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Effects of passive heat adaptation and moderate sweatless conditioning on responses to cold and heat*

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Summary. Two series of experiments were performed in physically untrained subjects. In series A (heat adaptation, HA), seven male subjects were adapted to dry heat (five consecutive days at 55° C ambient air temperature (T_a) for 1 h · day^{-1}) under resting conditions. Before and after HA, the subjects' shivering responses were determined in a cold test (T_a + 10 to 0° C). In series B, eight male subjects underwent mild exercise training (five consecutive days at a heart rate, HR, of 120 *b* · min^{-1}) under T_a conditions individually adjusted (T_a + 15 to + 5° C) to prevent both sweating and cold sensations. Before and after "sweatless training", the subjects were subjected to a combined cold and heat test. During HA the thresholds for shivering, cutaneous vasodilatation (thumb and forearm) and sweating were shifted significantly ($p < 0.05$) towards lower mean body temperatures ($\bar{T}_b$). The mean decrease in threshold $\bar{T}_b$ was 0.36° C. "Sweatless training" resulted in a mean increase in work rate (at HR 120 *b* · min^{-1}) and oxygen pulse of 13 and 8%, respectively. However, "sweatless training" did not change the threshold $\bar{T}_b$ for shivering or sweating. Neither HA nor "sweatless training" changed the slopes of the relationships of shivering and sweating to $\bar{T}_b$. It is concluded that the previously reported lowering of shivering and sweating threshold $\bar{T}_b$ in long-distance runners is not due to an increased fitness level, but is essentially identical with HA. The decreased shivering threshold following HA is interpreted as "cross adaptation" produced by the stressors cold and heat.

Key words: Shivering, vasodilatation, sweating thresholds — Thermal adaptation — Physical training

Introduction

Numerous publications in the last few decades have shown that heat adaptation (HA) changes the sweating response (for review see Henane 1981). The most characteristic modification is a decrease in threshold temperature (Adolph 1956; Davies 1981; Fox et al. 1963; Henane and Valatx 1973; Nadel et al. 1974; Roberts et al. 1977; Schwennicke and Brück 1976; Shvartz et al. 1979). Sometimes, a steepened slope of the relationship of sweat rate to body temperature has also been reported following HA (Fox et al. 1963; Roberts et al. 1977). In contrast to the well-documented HA effects on sweating and skin blood flow (Fox et al. 1963; Roberts et al. 1977), information on the effects of HA on cold defence responses is scarce. In a preliminary study from our laboratory (Schwennicke and Brück 1976) no shivering threshold change was found during heat adaptation; the exposure temperature was relatively mild (45° C), however.

Exercise training carried out at moderate air temperature also leads to some HA characteristics such as a lowered sweating threshold (Baum et al. 1976; Henane et al. 1977; Nadel et al. 1974; Roberts et al. 1977; Shvartz et al. 1979) and an increased slope of the sweating response (Henane et al. 1977; Nadel et al. 1974; Piwonka et al. 1965; Roberts et al. 1977; Senay and Kok 1977). From

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results in swimmers, however, who exhibit only minor HA features (Henane et al. 1977; McMurray and Horvath 1979; Piwonka et al. 1965), it has been postulated that the HA characteristics found in "air athletes" might not be due to exercise training, but rather to the intermittent internal heat load which is not effective at low water temperatures.

We have made a comparative study of the thresholds of both cold defence and heat loss responses, as well as of the slopes of the relationship between the response and body temperature, as follows: (i) before and after repeated heat exposure (55—60° C) under resting conditions, and (ii) before and after repeated moderate exercise at ambient air temperatures that were being manipulated to avoid, as far as possible, both sweating and feeling cold (see Hessemer and Brück 1983). The data from the present study, when compared with those obtained previously in long-distance runners (Baum et al. 1976) and in artificially cold-adapted subjects (Brück et al. 1976), provided an answer to the question as to whether or to what extent adaptive thermoregulatory modifications are specific (Adolph 1956) for the respective thermal (heat, cold) or non-thermal (exercise) stressors.

Methods

Subjects and procedures

Two series of studies were carried out in which the effects on thermoregulatory responses of (A) heat adaptation under resting conditions and (B) of physical training under "sweatless conditions" were investigated in physically untrained subjects. Seven male subjects (mean age 24.8 years, range 23—29; mean height 180.5 cm, range 175—188; mean weight 70.2 kg, range 55—80.7) volunteered to participate in series A, and eight male subjects (mean age 25.6 years, range 23—29; mean height 179.7 cm, range 170—188; mean weight 69.1 kg, range 58.5—82.9) in series B. All experiments were carried out in a climatic chamber between 9 A.M. and noon, in order to avoid any influence of diurnal temperature fluctuations. The subjects reported to the climatic laboratory after a light breakfast at home. In a preliminary experiment the subjects were familiarized with all test situations and laboratory procedures.

Series A. Two experimental protocols, the heat test (Fig. 1) and the cold test (Fig. 2), were employed. In both protocols, the subjects, wearing shorts and socks, rested in a plastic mesh chair in the supine position. The heat test, applied on five consecutive days (D 1 ... D 5), began with a 30-min period at a neutral temperature, 28° C, 50% relative humidity (r.h.) and was followed by a period of moderate cooling (Fig. 1) to achieve initial skin vasoconstriction. Thereafter, ambient temperature was increased by 1—2° C · min^{-1} up to 55—60° C (r.h. 20%), which temperature was maintained for about 1 h. On the day preceding (D 0) and the day following (D 6) this heat adaptation period, the subjects were subjected to the cold test according to Fig. 2, to determine the shivering threshold. Again beginning with the resting period at neutral temperature, chamber temperature was decreased to a range between + 10 and 0° C, depending on the individual's reaction to cold, until overt shivering occurred (Fig. 2).

Series B. The subjects were subjected to a physical training program consisting of 1-h exercise bouts performed in the upright position on a cycle ergometer (Siemens-Elema Ergometer 380) on five consecutive days. They were asked to exercise at a constant heart rate of 120 *b* · min^{-1}, which could be read from a meter on the handlebar. The work load, dependent on pedalling rate, required about 45—50% of the subjects' maximum oxygen uptake ($\dot{V}_{O_{2\max}}$). The experimenter outside the climatic chamber controlled the chamber temperature to compensate for the exercise-induced elevation of core temperature, with respect to thermoregulatory responses (sweat rate, thermal sensations), by a decrease in mean skin temperature. The manoeuver resulted in an almost constant mean body temperature throughout the exercise periods (Fig. 4). Furthermore, evaporative heat loss from the skin remained close to resting values (Fig. 4). Before and after the training period, shivering and sweating thresholds were determined in cold and warm exposures carried out consecutively in one session: following an initial period at 28° C, ambient temperature (T_a) was decreased until overt shivering was seen; after another period at 28° C, T_a was increased up to 45° C until sweating occurred. In four of the eight subjects, $\dot{V}_{O_{2\max}}$ was determined, using a standard incremental cycle ergometer test, before and after training.

Variables

Electrical muscle activity (EMA) was recorded by surface electrodes over latissismus dorsi and quadriceps femoris. EMA was integrated, and arithmetic means of EMA values from the two muscles were calculated. Oxygen uptake ($\dot{V}_{O_2}$, STPD) was measured by an open-circuit technique consisting of a plastic hood placed over the subject's head, a pump, a flowmeter and a paramagnetic O_2 analyzer (Servomex 0A. 184). Metabolic rate (MR) was calculated from $\dot{V}_{O_2}$ on the basis of a caloric equivalent of 20.4 kJ · l^{-1} (assuming a respiratory quotient of 0.86). Heart rate (HR) was calculated from the R-R intervals of a bipolar chest wall ECG. Sweat rate (SR) was measured on the chest using a capsule which covered a skin area of 7 cm^2. Dried heated air of constant temperature was drawn through the capsule and led to an infrared water vapour analyzer (URAS 2T, Hartmann & Braun). Oesophageal temperature (T_{es}) was measured (Hessemer and Brück 1985; Hessemer et al. 1984) at a level just above the cardia. The position of the probe was verified by an electroacoustic method. Tympanic temperature (T_{ty}) was measured by inserting a thermocouple close to the eardrum as in previous studies in our (Hessemer and Brück 1985; Hessemer et al. 1984) and other (Henane and Valatx 1973) laboratories. The auditory canal was plugged with absorbent cotton, and the ear was covered by a pad filled with absorbent cotton. Mean skin temperature ($\bar{T}_{sk}$) was calculated from four thermocouple temperatures on the chest (T_1), upper arm (T_2), thigh (T_3) and lower leg (T_4), according to the equation (Ramanathan 1964)

$$\bar{T}_{sk} = 0.3(T_1 + T_2) + 0.2(T_3 + T_4)$$

Mean body temperature ($\bar{T}_b$) was calculated according to the equation

$$\bar{T}_b = 0.87\ T_c + 0.13\ \bar{T}_{sk}$$

where T_c is the core temperature represented by either T_{es} or T_{ty} ($\bar{T}_{b(es)}$ and $\bar{T}_{b(ty)}$, mean body temperatures calculated from T_{es} and T_{ty}, respectively; see Figs. 1, 3, 4). As shown previously, $\bar{T}_b$ is a practical variable, combining the weighted values of T_c and $\bar{T}_{sk}$, for describing sweating (Baum et al. 1976; Hessemer and Brück 1985; Hessemer et al. 1984), skin blood flow (Hessemer and Brück 1985) and shivering responses (Baum et al. 1976; Brück et al. 1976; Hessemer and Brück 1985), the latter within a restricted temperature range, corresponding to the straight, approximately horizontal part of the shivering threshold line in Fig. 6. Similar relative contributions of T_c and $\bar{T}_{sk}$ to the control of sweating (Nadel et al. 1971) and peripheral blood flow (Wenger et al. 1975) have been demonstrated by others.

Venous occlusion plethysmography, using the mercury-in-silicone strain gauge technique, was employed to measure peripheral blood flow during the heat test in series A (Fig. 1). The gauge was applied to the left forearm, just proximal to the wrist. The arm was enclosed in a Plexiglas box held thermostatically at 32° C, to avoid direct temperature influences on skin blood flow. Hand blood flow was not cut off by arterial wrist occlusion. Thus, the present plethysmograph values represent the mean blood flow to the distal forearm and hand (Whitney 1954), designated as "arm blood flow" (ABF). Venous occlusions (50—70 Torr, 10—15 s) were made every 8—10 min with a pneumatic cuff on the upper arm.

The local heat clearance technique introduced by Hensel (see Golenhofen et al. 1963) was employed in its 6-plate version (Hensel and Brandt 1977) for continuous estimation of local skin blood flow during the heat test in series A. Simultaneous measurements of heat conductivity, λ, were made at the distal phalanx of the thumb and at the middle of the forearm. The recording elements were attached by adhesive tape to the skin of the left arm within the Plexiglas box. By inflating the pneumatic cuff on the upper arm to 250 Torr (lasting 3—4 min), the heat conductivity corresponding to zero blood flow, λ_0, was obtained from the distal areas (see asterisks in Fig. 1). The cutaneous heat conductivity increment ($\Delta\lambda$), i.e., the $\lambda - \lambda_0$ difference, has been demonstrated to be approximately linearly proportional to skin blood flow as measured by a plethysmograph (see Golenhofen et al. 1963).

Except for plethysmograph values, the physiological variables were sampled at 20-s intervals by a Hewlett Packard 9830 A calculator and stored in digital form on magnetic tape.

Statistics

Linear regression analysis was employed to obtain thresholds and slopes for the thermoregulatory responses (for details see Hessemer and Brück 1985). The responses were plotted in relation to $\bar{T}_b$. Regressions were calculated for the horizontal and linearly rising limbs of the relationship between the response and $\bar{T}_b$. The intersection points of the two regressions were taken as threshold values. In the cases of thumb vasodilatation and of the 1st forearm vasodilatory response (Fig. 1) the lowest data points were taken as threshold values.

The two-tailed Student's *t* test for intrapair differences was used for evaluation of threshold differences and of the data given in Fig. 5 and Table 2.

The Wilcoxon matched pairs signed rank test was employed for evaluation of slope differences. These data did not show normal distribution, as evidenced by the ratio of means to median values.

Results

A. Heat adaptation (series A)

A typical heat test employed to test the sweating and vasomotor responses to increasing ambient temperature (T_a) is shown in Fig. 1. Following a resting period at neutral temperature, initial cutaneous vasoconstriction was achieved by decreasing T_a to 18° C. During the subsequent heating period, skin vasodilatation occurred. Typically,

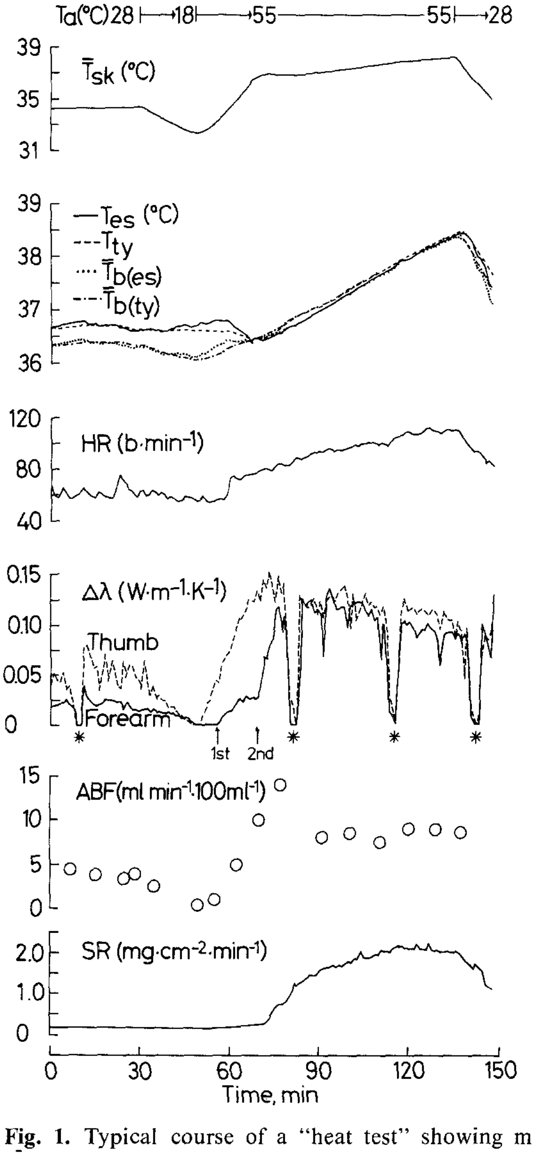

Fig. 1. Typical course of a "heat test" showing mean skin ($\bar{T}_{sk}$), oesophageal (T_{es}), tympanic (T_{ty}) and mean body temperatures ($\bar{T}_{b(es)}$ and $\bar{T}_{b(ty)}$), heart rate *(HR)*, heat conductivity increments ($\Delta\lambda$), arm blood flow *(ABF)*, and local chest sweat rate *(SR)*. Note that in the foream a "1st" and "2nd" vasodilatation are discernible, the latter coinciding with sweating onset. Figures at the top indicate changes in ambient temperature (T_a). * Arterial occlusion

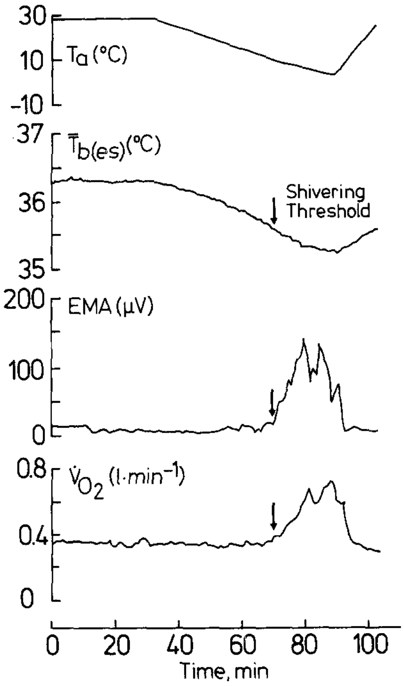

Fig. 2. Example of a "cold test" employed for determination of shivering threshold (↓). T_a, ambient, temperature; $\bar{T}_{b(es)}$, mean body temperature; *EMA*, integrated electrical muscle activity (mean from two muscle groups); $\dot{V}_{O_2}$, oxygen uptake

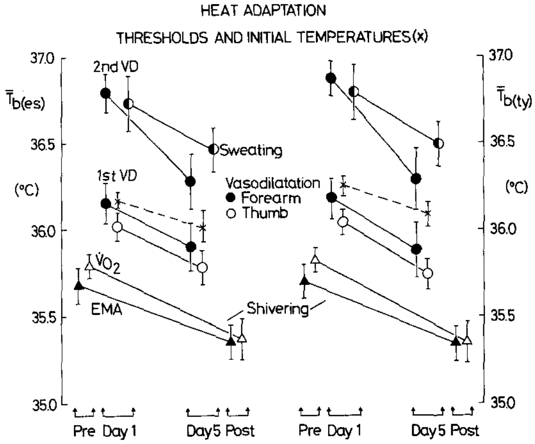

Fig. 3. Comparison of thresholds (means ± SE), in relation to $\bar{T}_{b(es)}$ (left) and $\bar{T}_{b(ty)}$ (right), for sweating and cutaneous vasodilatation (forearm and thumb) measured on day 1 and day 5 of the heat adaptation series; and for shivering ($\dot{V}_{O_2}$, *EMA*) on a day preceding *(pre)* and following *(post)* heat adaptation. In addition, initial $\bar{T}_{b(es)}$ and $\bar{T}_{b(ty)}$ measured at neutral temperature are given (×)

forearm skin vasodilatation in relation to time, as well as to $\bar{T}_b$ occurred as described by Roddie et al. (1957) in two phases designated as "1st" and "2nd" vasodilatation while thumb blood flow increased continuously in one phase. The 2nd forearm vasodilatation threshold approximated closely to the onset of sweat secretion. Five heat tests of the kind described in Fig. 1 were applied to produce heat adaptation. Preceding and following heat adaptation, cold tests as shown in Fig. 2 were applied for the determination of the thresholds of the cold-induced increases in $\dot{V}_{O_2}$ and electrical muscle activity (EMA).

Figure 3 summarizes the average threshold mean body temperatures for sweating, skin vasodilatation and shivering measured in the heat test on D 1 and D 5 and in the pre- and post-heat adaptation cold tests (D 0 and D 6), respectively. Sweating threshold temperatures decreased by 0.28 and 0.30° C ($p < 0.05$) when related to $\bar{T}_{b(es)}$ and $\bar{T}_{b(ty)}$ respectively. The threshold temperatures for vasodilatation in the thumb were decreased by 0.23 and 0.30° C ($p < 0.002$); and for the 1st forearm vasodilatation by 0.26 and 0.30° C ($p < 0.01$). The changes in threshold temperatures for the 2nd forearm vasodilatation were larger, i.e., 0.51 and 0.59° C ($p < 0.05$), again related to $\bar{T}_{b(es)}$ and $\bar{T}_{b(ty)}$. The threshold temperatures for the cold-induced increase in $\dot{V}_{O_2}$ were 0.42 and 0.48° C ($p < 0.01$) lower after heat adaptation; and those for EMA were 0.33 and 0.36° C ($p < 0.05$) lower, in relation to $\bar{T}_{b(es)}$ and $\bar{T}_{b(ty)}$. The changes in all threshold temperatures occurred in a continuous way in the course of the five heat adaptation sessions, so that by day 3 about one half of the final threshold temperature changes could be demonstrated. Resting $\bar{T}_{b(ty)}$ was also significantly decreased at the end of the heat adaptation period by 0.15° C ($p < 0.05$) (Fig. 3); $\bar{T}_{b(es)}$ showed a tendency in the same direction ($\Delta T = 0.13°$ C, $p = 0.08$). Notably, the decrease in resting mean body temperature was slightly less than the concomitant shift in threshold temperatures for the 1st vasodilatation and shivering, to the extent that the differences between resting temperature and the thresholds for vasodilatation and shivering increased (Fig. 3).

Table 1 summarizes the average threshold core and mean skin temperatures found on D 1 and D 5 of the heat adaptation series and in the pre- and post-heat adaptation cold tests. The data show that both core and mean skin temperatures contribute to the changes in mean body temperature demonstrated in Fig. 3.

The maximum body temperatures that were reached at the end of each heat test were not significantly decreased at the termination of the heat adaptation period (Table 2). Also, total sweat loss and maximum HR remained practically unchanged. Maximum arm blood flow, however, was markedly decreased at the end of the adapta-

Table 1. Oesophageal (T_{es}), tympanic (T_{ty}) and mean skin ($\bar{T}_{sk}$) temperatures in °C at the onset of heat dissipation and thermogenetic responses on the 1st and 5th day (D 1, D 5); and on a day before (PRE) and after (POST) heat adaptation. Values are means ±SE and differences. EMA, electrical muscle activity; $\dot{V}_{O_2}$, oxygen uptake rate. For 1st and 2nd forearm vasodilatation see Fig. 1

	T_{es}		T_{ty}		$\bar{T}_{sk}$	
Sweating	D 1	D 5	D 1	D 5	D 1	D 5
	36.64 ±0.14	36.39 ±0.12	36.70 ±0.14	36.42 ±0.12	37.37 ±0.52	36.55 ±0.68
Diff.	0.25		0.28		0.82	
Vasodilatation						
Thumb	36.61 ±0.10	36.40 ±0.08	36.64 ±0.09	36.38 ±0.06	32.13 ±0.33	31.72 ±0.42
Diff.	0.21		0.26		0.41	
1st, Forearm	36.54 ±0.09	36.44 ±0.07	36.57 ±0.07	36.30 ±0.14	33.60 ±0.86	32.30 ±0.95
Diff.	0.10		0.27		1.30	
2nd, Forearm	36.64 ±0.09	36.44 ±0.08	36.73 ±0.09	36.45 ±0.08	37.82 ±0.27	35.23 ±1.36
Diff.	0.20		0.28		2.59	
Shivering	PRE	POST	PRE	POST	PRE	POST
EMA	36.60 ±0.07	36.42 ±0.08	36.63 ±0.07	36.40 ±0.07	29.50 ±0.62	28.21 ±0.82
Diff.	0.18		0.23		1.29	
$\dot{V}_{O_2}$	36.58 ±0.08	36.44 ±0.09	36.62 ±0.06	36.40 ±0.08	30.54 ±0.62	28.32 ±0.89
Diff.	0.14		0.22		2.22	

Table 2. Means ±SE for body temperatures (oesophageal, tympanic, mean skin), heart rate and arm blood flow averaged over last 10 min of the heat test, and total sweat loss during the heat test, on day 1 (D 1) and day 5 (D 5) of heat adaptation

	Body temperatures, °C			Heart rate b · min^{-1}	Arm blood flow ml · min^{-1} · 100 ml^{-1}	Total sweat loss kg
	T_{es}	T_{ty}	$\bar{T}_{sk}$			
D 1	37.92 ±0.14	38.05 ±0.19	38.32 ±0.21	106.2 ±5.4	26.8 ±5.1	1.09 ±0.15
D 5	37.80 ±0.10	37.97 ±0.11	38.14 ±0.17	102.5 ±2.6	16.3 ±3.2	1.14 ±0.10
Diff.	0.12	0.08	0.19	3.7	10.5	0.05
p	0.5	0.7	0.5	0.5	0.02	0.75

tion period (Table 2). The slope of the relation SR: $\bar{T}_{b(es)}$ was not changed significantly during HA (median values 1.57 and 1.12 mg · cm^{-2} · min^{-1} · °C^{-1} on day 1 and 5, respectively). Also the slopes of the $\dot{V}_{O_2}$:$\bar{T}_{b(es)}$ and the EMA: $\bar{T}_{b(es)}$ relationships were not significantly changed during HA (median values −0.49 and −0.80 l · min^{-1} · °C^{-1} and −488 and −619 µv · °C^{-1} before and after HA, respectively).

B. Adaptation to "sweatless" exercise (series B)

Figure 4 shows an exercise test carried out on D 4 of the training period as an example. During exercise, the ambient temperature was continuously decreased to prevent sweating as far as possible. In fact, the skin evaporative heat loss (E_{sk}), estimated from the chest sweat rate, did not much increase. E_{sk} averaged maximally 15% (in the 2nd quarter of exercise) of the total heat production (H). On the other hand, care was taken not to let ambient temperature drop to a level evoking cold responses. Thus, the thermal sensations ranged from "slightly cool" to mostly "thermoneutral" during exercise. Figure 6 also shows that an increase in core temperature was not prevented by the external cooling, whereas $\bar{T}_{b(es)}$ and $\bar{T}_{b(ty)}$ remained almost constant or fell only slightly below resting values.

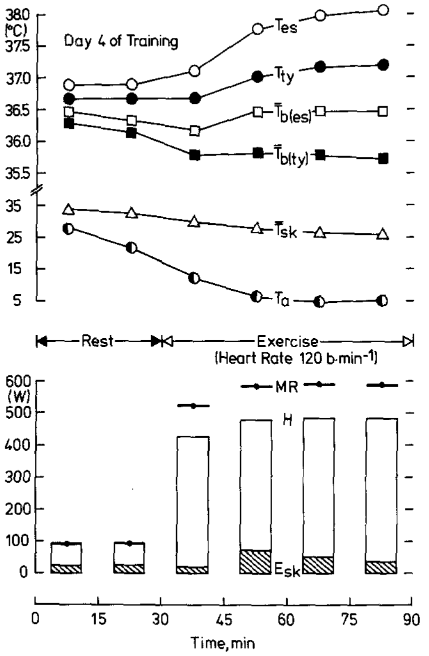

Fig. 4. "Sweatless exercise" experiment (median values of day 4 of the training period). Upper panel: T_{es}, oesophageal temperature (3 subjects only); T_{ty}, tympanic temperature. Note, mean body temperatures ($\bar{T}_{b(es)}$, $\bar{T}_{b(ty)}$) could be prevented from rising during exercise by decreasing ambient (T_a) and mean skin ($\bar{T}_{sk}$) temperatures. Lower panel: MR, metabolic rate; H, total heat production (=difference between MR and work rate). Skin evaporative heat loss (E_{sk}) could be maintained near the resting level

As shown in Fig. 5, the work rate and oxygen pulse increased significantly from the first to the last day of training by 13% and 8%, respectively. $\dot{V}_{O_{2\,max}}$, which was determined in only four subjects, showed a slight increase in three subjects, but remained unchanged in the fourth.

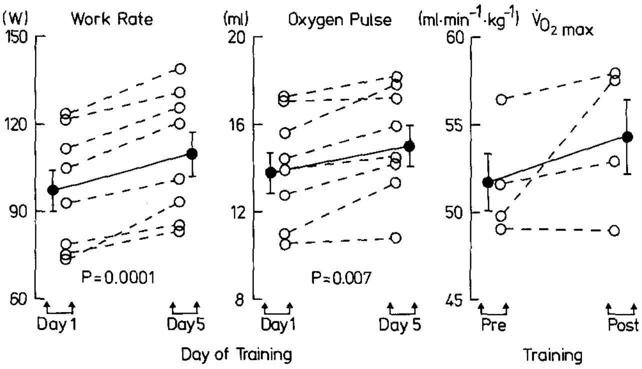

Fig. 5. Changes in work rate, oxygen pulse and $\dot{V}_{O_{2\,max}}$ (4 subjects only) during "sweatless training". Open circles: individual values; closed circles: means; bars indicate SE. p values from the paired t-test

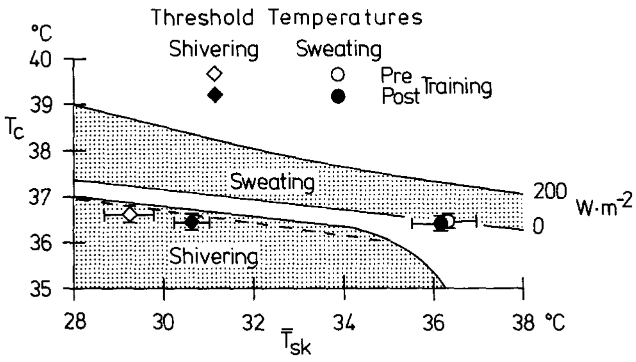

Fig. 6. Combinations of mean skin temperatures ($\bar{T}_{sk}$) and core temperatures (T_c) corresponding to the onset of sweating and shivering (*EMA*) before (open symbols) and after (closed symbols) "sweatless training". Values are means ±SE of tympanic temperatures (T_{ty}) standing for T_c, and of $\bar{T}_{sk}$. The contour lines enclosing the fields of shivering and sweating are based on data from Benzinger (1969) (T_{ty} for T_c) and Nadel et al. (1971) (T_{es} for T_c), respectively. The dashed line represents temperature combinations corresponding to $\bar{T}_b=35.9\,^\circ$C according to the equation $\bar{T}_b=0.87\cdot T_c+0.13\cdot\bar{T}_{sk}$ (see methods). Note that the increased post-training shivering threshold $\bar{T}_{sk}$ is offset by a decrease in T_c, thus there was no change in shivering treshold when related to $\bar{T}_b$; see text

Shivering and sweating thresholds, in relation to $\bar{T}_{b(ty)}$, were almost identical before and after the training period (shivering thresholds: 35.62 ± 0.13 and $35.67\pm0.09\,^\circ$C, $p=0.50$; sweating thresholds: 36.41 ± 0.16 and $36.36\pm0.15\,^\circ$C, $p=0.61$). In Fig. 6, the pre- and post-training threshold core temperatures (T_{ty}) are plotted against the threshold values of $\bar{T}_{sk}$. As for sweating, the T_c:$\bar{T}_{sk}$ threshold combinations were nearly identical for pre- and post-training conditions. For comparison, the sweating threshold temperatures found by Nadel et al. (1971) are given as a contour line. The diagram shows that, after training, shivering occurred at a 1.32 °C higher $\bar{T}_{sk}$ ($p=0.03$), but at a 0.13 °C lower T_c ($p=0.02$), so that $\bar{T}_b$ remained unchanged (note that the shift of temperature combination is parallel, not perpendicular to the dashed line in Fig. 6).

The slope of the relationship SR:$\bar{T}_{b(ty)}$ was not changed significantly due to "sweatless training" (1.88 and 1.17 mg · cm^{-2} · min^{-1} · °C^{-1} median values before and after training).

Discussion

In this study, the effects on thermoregulatory responses of a passive heat adaptation regimen and of mild exercise training without obvious stimulation of sweating were compared. In previous studies, comparing the effects of HA with those of exercise training (Nadel et al. 1974; Roberts et al. 1977; Senay and Kok 1977; Shvartz et al. 1979), the subjects exercised in both these conditions, and the ambient temperature during training (above 20° C) was not low enough to prevent sweating. It was thus impossible exactly to differentiate the adaptive effects of the two stressors, heat and exercise. Furthermore, there are few studies on the long-term effects of heat (Schwennicke and Brück 1976) and exercise (Adams and Heberling 1958) on cold defence responses.

The present study shows that during heat adaptation in resting conditions of only five days there was a shift in the thresholds of all autonomic thermoregulatory responses to lower body temperatures (Fig. 3, Table 1). The magnitudes of the threshold changes for shivering (EMA and $\dot{V}_{O_2}$ thresholds) and skin vasodilatation in the thumb, not described previously, were similar to the known threshold changes for sweating (for literature see Introduction) and forearm skin vasodilatation (Roberts et al. 1977). In addition, the present study demonstrates that, in the forearm, both the 1st and 2nd vasodilatation thresholds were lowered following heat adaptation. It should be remembered that the 1st vasodilatory response in the forearm, which occurs simultaneously with vasodilatation in the thumb, is related to a release of sympathetic vasoconstrictor tone, whereas the 2nd vasodilatation is thought to be due to an active vasodilator mechanism (Roddie et al. 1957).

In contrast, in a preliminary heat adaptation study, no change in shivering threshold could be seen, although the sweating threshold had been lowered (Schwennicke and Brück 1976): this appears to be due to the fact that the heat load employed was relatively mild (T_a 45° C, maximum T_{es} 37.7 and 37.4° C at the first and final exposure, respectively) compared with the present study. The concomitant and quantitatively almost identical alterations in all autonomic thermoregulatory thresholds, along with a tendency toward lower resting body temperatures (Fig. 3), suggest that these heat-adaptive changes depend on the alteration of some central nervous mechanisms that control the effector actions of the thermoregulatory system (Brück and Hinckel 1984). Alternatively, one might think of changes in the temperature responses of thermal receptors. No evidence has been found, however, for differences in the cutaneous cold receptor characteristics of two groups of cats maintained at ambient temperatures of +5 and +35° C, respectively, for two months (Hensel and Banet 1978). Also, no long-term thermoadaptive changes in internal receptors have been reported.

Total sweat loss did not change significantly during HA: this may have been due to the relatively short period of HA, although inconsistent results have been reported regarding changes in sweating rate in HA (for review see Henane 1981). The heat-induced rise in arm blood flow was diminished during HA (Table 2). In contrast to this result, Fox et al. (1963) reported increases of 35 and 11% in hand and arm blood flows respectively during a 12—24 d HA under resting conditions. These two extreme results are examples of a large number of such divergent results to be found in the literature (for review see Henane 1981). To explain these apparent discrepancies one has to consider that the HA process may have to be subdivided into several phases (Wyndham et al. 1976). Acute exposure to heat leads to a reduction in plasma volume with a consecutive decrease in stroke volume (Senay and Kok 1977; Wyndham et al. 1976). During a few days of repeated exercise in hot conditions, plasma volume and plasma protein levels increase considerably (Senay and Kok 1977; Wyndham et al. 1976), to the extent that circulation stabilizes. An increasing venous tone also appears to contribute to this stabilization of the circulation (for review see Rowell 1983). In another phase of the acclimatization process, partly in parallel with the 1st phase, the "classical" features of heat adaptation develop, i.e., increased sweat rate, reduction in the final elevation of body core temperature and reduction in heart rate. It thus appears that it is only after stabilization of the circulation that the organism can afford an elevated maximum skin blood flow.

In contrast to heat adaptation and "conventional" training regimens (for literature see Introduction), "sweatless training" failed to cause any threshold changes. The unchanged threshold temperatures for sweating are in accordance with preliminary results in three subjects, reported by Nielsen (1982), who found no change in sweating threshold (related to T_{es}) and total sweat rate following strenuous exercise training performed at 2—5° C air temperature. Furthermore, Avellini et al. (1982) reported that subjects trained on a cycle ergometer in cold water did not increase their sweat rates. Reference is made in the Introduction to similar results obtained in swimmers (Henane et al. 1977; McMurray and Horvath 1979; Piwonka et al. 1979). The increased $\bar{T}_{sk}$ combined with a decreased T_c at the onset of shivering (Fig. 6) following "sweatless training" indicates a tendency to increased peripheral blood flow under cold conditions. These characteristics resemble those described after physical training by Adams and Heberling (1958). They may be taken as modifications typical for the stress of exercise per se.

It should be noted that work rates requiring more than about 50% $\dot{V}_{O_{2\,max}}$ were not compatible with the aim of our protocol because sweating could not be suppressed at exercise intensities higher than 50% $\dot{V}_{O_{2\,max}}$, unless T_a was decreased to such an extent that the subjects experienced cold discomfort. Such a dissociation between autonomic and behavioual responses has been described previously by Bleichert et al. (1973).

The slope of the relationship between sweat rate and body temperature remained unchanged following both "sweatless training" and HA. The unchanged slope after "sweatless training" fulfills the prediction of Nadel et al. (1974) that steepening of the slope of the sweating response will not occur, in contrast to "conventional" training regimens (for literature see Introduction), if the training is performed without increased sweating. The same result was obtained in the preliminary study by Nielsen (1982). The unchanged slope during the present HA regimen is in accordance with some studies (Henane and Valatx 1973; Nadel et al. 1974), but in contrast to others, in which an increased slope has been reported due to HA (see Introduction).

The concomitant decrease in threshold temperatures for all autonomic thermoregulatory responses, found after the present heat adaptation regimen, is not self-evident: *independent* changes in the thresholds for heat loss and cold defence responses have been found after adaptation to moderate heat in man (Schwennicke and Brück 1976), and after cold adaptation in the guinea-pig (Brück et al. 1970; Zeisberger and Ewen 1983). On the other hand, a concomitant lowering of the threshold temperatures for both heat loss and cold defence responses has been found in long-distance runners (Baum et al. 1976). The quantitatively comparable threshold alterations found in "air athletes" and after the present heat adaptation regimen suggest that the athletes' thermoregulatory characteristics are a corollary of the internal heat load accompanying endurance exercise, and are, in essence, identical with heat adaptation. Shivering threshold deviations can be brought about by both cold (Brück et al. 1976) and heat adaptation (this study), so that there must be cross adaptation between heat and cold. Exercise *per se* does not seem to have any stressor property which could change thermoregulatory thresholds. Thus, the thermoregulatory threshold deviations can be thought of as *temperature-specific modifications* (Adolph 1956).

The biological significance of the concomitant shift in shivering threshold during heat adaptation may be seen in the extension of the gap between resting body temperature and shivering threshold (Fig. 3). If shivering threshold remained unchanged, slight cooling episodes would be more likely to cause shivering after heat adaptation. As for the heat-adaptive decrease in initial body temperature, the reader is referred to the demonstration of improved submaximum exercise performance with slightly below-normal body temperatures (Hessemer et al. 1984).

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