 2.3†	52.0 ± 1.8†	70.5 ± 2.1*†	52.3 ± 2.0†	71.3 ± 2.3*†	51.1 ± 1.8†
Local sweat rate, $mg \cdot cm^{-2} \cdot min^{-1}$									
Y	0.19 ± 0.03	0.66 ± 0.07	0.29 ± 0.05	0.79 ± 0.10‡	0.32 ± 0.06	0.81 ± 0.10	0.37 ± 0.07	0.81 ± 0.10	0.40 ± 0.08
MA	0.24 ± 0.03	0.66 ± 0.07	0.36 ± 0.06	0.79 ± 0.08‡	0.40 ± 0.05	0.81 ± 0.07‡	0.42 ± 0.06	0.82 ± 0.07‡	0.44 ± 0.06
O	0.33 ± 0.06	0.79 ± 0.07	0.52 ± 0.07	0.86 ± 0.06	0.52 ± 0.07	0.87 ± 0.07	0.53 ± 0.08	0.86 ± 0.07	0.51 ± 0.08
Skin blood flow, $\%PU_{max}$									
Y	28.3 ± 4.2	43.5 ± 4.3	27.9 ± 4.2	46.5 ± 6.2	24.2 ± 2.9	45.1 ± 6.2	21.4 ± 1.8	39.2 ± 4.1	21.7 ± 2.2
MA	23.8 ± 1.9	46.3 ± 4.8	26.5 ± 2.9	47.8 ± 6.0	26.2 ± 4.4	44.3 ± 5.8	25.0 ± 4.5	41.5 ± 6.0	23.2 ± 4.7
O	23.1 ± 2.9	48.0 ± 5.9	28.1 ± 4.1	47.7 ± 5.1	28.9 ± 3.9	48.3 ± 5.7	27.9 ± 3.3	45.8 ± 5.1	26.3 ± 3.3
Onset threshold of evaporative heat loss, °C									
Y		36.7±.0.1		36.9 ± 0.1		37.0 ± 0.1		37.1 ± 0.1	
MA		36.7±.0.1		36.9 ± 0.1		37.0 ± 0.1		37.1 ± 0.1	
O		36.8 ± 0.1		37.0 ± 0.1		37.2 ± 0.0		37.2 ± 0.0	

Values are expressed as means ± SE. The values represent the average of the last minute of each exercise (Ex1, Ex2, Ex3, Ex4) and rest (R1, R2, R3) periods with the exception of R4, which is the value at the 15-min mark of the finale 60-min recovery. Y, young; MA, middle-aged; O, older; $\%HR_{max}$, percentage of maximal hear rate; $\%PU_{max}$, percentage of maximal skin blood flow measured in units of perfusion. *Significant difference between young and older males. †Significant difference between middle-aged and older males. ‡Significantly different than the previous exercise bout. Significance level was accepted at $P \leq$ 0.05.

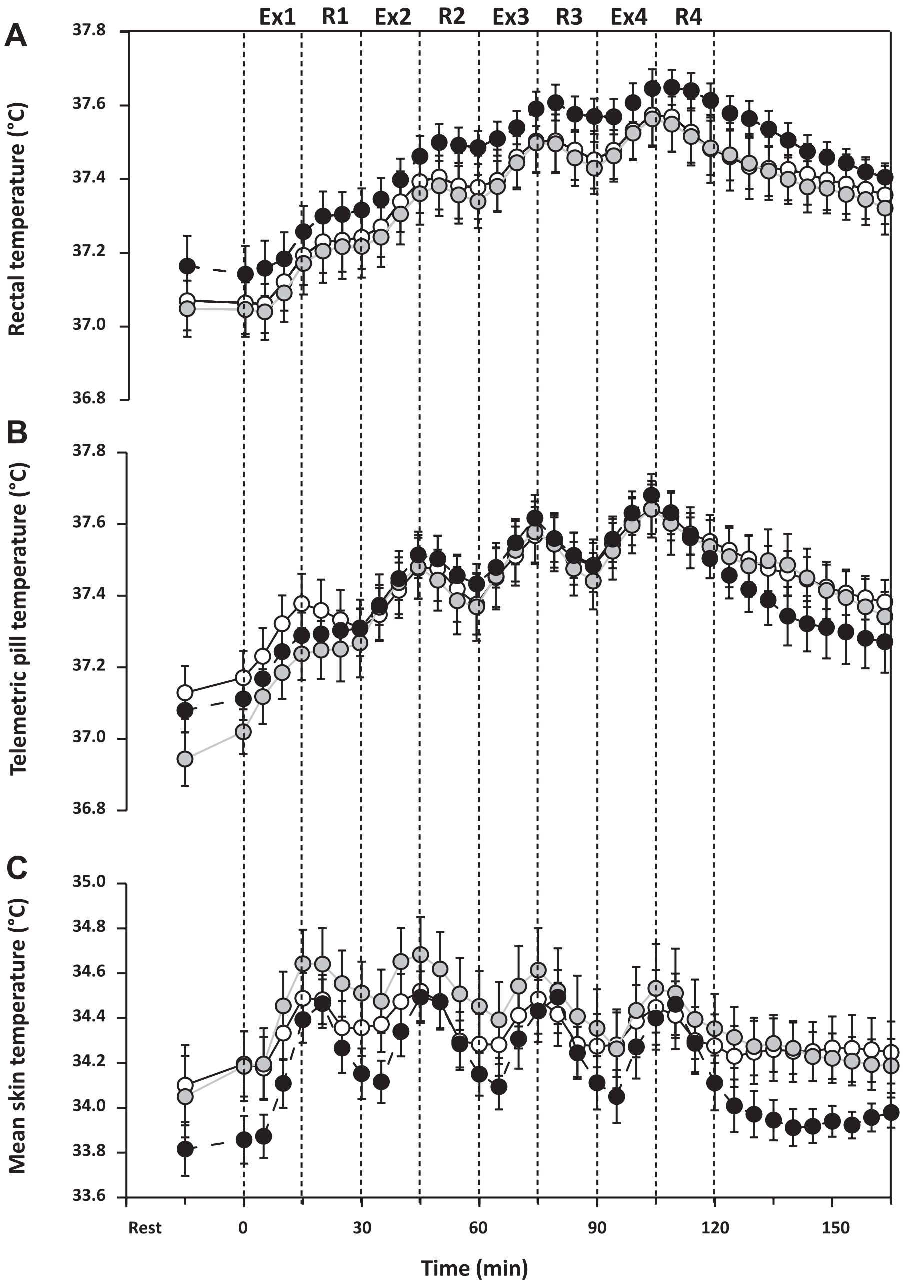

Fig. 3. Values are presented as means ± SE. Rectal (T_{rec}; *A*), telemetric pill (T_{pill}; *B*), and mean skin (T_{sk}; *C*) temperatures for young (white), middle-aged (gray) and older (black) males throughout a 165-min intermittent exercise protocol at 35°C/20% RH.

(P = 0.043), Ex3 (P = 0.022), and Ex4 (P = 0.051). Young and middle-aged males exercised at similar percentages of maximum heart rate throughout the exercise bouts.

Recovery. Local sweat rate did not significantly change with successive recovery periods and was not significantly different between groups. The relative change in local sweat rate from baseline was also not significantly different between groups.

Skin blood flow did not change with each recovery period and was not significantly different between age groups.

Heart rate response did not significantly increase during successive recovery periods and was similar between groups. Heart rate expressed as a percentage of maximum heart rate also did not increase during the recovery periods, but there was a significant difference between age groups (P = 0.043). A post hoc analysis demonstrated that older males were at a greater percentage of maximum heart rate compared with middle-aged males at the end of R2 (P = 0.049), R3 (P = 0.033), and R4 (P = 0.050). No differences were found between young and middle-aged or young and older males.

Core and Skin Temperatures

Exercise. One young male was excluded from the analysis for rectal temperature as the probe malfunctioned during the experimental session. Data from 10 young males, as well as 11 middle-aged and older males are presented in Fig. 3*A*. T_{rec} increased with repeated exercises ($P < 0.001$). T_{rec} was significantly elevated at the end of Ex2 vs. Ex1, Ex3 vs. Ex2, and Ex4 vs. Ex3 in each age group (all $P \leq 0.05$). Absolute T_{rec}

values and T_{rec} expressed as a relative change from baseline were not different between groups.

One older male participant was excluded from the analysis of visceral temperature as the ingestible thermometer capsule monitor failed to record the data during the experimental session. Data from 11 young and middle-aged, as well as 10 older males, are presented in Fig. 3*B*. T_{pill} significantly increased with successive exercises ($P < 0.001$). T_{pill} was significantly elevated at the end of Ex2 vs. Ex1 and Ex3 vs. Ex2 in each age group (all $P \leq 0.05$). Absolute T_{pill} values and T_{pill} expressed as a relative change from baseline did not differ between groups.

Mean skin temperature is presented in Fig. 3*C*. T_{sk} did not significantly change over time nor did it differ between groups.

Recovery. T_{rec} significantly increased with successive recovery periods ($P < 0.001$). In young males, T_{rec} was significantly more elevated at the end of R2 vs. R1 ($P = 0.001$) and R3 vs. R2 ($P = 0.001$). In middle-aged males, T_{rec} was significantly more elevated at the end of R2 vs. R1 ($P = 0.018$), R3 vs. R2 ($P < 0.001$), and R4 vs. R3 ($P = 0.027$). In older males, T_{rec} was significantly more elevated at the end of R2 vs. R1 ($P = 0.001$) and nearly significantly greater at the end of R3 vs. R2 ($P = 0.061$). The difference between age groups when T_{rec} was expressed in absolute values or as a relative change from baseline was not significant.

T_{pill} also significantly increased over the recovery periods ($P < 0.001$). There was a trend for T_{pill} to be more elevated at the end of R2 compared with R1 in young ($P = 0.072$) and middle-aged males ($P = 0.066$), whereas in older males, this was significantly different ($P = 0.001$). The difference between age groups when T_{pill} was expressed in absolute values or as a relative change from baseline was not significant.

There were no significant differences in T_{sk} between recovery periods or between age groups.

DISCUSSION

The present study demonstrated that whole body heat loss was attenuated in older adults during each exercise bout. This was evident as early as 10 min following the onset of exercise and persisted until the end of each exercise bout. As a result, the rate of heat storage during the exercises was substantially greater in older males compared with young males. Whole body heat loss and changes in body heat content in middle-aged males during each exercise period were intermediate to that of young and older males. Across age groups, the amount of heat stored in the body was significantly less during Ex2, Ex3, and Ex4 relative to the first exercise bout. The rate of heat loss and the changes in body heat content during the recovery periods were not significantly different between age groups. Over the 2-h period, the cumulative change in body heat content was 1.6- and 1.5-fold greater in older and middle-aged adults, respectively, compared with young adults.

Whole Body Heat Loss During Short Exercise Bouts

A previous study compared local sweat rate between young and older adults during a single short exercise bout of 20 min (33). Two groups of older males, one highly fit group (age: 64 ± 1.9 yr, $\dot{V}O_{2\,max}$: 46.4 ± 2.1 ml·kg^{-1}·min^{-1}) and one normally fit group (age: 66 ± 1.4 yr, $\dot{V}O_{2\,max}$: 32.9 ± 2.1 ml O_2·kg^{-1}·min^{-1}), were compared with a group of young males (age: 29 ± 0.9 yr, $\dot{V}O_{2\,max}$: 44.0 ± 2.7 ml O_2·kg^{-1}·min^{-1}) during recumbent cycling at 65% $\dot{V}O_{2\,max}$ in the heat (30°C/50–60% RH). Local sweat rate was significantly reduced in normally fit older males compared with young males. Given that exercise was performed at a fixed percentage of $\dot{V}O_{2\,max}$, it is not surprising that the less fit older males had a lower sweat rate, considering that they exercised at a lower rate of heat production. Local sweat rate was also lower in the group of highly fit older males who exercised at a similar rate of metabolic heat production as the young males, although this was not statistically significant. In the present study, we observed a disparity in whole body evaporative heat loss between young and older males after 10 min of exercise, and this persisted until the end of each 15-min bout (see Fig. 1). In addition, although the onset threshold of evaporative heat loss occurred at the same mean body temperature in each age group (see Table 3), the exponential response of evaporative heat loss with time during exercise was greater in middle-aged and older males. During Ex1, for example, for the same rate of heat production (i.e., ~400 W), the time taken to reach ~63% of the total amplitude of change in evaporative heat loss from the start to the end of Ex1 was 6.9 ± 0.4 and 6.6 ± 0.5 min in middle-aged and older males, respectively. This exponential rise in evaporative heat loss occurred at a rate ~1 min slower than young males (5.8 ± 0.4 min) and for a reduced amplitude of change. The evaporative heat loss value representing ~63% of the total amplitude of change during Ex1 was lower in middle-aged (207 W) and older males (177 W) than young males (238 W), yet it took the older groups more time to achieve this rate. Over the sum of each 15-min exercise bout (1 h in total), older males gained 132 kJ (25%) more heat, whereas middle-aged males gained 66 kJ (14%) more heat than young males.

Whole Body Heat Loss With Successive Exercise Periods

Previous studies have demonstrated that the time taken to balance the differential rates of whole body heat production and heat loss (i.e., thermal inertia) is reduced when core temperature is elevated and the body is already warm (7, 21, 22). The greater rate of whole body heat loss with repeated exercise, known as the priming effect (7), has been shown to reduce the amount of heat gained during the subsequent exercise periods (21). Although this was observed in young adults, it was unclear whether this response remained intact in middle-aged and older adults, despite reductions in whole body heat loss during exercise. A limited number of studies have examined thermoregulatory function using an intermittent exercise protocol between age groups. Hellon et al. (12) estimated evaporative rate (from measurements of preexercise and postexercise recovery weight loss) of young (19–31 yr) and middle-aged males (39–45 yr). The intermittent exercise protocol involved four exercise periods of 30 min in duration (except fourth exercise: 20 min) separated by 30-min recovery periods (except third recovery: 20 min and final recovery: 40 min) and was performed in 37.8°C/50–55% RH. Lind et al. (26) used a simulated underground mining shift protocol involving six exercise periods (two 50-min periods of walking and four 45-min periods of shoveling) separated by five rest periods (45 min each) to examine the level of thermal strain experienced by young (23–31 yr) and middle-aged males

(39–53 yr) in five different climates (25°C/55% RH, 31°C/64% RH, 33°C/64% RH, 35°C/62% RH, and 36°C/63% RH). In the study by Hellon et al. (12), although sweat loss was reduced in middle-aged males during the exercise bouts, it appears from data reported in a figure only that sweat loss was greater by roughly 40% during the second and third exercise periods compared with the first exercise bout in both age groups. Unfortunately, Lind et al. (26) only reported the overall weight loss during exercise in each ambient condition; thus, it is not possible to determine whether the priming effect influenced the rate of heat loss with successive exercise in their study. In the present study, we show that the exponential increase in whole body evaporative heat loss became faster with successive exercise in each age group. Specifically, the time constant for the exponential increase in evaporative heat loss was reduced in young and middle-aged males during Ex2 (4.3 ± 0.4 and 5.4 ± 0.4 min, respectively) compared with Ex1 (5.8 ± 0.4 and 6.9 ± 0.4 min, respectively). A similar trend was observed in older adults (Ex2: 5.3 ± 0.4 vs. Ex1: 6.6 ± 0.5 min). Across age groups, a faster increase in evaporative heat loss at the start of exercise combined with a greater rate of heat loss during Ex2, Ex3, and Ex4 relative to Ex1 led to a concomitant reduction in heat storage with successive exercises (see Fig. 2). Thus, there does seem to be a benefit to performing intermittent bouts of exercise for middle-aged or older adults reflected by an enhanced rate of heat loss with successive exercise bouts.

Whole Body Heat Loss During Postexercise Recovery

A growing number of recent studies have demonstrated a consistent and rapid attenuation of local and/or whole body heat loss at the onset of recovery in young adults (21–23). Kenny et al. (21) demonstrated that the attenuation in heat loss occurring at the start of recovery was the same for each recovery period in young adults who engaged in three 30-min bouts of cycling separated by 15-min inactive recovery periods at an ambient air temperature of 30°C/30% RH. Consistent with these findings, we observed that whole body heat loss was markedly attenuated at the cessation of each exercise bout and that this occurred to a similar extent between age groups. For example, at the end of the first exercise bout, whole body heat loss rapidly declined in young, middle-aged, and older males, such that only 23% (young), 20% (middle-aged), and 21% (older) of the heat gained during this first exercise bout was dissipated during the first recovery period. In the study by Kenny et al. (21), similar changes in body heat content were measured between recovery periods. In the present study, the change in body heat content was reduced during the second recovery period in young (53%), middle-aged (43%), and older males (51%) compared with the first rest period. The change in body heat content was, however, similar during R2, R3, and R4 in all age groups. This study was the first to show that in accordance with results obtained in young adults (21–23), even older adults have a compromised ability to dissipate heat during postexercise recovery, irrespective of the age-related impairments in thermoregulatory function observed during exercise. Hellon et al. (12) and Lind et al. (26) previously reported that sweat loss during the postexercise recovery periods tended to be greater in middle-aged adults relative to young adults. For example, Lind et al. (26) reported that the average sweat loss was ~13% greater in middle-aged males during the rest periods relative to young males. In the present study, we did not find a significant difference in heat loss or change in heat content between groups. However, we did observe that the exponential decay in heat loss, as reflected by τ, was slower in older males during each recovery period compared with both young and middle-aged males (see Table 2). As a result, the older group maintained an elevated rate of heat loss during the recovery periods compared with the other two groups, which is reflected by a lower total amplitude of change in heat loss from the end of each exercise bout to the start of the next. The negative change in body heat content over the sum of each recovery period in older males was greater by 11% and 14% compared with young and middle-aged males, respectively. Nonetheless, this slightly elevated rate of heat loss during the recovery periods was not sufficient to offset the greater rate of heat storage during the exercise bouts.

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

The reduced rate of heat loss observed in older males during exercise, and to some extent in middle-aged males, was not paralleled by lower local sweating or skin blood flow responses. It has been repeatedly shown that a high degree of heterogeneity in local sweating and skin blood flow responses occur with aging (14, 15). Because we only measured local sweat rate and skin blood flow at one site, it is likely that our results simply reflect regional differences in local sweat rate and/or skin blood flow. Additionally, our measurements of core and skin temperature were not significantly different between age groups despite the large differences in body heat storage measured in young vs. middle-aged and older males. Again, it is well established that core and skin temperature measurements underestimate changes in mean body temperature (17–19) and that these measurements do not accurately represent the magnitude of residual heat storage especially in the early stages (non-steady-state period) of exercise (2, 19). As demonstrated by a growing number of recent studies (6, 8, 21, 23), the use of whole body calorimetry is the optimal way to assess changes in whole body heat loss capacity and heat storage to eliminate the potential confounding effects of regional variations in local heat loss responses and heat distribution when studying independent groups. In fact, had we only relied on measurements of local sweating and skin blood flow, as well as core/skin temperature, our conclusions would have been markedly different, that is, the capacity to dissipate heat appears unaffected by advancing age. It is important to consider that with the heat load employed in the present study, the measures of local heat loss and core temperature were not responsive enough to show differences in this period of thermal imbalance, where the rate of heat loss is still rising exponentially. This is not to say that a separation in core temperature would not become apparent earlier at a higher rate of heat gain (i.e., higher heat load) or that important differences in local heat loss would not be evident with longer exercise bouts when a steady-state rate of heat loss is achieved (6, 8).

Consideration

The older males in the current study had a significantly lower $\dot{V}O_{2\,max}$ and as a result, exercised at a greater relative (%$\dot{V}O_{2\,max}$) exercise intensity compared with middle-aged and young males. It is well established, however, that whole body sweating is defined by the evaporative heat loss required to achieve heat balance (E_{req}) during exercise, irrespective of the $\%\dot{V}O_{2\,max}$ incurred (6, 8, 10, 16, 27, 28). In the present study, we employed a fixed rate of metabolic heat production under fixed environmental conditions to elicit the same E_{req} in our age groups. If the effect of $\dot{V}O_{2\,max}$ on thermoregulatory capacity was more pronounced than aging per se, we would expect heat loss and changes in body heat content to be similar between young and middle-aged subjects considering that $\dot{V}O_{2\,max}$ was not significantly different between these two groups. We also would expect a significantly reduced rate of heat loss and a greater change in body heat content in older males compared with both middle-aged and young males. Conversely, the cumulative change in body heat content over the 2-h experimental session was 39% and 33% greater in older and middle-aged males, respectively, compared with young males. The difference in heat storage between middle-aged and older males was only ~8%.

Perspectives and Significance

Intermittent exercise is typical of many daily and/or occupational activities. Intermittent exercise is also used by many health and safety industries as a measure to reduce the risk of exertional heat strain when work-related activities are performed in elevated ambient air conditions. The majority of current guidelines for heat exposure safety do not account for a number of important factors, notably the age of the individual, which may affect a person's capacity to thermoregulate during work in the heat. In the present study, we determined that heat loss capacity was compromised in older adults and that noticeable decrements in heat dissipation were also evident in the middle-aged group during exercise. It is important to consider that heat loss responses and changes in body heat content were only examined over a relatively short period of time (2 h). A typical work shift in various industrial settings ranges anywhere from 8 to 12 h (24). If we extrapolated our results over an 8-h period, it is likely that older and middle-aged adults would be at an elevated risk of sustaining a heat-related injury relative to their younger counterparts, unless appropriate heat exposure guidelines are in place. Our results, therefore, support the need to include age-specific heat exposure guidelines for safe work and/or exercise in the heat. Of note, the participants recruited for the purpose of this study were active, healthy, and free of any known medical conditions. It is plausible that for middle-aged and older adults with chronic medical conditions (e.g., Type 2 diabetes, cardiovascular disease, etc.) or lower levels of aerobic fitness, the risk for heat-related injury may be even greater (25). Moreover, a greater proportion of older adults were tested during the spring/summer season yet had a lower capacity to dissipate heat compared with their younger counterparts, who for the most part were tested in the fall/winter. This supports previous findings suggesting that minimal heat acclimatization occurs in healthy individuals who are nonathletes living in temperate climates despite warm outdoor environmental conditions during the summer. This has been attributed to modern behavioral adaptations, notably the prevalence of air-conditioned living and avoidance of outdoor activity during hot days (1).

Conclusion. As a result of a reduced capacity to dissipate heat during exercise, which was not compensated by a sufficiently greater rate of heat loss during the recovery periods, both older and middle-aged males had a progressively greater rate of heat storage compared with young males over a 2-h intermittent exercise protocol. Age-related decrements in heat dissipation during exercise were pronounced in males >60 yr, but our findings also suggest that heat loss capacity may be compromised as early as the fourth decade of life.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

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

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