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Relevance of individual characteristics for human heat stress response is dependent on exercise intensity and climate type

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Abstract Multiple heterogeneous groups of subjects (both sexes and a wide range of maximal oxygen uptake $\dot{V}O_{2\max}$, body mass, body surface area (A_D), % body fat, and A_D /mass coefficient) exercised on a cycle ergometer at a relative (% $\dot{V}O_{2\max}$, REL) or an absolute (60 W) exercise intensity in a cool (CO 21°C, 50% relative humidity), warm humid (WH 35°C, 80%) and a hot dry (HD 45°C, 20%) environment. Rectal temperature (T_{re}) responses were analysed for the influence of the individual's characteristics, environment and exercise intensity. Exposures consisted of 30-min rest, followed by 60-min exercise. The T_{re} was negatively correlated with mass in all conditions. Body mass acted as a passive heat sink in all the conditions tested. While negatively correlated with $\dot{V}O_{2\max}$ and $\dot{V}O_{2\max}$ per kilogram body mass in most climates, T_{re} was positively correlated with $\dot{V}O_{2\max}$ and $\dot{V}O_{2\max}$ per kilogram body mass in the WH/REL condition. Thus, when evaporative heat loss was limited as in WH, the higher heat production of the fitter subjects in the REL trials determined T_{re} and not the greater efficiency for heat loss associated with high $\dot{V}O_{2\max}$. Body fatness significantly affected T_{re} only in the CO condition, where, with low skin blood flows (measured as increases in forearm blood flow), the insulative effect of fat was pronounced. In the warmer environments, high skin blood flows offset the resistance offered by peripheral adipose tissue. Contrary to other studies, T_{re} was positively correlated with A_D /mass coefficient for all conditions tested. For both exercise types used, being big (a high heat loss area and heat capacity) was apparently more beneficial from a heat strain standpoint than having a favourable A_D /mass coefficient (high in small subjects). The total amount of variance in

T_{re} responses which could be attributed to individual characteristics was dependent on the climate and the type of exercise. Though substantial for absolute exercise intensities (52%–58%) the variance explained in T_{re} differed markedly for relative intensities: 72% for the WH climate with its limited evaporative capacity, and only 10%–26% for the HD and CO climates. The results showed that individual characteristics play a significant role in determining the responses of body core temperature in all conditions tested, but their contribution was low for relative exercise intensities when evaporative heat loss was not restricted. This study demonstrated that effects of individual characteristics on human responses to heat stress cannot be interpreted without taking into consideration both the heat transfer properties of the environment and the metabolic heat production resulting from the exercise type and intensity chosen. Their impact varies substantially among conditions.

Key words Dry and humid heat · Heat tolerance · Physical fitness · Body surface area and mass · Sex

Introduction

Large inter-individual differences in human responses to exercise in the heat have been described in the literature (Kenney 1985; Wenzel et al. 1989; Havenith et al. 1995a,b), differences which can in part be ascribed to differences in specific personal characteristics of the subjects tested. Research aimed at elucidating the effect of individual characteristics such as age, sex, body size, adiposity, and aerobic power has been extensive. Several recent studies have proposed that aerobic power, adiposity, and anthropometrics are the main determinants of the response to heat stress and that most of the effects that have been observed to be related to age and sex differences were really due to concomitant differences in the first three above-mentioned parameters (Pandolf et al. 1988; Kenney and Havenith 1993; Havenith et al.

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1995a,b). Limited attention has as yet been given to the question of how these individual differences influence thermal responses for different exercise intensities or climate types. Common paradigms in thermophysiological research have been the use of hot-dry versus warm-humid climates, both with equal thermal load, as for example defined by the wet bulb globe temperature (WBGT), or the use of fixed exercise intensities for all, as against an intensity relative to the individual's maximum.

As to the exercise type, it has been shown that in respect of the widely accepted concept that body core temperature during exercise is determined by the relative exercise intensity (Åstrand 1960; Saltin and Hermansen 1966) and sweat loss by absolute exercise intensity (Drinkwater and Horvath, 1979), it has not been possible to generalize because individual characteristics have been found to contribute significantly as well (Havenith et al., 1995b). With respect to the climate, indications that an interaction between individual characteristics and climate type was present have been suggested in experiments on male-female differences in exposure to hot-dry and warm-humid heat stress: for example, the higher body surface to body mass coefficient for women has been suggested to be an advantage in a warm-humid climate, but not in a hot-dry climate (Shapiro 1980).

In many cases experiments published in the literature, using different types of exercise (relative versus fixed intensities) and climate, are difficult to compare for the effect of individual differences due to differences in the characteristics of the groups of subjects used. Therefore, the present study attempted to compare body core temperatures from five experiments on comparable groups of subjects, but performed in different climates (cool, warm-humid and hot-dry), and with different exercise intensity types (a fixed intensity for all subjects and an intensity relative to the individuals' maximal aerobic power). The data from these studies were analysed for the contributions of individual characteristics to the thermoregulatory response, and more specifically, were examined for possible interactions among the effects of individual characteristics, the type of exercise intensity, and climate. The questions asked were therefore: "how much of the differences in heat stress response can be explained by selected individual characteristics? What is the relative contribution of different parameters quantitatively? Is it the same in different climates and for different work types?"

To compare the influence of several individual characteristics simultaneously, instead of one in each experiment as has been common in most previous research on individual characteristics, heterogeneous subject groups were used, with multiple regression as the method of analysis. This technique has previously been described in this journal by Havenith and van Middendorp (1990) and Havenith et al. (1995a,b).

Methods

This paper presents an integrated analysis of the combined data from five separate experiments covering various combinations of climate and exercise intensity. Two types of exercise intensity were used in the experiments, a fixed absolute intensity (ABS) of 60 W on a reclining cycle ergometer for 60 min after 30-min rest, and an intensity relative to the individual's maximal capacity [REL, a ramp exposure of 30 min each at rest, 25%, and 45% maximal oxygen uptake ($\dot{V}O_{2\max}$) in sequence].

Three types of climate were used: a warm humid [WH 35°C, 80% relative humidity (rh) and a hot dry (HD 45°C, 20% rh) climate, both with similar WBGT value ($\pm 31.6^\circ\text{C}$) and a cool climate (CO 21°C, 50%). All conditions were without added radiation and had an air velocity less than $0.2 \text{ m} \cdot \text{s}^{-1}$. For the ABS trials, the subjects were exposed to WH and HD. For the REL experiments, the subjects were exposed to WH, HD, and CO.

Subjects

Three groups of subjects of mixed sex were tested. One group participated in all REL tests ($n = 24$), a second participated in the WH/ABS condition ($n = 27$), and a third group in the HD/ABS condition ($n = 30$). The subject groups were recruited using the same criteria to allow between-groups comparisons.

Protocol

With the obvious exception of climate and exercise intensity, comparable procedures and methods were used in all the experiments. Differences in methods were due to differences in equipment available at the time when the tests were performed. A detailed description of the methods of the separate tests is given in Table 1. Of the studies mentioned, data of four (CO/REL, HD/REL, WH/REL and WH/ABS) have been published previously (Havenith and van Middendorp 1990; Havenith et al. 1995a,b), with emphasis on the single condition used. The data for the condition HD/ABS and the discussion of the interactions between the individual's parameters, climate and exercise type are new.

Screening

In the screening procedure before the actual exposures, the subjects' individual characteristics were determined. The subjects were all volunteers, and the studies were all approved by the Institute's Medical Ethics Committee. Before participation, each subject gave informed consent and was medically screened. This screening included medical questionnaires or a full physical examination. The following individual characteristics were determined: anthropometric data (height and mass), body surface area (A_D), $\dot{V}O_{2\max}$, average skinfold thickness (of four sites) and adiposity, and finally a habitual level of physical activity score using a validated questionnaire. Natural heat acclimatization of all the subjects was presumed to be equivalent, as all tests were performed in the spring and the subjects had not been exposed to heat for several months. Exercise induced acclimation was allowed for by the use of the activity score mentioned above.

Heat stress test

For all heat stress tests, each subject reported to the laboratory, changed into shorts (women also wore a halter top) and had sensors attached. Next, they entered a climatic chamber set at the conditions for the WH, HD or CO climate. The subjects rested for 30 min in a semi-reclining chair mounted behind a cycle ergometer, then exercised (ABS or REL) for 60 min on the cycle ergometer, or until reaching one of the safety criteria (rectal temperature,

Table 1 Description of methods of the five experiments. *REL* Relative, *ABS* absolute exercise intensities. *WH* Warm humid, *HD* hot dry, *CO* cool environments, $\dot{V}O_{2\max}$ maximal O_2 uptake

Condition	REL (HD, WH and CO)	WH/ABS	HD/ABS
<i>Subjects</i> Screening: $\dot{V}O_{2\max}$	$n = 24$; 12♂, 12♀	$n = 27$; 19♂, 8♀	$n = 30$; 14♂, 16♀
	O_2 uptake measured by custom built closed circuit oxygen system, using a polarographic oxygen analyser (Servomex). Maximum determined by extrapolation of the results of an incremental exercise test on a Monark power regulated cycle ergometer at submaximal levels of intensity (Åstrand and Rodahl 1970).	$\dot{V}O_{2\max}$ (Oxycon sigma, Mijnhardt) in incremental exercise test on treadmill with modified Balke protocol [2.5% gradient changes ($= 1.23 \text{ W} \cdot \text{kg}^{-1}$ at $5 \text{ km} \cdot \text{h}^{-1}$), every 2 min after 5-min warmup at 5% gradient, until exhaustion.	$\dot{V}O_{2\max}$ was derived from the maximally achieved exercise intensity during an incremental exercise test on a Lode cycle ergometer (Binkhorst 1993)
Body fat content	Sum of four skinfolds (Durnin and Womersley 1974)	Sum of four skinfolds (Durnin and Womersley 1974)	Sum of four skinfolds (Durnin and Womersley 1974)
Body surface area	From height ($\pm 0.5 \text{ cm}$) and mass ($\pm 10 \text{ g}$) (DuBois and DuBois 1916)	From height ($\pm 0.5 \text{ cm}$) and mass ($\pm 10 \text{ g}$) (DuBois and DuBois 1916)	From height ($\pm 0.5 \text{ cm}$) and mass ($\pm 10 \text{ g}$) (DuBois and DuBois 1916)
Habitual activity	Questionnaire describing physical activity level and participation in exercise programmes. Scored on a 7-point scale, ranging from "avoid walking or exertion" to "run over 10 miles each week or exercise over 3 h each week" (Ross and Jackson 1990)	Questionnaire describing physical activity level and participation in exercise programmes. Scored on a 7-point scale, ranging from "avoid walking or exertion" to "run over 10 miles each week or exercise over 3 h each week" (Ross and Jackson 1990)	Questionnaire describing physical activity level and participation in exercise programmes. Scored on a 7-point scale, ranging from "avoid walking or exertion" to "run over 10 miles each week or exercise over 3 h each week" (Ross and Jackson 1990)
<i>Heat stress test</i> Temperature/Humidity/ Wind speed	WH: $35^\circ\text{C}/80\%/ < 0.2 \text{ m} \cdot \text{s}^{-1}$ HD: $45^\circ\text{C}/20\%/ < 0.2 \text{ m} \cdot \text{s}^{-1}$ CO: $21^\circ\text{C}/50\%/ < 0.2 \text{ m} \cdot \text{s}^{-1}$	$35^\circ\text{C}/80\%/ < 0.2 \text{ m} \cdot \text{s}^{-1}$	$45^\circ\text{C}/20\%/ < 0.2 \text{ m} \cdot \text{s}^{-1}$
Exercise intensity regime	30-min rest on wire chair behind an electronically controlled cycle ergometer (modified, power regulated, Monark, Monark-Crescent AB, Varburg, Sweden) in a reclining position, followed by 30-min work at $25\% \dot{V}O_{2\max}$, and 30-min work at $45\% \dot{V}O_{2\max}$	60 W on reclining cycle (electrically braked Lode) for 60 min after a 30-min rest period	60 W on reclining cycle (electrically braked Lode) for 60 min after a 30-min rest period
Oxygen uptake	Custom built closed circuit oxygen system, using a polarographic oxygen analyser (Servomex)	Oxygen uptake by analysis of expired gases during two 5-min periods (after 15-min and after 45-min exercise) using a Mijnhardt Oxycon Sigma system	Oxygen uptake by analysis of expired gases during two 5-min periods (after 15-min and after 45-min exercise) using a Mijnhardt Oxycon Sigma system
Core temperature	Yellow Springs Instruments 700 Thermistor inserted 12 cm beyond anal sphincter	Yellow Springs Instruments 700 Thermistor inserted 12 cm beyond anal sphincter	Yellow Springs Instruments 700 Thermistor inserted 12 cm beyond anal sphincter
Skin temperature	Average skin temperature was calculated from seven (head, upper arm, lower arm, chest, back, upper leg, lower leg) separate measurements (Yellow Springs Instruments 700 skin thermistors), weighted for the surface area they represented (Hardy and DuBois 1938).	Surface weighted average of 4 YSI 700 series thermistors placed on the arm, upper leg, chest and back (Hardy and DuBois 1938).	Surface weighted average of 4 YSI 700 series thermistors placed on the arm, upper leg, chest and back (Hardy and DuBois 1938).
Heart rate	The electrocardiogram (CM5 lead) was monitored continuously, from which heart rate was deduced and recorded	The electrocardiogram (CM5 lead) was monitored continuously, from which heart rate was deduced and recorded	The electrocardiogram (CM5 lead) was monitored continuously, from which heart rate was deduced and recorded

$T_{re} > 39^{\circ}\text{C}$ or heart rate, $\text{HR} > 90\%$ of the individual's maximum as determined in the aerobic power test, or any adverse symptomology).

Physiological variables were measured and stored using a calibrated data acquisition system: T_{re} , mean skin temperature (\bar{T}_{sk}), HR, and oxygen uptake. Body heat storage was calculated from T_{re} and \bar{T}_{sk} as: $\text{Store} = C_b \cdot [0.8 \cdot (T_{re} - 37.) + 0.2 \cdot (\bar{T}_{sk} - 34)](\text{J} \cdot \text{g}^{-1})$, with C_b as average heat capacity of body tissue defined as $C_b = [(\text{fat mass}/\text{body mass}) \cdot 2.51 + (\text{body mass} - \text{fat mass})/\text{body mass} \cdot 3.65]$ (joules per gram). Sweat loss was determined by weighing subjects before and after the heat exposure, corrected for metabolic and respiratory mass losses. Forearm blood flow (FBF), mean arterial pressure and forearm vascular conductance were also determined, but will be reported on separately.

Data were stored at 60-s intervals. The final statistical analyses were performed using the data collected at and averaged over the last 3 min of the test.

Statistics

For the statistical analyses, correlation and multiple regression analysis modules of the package SYSTAT (Wilkinson 1990) and STATISTICA (1995) were used. Distributions of data were tested for normality using probability plots and skewness and kurtosis calculations. Differences in correlation coefficients between physiological responses and individual characteristics were tested only for comparisons within the climate type (WH/REL vs WH/ABS and HD/REL vs HD/ABS) or within an intensity (CO/REL vs WH/REL vs HD/REL and WH/ABS vs HD/ABS). For the correlation, significance levels of $P < 0.05$ were accepted. All P values between 0.05 and 0.1 were considered as a trend.

The multiple regression analysis was performed in a stepwise, interactive mode. Outliers were identified using Studentized residuals and Cook's D-statistic. Parameters were included based on their correlation with the residual ($P < 0.1$), and their intercorrelation (tolerance) with parameters already in the equation. The regression equations produced were accepted at a significance level of $P < 0.05$.

For comparison of the importance of different parameters in relation to each other, standardized regression coefficients were used (Havenith and van Middendorp 1990). The value of the standardized regression coefficient represents the change in the dependent variable (e.g. T_{re}) expressed in units of its standard deviation, when the independent parameter (mass, $\dot{V}O_{2\max}$, etc.) changes by 1 standard deviation. With this method, problems in comparing the effect of different parameters related to differences in their ranges and in the units in which they are expressed are solved. Using the standardized regression coefficients, the relative contribution of the different parameters to the variance explained was calculated as:

$$\text{partial contribution } r^2 = \frac{|\text{standardized regression coefficient for parameter}|}{\sum |\text{of all standardized regression coefficients in equation}|} \cdot r^2$$

Adjusted r^2 values are given; which are r^2 values adjusted for the number of cases and the number of parameters in the analysis. These are lower than the usual r^2 values.

Results

The subject group (Table 1) characteristics are illustrated in Fig. 1. The subject groups did not show any significant differences in personal characteristics, thus allowing good comparisons among experiments. Though an attempt was made to minimize correlations between individual characteristics within groups by subject selection, $\dot{V}O_{2\max}$ and mass were significantly

correlated. Thus, these parameters had to be treated with caution in the analyses. Also, the relationship of A_D to mass and height could obviously not be avoided. The $\dot{V}O_{2\max}$, expressed per kilogram of body mass did not show any correlation with mass, however. Also % body fat was not correlated with $\dot{V}O_{2\max}$, body mass, or A_D .

The physiological response to be discussed is T_{re} , as a representative of body core temperature. The distribution of this response, as measured at the end of the exposures, together with a normal distribution with same average and standard deviation is illustrated in Fig. 2. The individual characteristics to which it was related were: $\dot{V}O_{2\max}$, $\dot{V}O_{2\max} \cdot \text{kg}^{-1}$, body mass, % body fat, A_D and surface area to mass coefficient. As the number of data and relationships to be presented in this paper is quite large, we have chosen to focus on the effects which showed differences among climate types or among exercise intensities. The most interesting (and significant) differences have been illustrated in the figures.

Correlation analysis

In Fig. 3a the correlation coefficients of the relationship between T_{re} and $\dot{V}O_{2\max}$ are given for the five climate/intensity conditions. For ABS, significant negative correlations were present; for REL, only the positive cor-

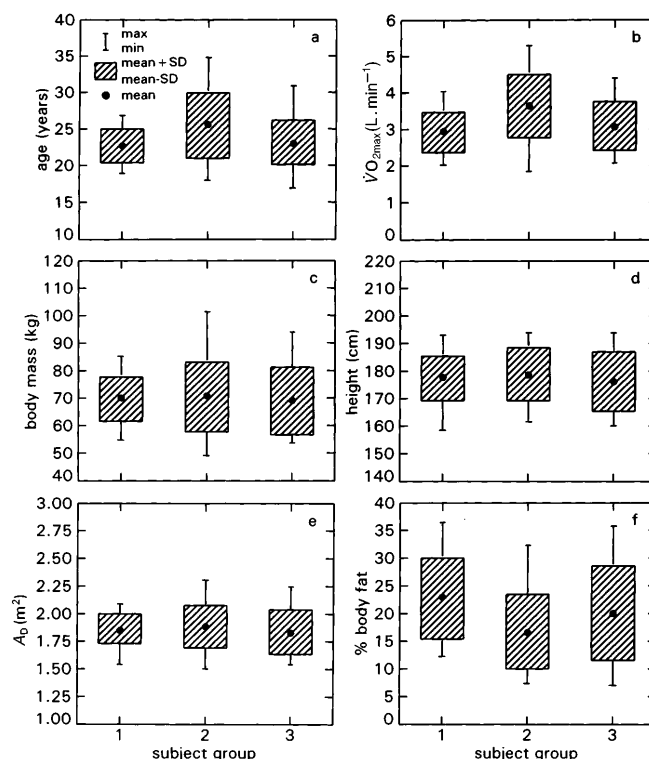


Fig. 1 Mean, standard deviation SD, minimal and maximal values for physical and physiological characteristics of the subject groups used in the analysis. % Body fat fat percentage; A_D body surface area, group 1 all REL conditions, group 2 WH/ABS, group 3 HD/ABS. See Table 1 for definitions

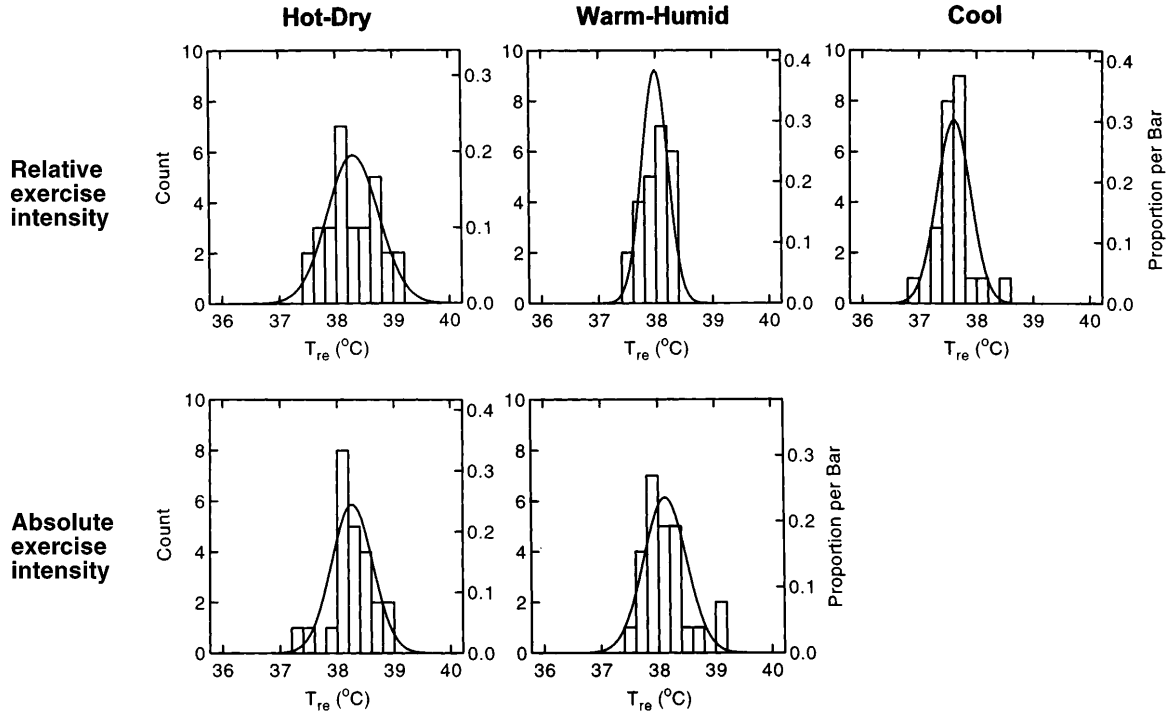


Fig. 2 Distribution of rectal temperature (T_{re}) at the end of the heat exposures for the different conditions. The curves drawn represent normal distributions with the same mean and standard deviation as the results observed

relation for the WH/REL condition approached significance ($P = 0.08$). This positive correlation for the WH/REL condition differed significantly from all other conditions, except from HD/REL, which difference approached significance ($P = 0.08$).

The relationship between T_{re} and body mass is given in Fig. 3b. The relationships (negative correlation) were similar for all trials in the heat (ABS and REL). For the cool climate the correlation was not significant. The relationship of T_{re} with $\dot{V}O_{2max}$ standardized for body mass ($\dot{V}O_{2max} \cdot \text{kg}^{-1}$) are shown in Fig. 3c. In this case, only the correlation for the WH/REL was significant (WH/ABS approached significance; $P = 0.07$) and this WH/REL condition differed significantly from all other conditions compared. In Fig. 3d, the relationship of T_{re} with % body fat is given. Only for the CO/REL condition was this positive correlation significant, and significantly different from WH/REL. The relationship of T_{re} and A_D was similar to that for T_{re} and body mass. Also the relationships between T_{re} and A_D/mass were similar to those between T_{re} on the one hand, and mass or A_D on the other, but the sign was opposite. A higher A_D/mass coefficient resulted in a higher T_{re} .

Multiple regression analyses

In Figs. 4 and 5, a selection of the results for the multiple regression analyses is given as pie charts. These pie charts show the percentages of explained and unexplained variance due to individuals' characteristics in the

data for T_{re} for the respective conditions. The percentage of the variance explained (= adjusted r^2) is distributed over contributing parameters according to the size of their standardized regression coefficients as explained in Methods.

In Fig. 4 the analysis commenced with $\dot{V}O_{2max}$, being a relevant parameter in the correlation analysis. In that case, mass usually was the second relevant parameter, or for HD/REL, the only parameter. For CO/REL, body fat content was the only parameter. It was also possible to construct equations including the A_D/mass coefficient instead of mass. These equations produced very similar explained variances to those with mass. The important difference was that A_D/mass had a positive regression coefficient, whereas mass had a negative one.

The results of the analyses indicated an inter-correlation between $\dot{V}O_{2max}$ and mass in the regression equation (tolerance = 0.35). When the analyses was started from $\dot{V}O_{2max} \cdot \text{kg}^{-1}$ (Fig. 5) this problem of a correlation with mass was not present (tolerance > 0.95), providing a statistically more robust analysis. Also in this analysis, mass was the best predictor in sequence, except for HD/REL and CO/REL. In these conditions, $\dot{V}O_{2max} \cdot \text{kg}^{-1}$ did not contribute at all.

Identical to the observation in the correlation analysis (Fig. 3), the contribution of $\dot{V}O_{2max}$ or $\dot{V}O_{2max} \cdot \text{kg}^{-1}$ was opposite in sign between the WH/REL condition versus all others. In the WH/REL condition a higher $\dot{V}O_{2max}$ or $\dot{V}O_{2max} \cdot \text{kg}^{-1}$ resulted in higher T_{re} values and in all other measured conditions in lower T_{re} .

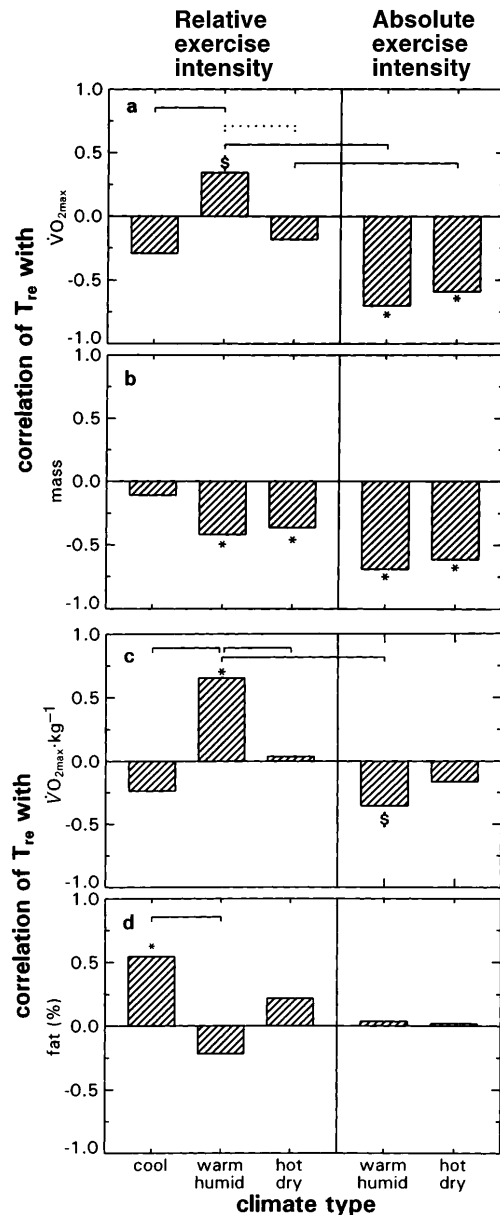


Fig. 3 Correlations of rectal temperature (T_{re}) with **a** maximal oxygen uptake ($\dot{V}O_{2max}$), **b** body mass, **c** maximal oxygen uptake per kg of body mass ($\dot{V}O_{2max} \cdot kg^{-1}$), and **d** body fat. * $P < 0.05$, \$ $0.05 < P < 0.10$; lines connect conditions which are significantly different (comparison within climate or work type only; see Methods). Dotted line difference at $0.05 < P < 0.10$ level

Analysis of body heat storage in the same way provided almost identical results, with similar explained variance numbers and identical contributing parameters. In this case, however, none of the individual parameters contributed in the CO/REL condition.

Discussion

Methodology

The methodology of using heterogeneous subject groups, including men and women, instead of groups matched for all but one parameter has been discussed by Havenith et al. (1995a). In this type of experiment, analyses by multiple regression have been used. For the present approach, aiming at comparisons of responses over climates and types of exercise intensity and their combinations, the choice was made to present the data first in a simple correlation analysis approach to get an overview of the relevant factors, followed by a multiple regression analysis which usually includes fewer parameters.

The subject groups were chosen with a large variation in individual characteristics ($\dot{V}O_{2max}$, $\dot{V}O_{2max} \cdot kg^{-1}$, mass, A_D , $A_D/mass$, adiposity, regular activity level) within each group. Both sexes were included, but not analysed separately. This decision was based on conclusions in numerous previous publications (e.g. Avellini and Kamon 1980; Frye and Kamon 1981; Frye et al. 1982; Havenith and van Middendorp 1990), that sex differences in thermoregulatory response during exercise and heat exposure are in fact due to differences in fitness and anthropometry. Sex differences observed at rest, related to for example hormone differences, have been shown to disappear during stress (Frye and Ramon, 1981). Also in the present study, once data were corrected for effects of other individual characteristics, no effect of sex could be observed. Inclusion of both sexes resulted in a wider range of individual characteristics within the subject groups than would have been possible with a single sex.

Among the groups used in the different experiments, the ranges of the individual characteristics ($\dot{V}O_{2max}$, mass, height, %fat, age, A_D) as well as their mean and standard deviations were similar and not significantly different (Fig. 1). Furthermore, though some measuring methods for the definition of the individual characteristics differed among groups (e.g. $\dot{V}O_{2max}$, Table 1), the ranking of individuals for these parameters would have been expected to be equal between methods for the type of subjects used (no athletes). Therefore, correlations between responses and individual parameters were valid measures for comparison over climates and work types. Experiments were sufficiently long to allow development of typical (heat) stress responses.

As $\dot{V}O_{2max}$ and mass were significantly correlated in all data sets, these parameters had to be treated with caution in the analyses. In part, this was approached by standardizing $\dot{V}O_{2max}$ for the mass effect, using $\dot{V}O_{2max} \cdot kg^{-1}$, which does not show a correlation with mass. For each level of $\dot{V}O_{2max}$ a large variation in masses was present. This explains why it was possible that different effects for $\dot{V}O_{2max}$ and mass were observed (Fig. 3a vs 3b) even though they were correlated, as will

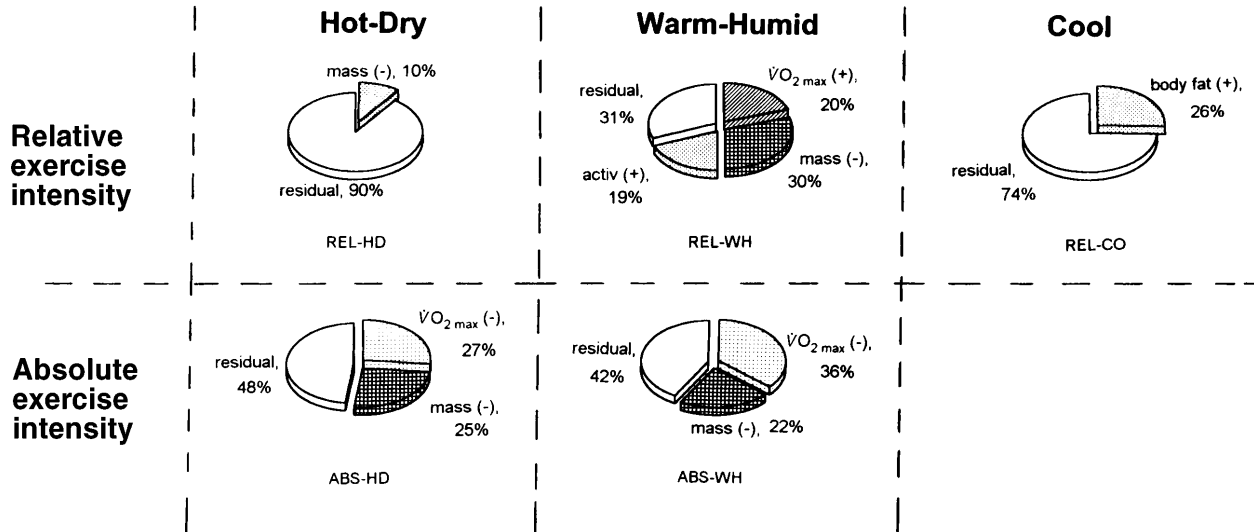


Fig. 4 Results from multiple regression analysis of rectal temperature (T_{re}) response, starting with maximal O_2 uptake ($\dot{V}O_{2\max}$). Pie charts show amounts of variance explained in T_{re} (adjusted r^2) due to individual characteristics, and the variance unexplained. *mass* body mass, *activ* regular activity score, (+) positive correlation, (-) negative correlation, *REL* relative work load, *ABS* absolute work load, *CO* cool, *WH* warm humid, *HD* hot dry climate

sent, as mentioned in the results, our observations of relationships with body heat storage were almost identical to those with T_{re} . For this reason body heat storage analysis has not been presented separately.

be discussed below. Percentage body fat on the other hand did not correlate with $\dot{V}O_{2\max}$ body mass, or with A_D , due to selection of subjects within the test groups (Havenith et al. 1995b), allowing an unbiased comparison of these effects.

Results presented are those for the T_{re} response. Depending on the beliefs of different authors on the mechanism of thermoregulation (regulation around a setpoint versus regulation of body heat content), they have chosen for analysis of either core temperature or total body heat storage. For the experiments pre-

Correlation analysis

T_{re} and aerobic power

A clear difference in the relationship between T_{re} and aerobic power ($\dot{V}O_{2\max}$ or $\dot{V}O_{2\max} \cdot \text{kg}^{-1}$) for the five climate/exercise intensity conditions was observed (Fig. 3a,c). For the ABS exercise intensities, a significant negative correlation existed in both climates for the correlation with $\dot{V}O_{2\max}$. This was almost significant for the WH/ABS condition ($P = 0.07$) and insignificant for

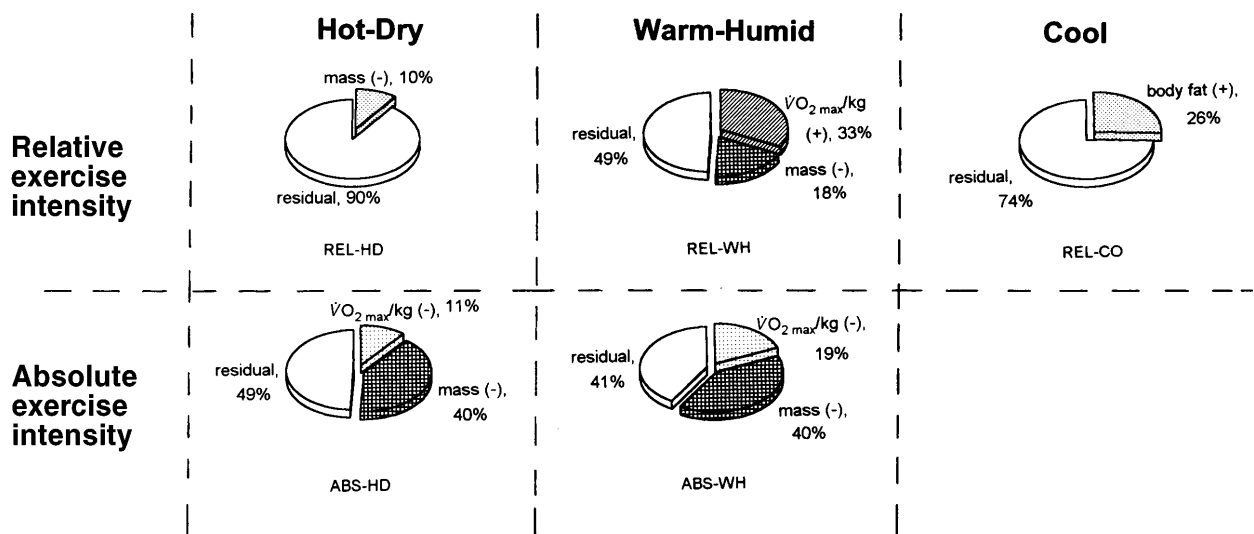


Fig. 5 Results from multiple regression analysis of rectal temperature response starting with $\dot{V}O_{2\max} \cdot \text{kg}^{-1}$. For further explanation see Fig. 4

the HD/ABS condition when aerobic power was expressed as $\dot{V}O_{2\max} \cdot \text{kg}^{-1}$.

For the REL exercise intensities, where according to the literature (see Åstrand 1960; Saltin and Hermansen 1966) one would expect no correlation between T_{re} and aerobic power, significant correlations were still present. Furthermore these differed among climate types. While for REL only insignificant negative correlations were present for CO and HD, a positive correlation was observed for $\dot{V}O_{2\max}$ ($P < 0.1$) and for $\dot{V}O_{2\max} \cdot \text{kg}^{-1}$ (significant) in WH. The higher the subject's aerobic power, the higher was the T_{re} in this condition. These findings can be explained as follows: for the ABS exercise intensity, the heat liberation in all subjects (assuming equal mechanical work efficiencies) was equal. Any advantage in the capacity for heat loss in fitter subjects in all climates should thus become visible as a reduced T_{re} . This was indeed observed (Fig. 3a). For relative exercise intensities, the heat liberated in the body would have been dependent on the subject's $\dot{V}O_{2\max}$. The subject's capabilities for heat dissipation have also been shown to be positively related to his $\dot{V}O_{2\max}$ (Avellini et al. 1982; Yoshida et al. 1995). Thus if these two relationships were equally strong, no correlation should be found between T_{re} and $\dot{V}O_{2\max}$ for relative exercise intensities. The latter was the case for the CO/REL and the HD/REL condition, where the effects of $\dot{V}O_{2\max}$ on heat production and on heat loss were apparently balanced. In WH however, the heat dissipation from the body was not limited by the body's capacity for heat loss (e.g. sweat rate), but by the climate. Due to the high water vapour pressure the evaporative capacity of the environment was strongly reduced in this climate. In this case subjects with a high $\dot{V}O_{2\max}$ should have had a high exercise intensity and high heat production in the body, but be unable to dissipate substantially more than less fit subjects due to climate restrictions. Therefore T_{re} should rise with heat production, and consequently should T_{re} also increase relative to $\dot{V}O_{2\max}$, as observed.

T_{re} and body size

For the relationship between T_{re} and body mass (Fig. 3b) one might say that for the conditions used, in general, the bigger the body (larger mass, but also larger A_{D}), the smaller was the increase in T_{re} . However, the interpretation of this finding is critical as positive correlations between body mass and $\dot{V}O_{2\max}$ were present in the subject groups. Thus one might argue that the mass effect was not due to, for example, the higher capacity for heat storage or high A_{D} which is concomitant with high mass, but acted through the mechanisms associated with the concomitant high $\dot{V}O_{2\max}$, or vice versa. Surprisingly however, the relationships of mass

and $\dot{V}O_{2\max}$ with T_{re} were not similar for all conditions: they were opposite in sign for the WH/REL condition, but had the same sign in all others.

This could be explained as follows: for the ABS intensities the effect of $\dot{V}O_{2\max}$ and body mass on T_{re} worked in the same direction: while the aerobic power level affected the active processes of heat dissipation (higher sweat output, etc. resulting in a negative correlation with T_{re}), body mass had (for the cycling exercise used) a more passive effect: when heat accumulated in the body, the increase in T_{re} would have been lower when heat capacity of the body (\approx mass) and cooling area ($= A_{\text{D}}$) were higher. For the REL intensities, where the effect of $\dot{V}O_{2\max}$ was the result of the balance of greater heat dissipation and of increasing heat production with increasing $\dot{V}O_{2\max}$, the net effect was dependent on the climate type. When the climate limited heat loss, the effect on heat production would have prevailed over that on heat dissipation, as described earlier. A high $\dot{V}O_{2\max}$ would therefore have been a disadvantage when working at a relative intensity in a WH climate, producing a positive correlation of T_{re} with $\dot{V}O_{2\max}$. A big mass however would still imply a high heat storage capacity and thus the correlation of T_{re} with mass, as a separate parameter, would remain negative. This difference between conditions is well illustrated in Fig. 3c, where the correlations of T_{re} with the coefficient of aerobic power to body mass are given. The $\dot{V}O_{2\max} \cdot \text{kg}^{-1}$ and mass were not correlated in the subject groups, thereby avoiding the interpretation problems discussed earlier. However, the aggravating effect of a high aerobic power for heat strain in the WH/REL condition was even more pronounced when this adjustment of $\dot{V}O_{2\max}$ for mass was applied.

While T_{re} showed a negative correlation with both A_{D} and mass, a positive correlation ($r = 0.3-0.45$ for HD and WH) was present with the surface to mass coefficient of subjects. This was highest for the ABS conditions and slightly lower for the REL conditions. The higher the surface to mass coefficient (the smaller the subject) the higher also was T_{re} . This observation was consistent over all conditions in the current experiments (all significant, except the CO). For cycling exercise, a high value of mass and A_{D} (heat storage capacity and cooling surface respectively) as found in big subjects, would seem more beneficial in reducing heat strain than a high coefficient for the two (high cooling surface area for a low heat producing mass) as found in small subjects.

The observation described above, although it has been supported by earlier results (Austin and Ghesquiere 1976), is opposite to classical (evolutionary) descriptions of the relationship between core temperature and A_{D} /mass. According to Bergman's (1847) and Allen's (1906) rules, a negative correlation between core temperature and A_{D} /mass for heat exposure would be expected. Most earlier studies on this subject (Shvartz et al. 1973; Shapiro et al., 1980; Austin and Lansing, 1986) have indeed observed such a negative correlation

between T_{re} and $A_D/mass$ for warm humid climates or work in vapour barrier clothing. Re-evaluation of the data in those studies has shown that a methodological problem might be present in the comparison of these different experiments. They have all used a walking protocol on a treadmill, with fixed speed and a gradient. The smaller the subject (low mass; high $A_D/mass$), the lower the metabolic rate. For example, in the experiment of Shapiro et al. (1980) the high $A_D/mass$ groups (difference in $A_D/mass \pm 10\%$) showed a 27% lower metabolic rate than the low $A_D/mass$ group. Thus it is not unlikely that the lower heat load in the small subjects was responsible for the lower increase in T_{re} , and not the high $A_D/mass$ coefficient in these subjects. In our comparable WH/REL condition, differences in metabolic rate between low and high $A_D/mass$ groups were insignificant. Thus, as heat loss in WH was very limited, equivalent metabolic rates would have resulted in higher T_{re} for the small subjects due to their smaller storage capacity.

Thus in our opinion, the negative correlation of T_{re} with $A_D/mass$ observed in the above-mentioned walking type experiments was actually due to the substantial differences in metabolic rate between different $A_D/mass$ groups and was incorrectly generalized to all heat stress conditions. Shvartz et al. (1973) have already indicated this alternative explanation of their findings. Also, the validity of the rules of Bergman (1847) and Allen (1906) when considering a single species (humans) has been questioned and criticized (Scholander 1955). Though it may be valid at rest in cool environments, it has been shown to be invalid during heat exposure (Schreider 1975). Thus a high $A_D/mass$ coefficient as present in small subjects is by itself a disadvantage in the ability to cope with heat stress during exercise.

T_{re} and body fat

A significant effect of body fat on T_{re} (high %fat – high T_{re}) was only observed in the CO condition. If one considers subcutaneous fat as a potential insulating layer, the insulating effect will be strongly dependent on the blood perfusion of this layer (see Burse 1979; Havenith 1997). In the CO climate, FBF taken as representative of skin blood flow, were low (maximum $7 \text{ ml} \cdot 100 \text{ ml}^{-1} \cdot \text{min}^{-1}$). In this case fat could have exerted its insulating effect, resulting in higher body temperatures for the fatter subjects. For the warmer climates, FBF were substantially raised (averages $14\text{--}21 \text{ ml} \cdot 100 \text{ ml}^{-1} \cdot \text{min}^{-1}$). This shortcut for heat transport would have reduced the contribution of the fat layer to the heat resistance to close to zero and thus have resulted in insignificant effects of body fat on T_{re} . The latter finding was in accordance with observations of Burse (1979), who has observed that differences in the thickness of fat layers due to sex had no effect on the responses to exercise in the heat.

It should be noted that in studies using body mass bearing exercise (treadmill) body fat may exert an effect on the response to heat stress through its passive mass, which has to be carried by the subject. The higher the passive mass, the higher the metabolic rate needed to carry it. This effect of increased heat production comes in addition to the insulating effect. Also the specific heat of adipose tissue, in which water content is low, is about half that of the fat-free mass. Therefore, it has been reported that a given heat load per kilogram of body mass will cause higher temperature elevations in the obese than in lean subjects (Bar-Or et al. 1969).

Multiple regression analysis

The multiple regression analyses for T_{re} , using the individual's characteristics as independent parameters, showed large differences among the conditions tested (see Results section and Figs. 4, 5). Firstly, the total variance in the T_{re} data which could be explained by the characteristics tested (100 minus unexplained variance in Figs. 4, 5) showed a wide range. The highest range of explained variance was found for the WH conditions: 58% (ABS) to 69% (REL). The lowest (10%–26%) was found in those REL conditions where evaporative heat loss was not the limiting factor of the climate (HD and CO). Secondly, though the sign of the contribution of several parameters was equal over conditions [mass (–, Fig. 3b), A_D (–), $A_D/mass$ (+)], that of $\dot{V}O_{2max}$ or $\dot{V}O_{2max} \cdot \text{kg}^{-1}$ was negative in all conditions but WH/REL (Fig. 3a,c). This was identical to the results of the correlation analysis, even with inclusion of more parameters simultaneously. This once more substantiates the suggestion that aerobic power was important in determining body core temperature when the exercise intensity was equal for all subjects (ABS). When the exercise intensity was relative to the individual's maximum, however, aerobic power would not seem to have contributed significantly to the T_{re} response when evaporative heat loss was not limited by the climate. When heat loss was limited (WH), a high aerobic power went together with a high T_{re} when the exercise intensity was relative.

Comparing the relative contributions of different parameters, Fig. 4 shows that $\dot{V}O_{2max}$ had a higher influence on T_{re} than mass in the ABS conditions, whereas mass was more relevant in the REL heat conditions. For $\dot{V}O_{2max} \cdot \text{kg}^{-1}$ (Fig. 5) this was the reverse – a smaller effect than mass in the ABS condition, but a much larger one (and opposite in sign) in the REL-WH condition. In this last condition aerobic power was mainly representing the actual heat liberation in the body per kilogram body mass, whereas in the ABS condition, with its identical heat production for all, it represented the better heat loss capacity for the subjects with higher aerobic power. Mass, in all conditions contributed as a passive heat sink, and as mass and A_D could be exchanged in the

analyses with little change in the results, mass also contributed through its relationship with the heat exchange area (A_D). Thus big subjects with a high heat sink and a high heat exchange area (all other things being equal) were at an advantage in the conditions tested here.

The results showed that the individual's characteristics played a significant role in the determination of body core temperature response in all the conditions tested, but their contribution was low in our experiments for relative exercise intensities where heat loss was not restricted. Typically, the conditions where the individual's characteristics explained a substantial part of the variance in T_{re} were those where heat loss was limited, and where the passive system characteristics (mass, A_D , $A_D/mass$) defining the size of the heat sink and the heat exchange surface were of importance.

General discussion

To understand the findings in terms of physiological and biophysical mechanisms, one may try to develop a general model of these responses, involving heat production, loss and storage. If one considers the body as a box with a certain mass, this mass will determine the heat storage capacity as well as the heat loss area ($= A_D$). All other things being equal, a big subject will be at an advantage over a small subject. It has been shown that maximal heat production levels (related to total muscle mass) as well as heat dissipation mechanisms (sweat production, sweat evaporation efficiency) are related to $\dot{V}O_{2max}$ (Avellini et al. 1982; Yoshida et al. 1995). The net effect of $\dot{V}O_{2max}$ depends on the balance between heat production and heat loss.

At ABS exercise intensities, heat production is equal for all, and the higher heat loss efficiency of subjects with high $\dot{V}O_{2max}$ will then result in lower T_{re} . At REL exercise intensities, the higher heat productions of subjects with high $\dot{V}O_{2max}$ will be balanced by the higher heat loss efficiency, resulting in the absence of a net $\dot{V}O_{2max}$ effect (see Åstrand 1960; Saltin and Hermansen 1966). When the heat loss is limited by the climate, the balance will even go the opposite way in these REL conditions. The higher heat production of subjects with high $\dot{V}O_{2max}$ will result directly in higher T_{re} as seen in the present study.

Body fat and skin blood flow can be seen as parallel resistances between core and skin. Body fat is therefore only active as an insulator when skin blood flow is low (high parallel resistance), as observed in CO.

This simple model describes the findings well. In other conditions than studied here (e.g. walking at a certain speed and gradient), an increase in mass and %fat also have indirect effects: they increase the (passive) mass that has to be carried and thereby metabolic rate. This would lead to an increased T_{re} for big or obese subjects in those conditions. These effects are also covered by the mechanism presented above.

In conclusion, this study has shown that effects of the individual's characteristics on the human response to heat stress cannot be defined without taking into consideration the heat transfer properties of the climate experienced and the metabolic rate resulting from the type of exercise. Taking this into consideration, seemingly contradictory results from different studies can be explained using a simple model. Our results showed that the individual's characteristics played a significant role in the determination of body core temperature response in all the conditions tested, but that their contribution was small for relative exercise intensities when evaporative heat loss was not restricted.

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