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Thermoregulatory Behavior of Man during Rest and Exercise

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Summary. The thermoregulatory behavior of two highly trained racing cyclists and of five untrained male subjects was investigated. The subjects were totally immersed in a water bath. They could regulate the water temperature according to their sensation of thermal comfort. At rest, in the state of thermal comfort, no thermoregulatory events—as sweating—could be observed. During exercise, esophageal temperature rises and consequently the subjects lower the water temperature. The resulting skin and deep-body temperatures caused an increase in sweat rate and heat conductance. Thus, during exercise, thermoregulatory responses increase as a function of oxygen uptake although the subjects are at thermal comfort. The different function of the two systems regulating sweat rate and thermoregulatory behavior respectively may arise from different weighting factors of skin and deep-body temperature as input variables to both systems. In the correlation equation

$$\text{Output} = a_O + a_1 T_{oe} + a_2 T_s$$

the ratio $a_1 : a_2$ is about 12—15 in the case of sweat rate, and about 4 in the case of behavior.

Key words: Thermoregulatory Behavior — Exercise — Water Immersion.

In recent papers (Kitzing *et al.*, 1972; Behling *et al.*, 1972) we studied input-output correlations in the system of physiological thermoregulation of man. By means of correlation equations sweat rate, heat conductance and thermoregulatory heat production can be predicted when mean skin and deep-body temperature are used as the only input variables. Since these equations are valid under steady-state conditions both during rest and exercise we concluded that the set-point of the system does not change during exercise.

Experiments with men and animals have shown that thermoregulatory behavior is also influenced by deep-body and mean skin temperature (Carlton and Marks, 1958; Weiss and Latties, 1961; Carlisle, 1968; Epstein and Milestone, 1968; Fanger, 1970; Corbit, 1969; Gagge *et al.*, 1969; Gale *et al.*, 1970; Adair, 1971; Cabanac, 1972 and others). Man has a sensation of thermal comfort only within a limited range of ambient temperature. In the resting state, this range coincides fairly well with the neutral zone of physiological thermoregulation, i.e. under climatic conditions of thermal comfort, the output of physiological thermoregulation is zero. During exercise, however, the sensation of thermal comfort can be achieved only under conditions which induce an increase in sweat rate. This striking difference between the state of rest and exercise may be due to the fact that the sensation of comfort is governed not only by thermal perception but also by sensations of other origins. For instance, during heavy exercise, thermoneutral conditions (sweat rate = zero) are present only in a rather cold climate. At such low temperatures, however, undressed persons have strong, even painful cold sensations in hands and feet, without adequate reactions of metabolic regulation. This discrepancy between behavioral and physiological regulation may be attributed to the non-uniform skin temperature over the whole surface with a predominant effect of the cold receptor field of hands and feet on pure sensation and with a rather small effect on thermoregulatory events. For this reason, a comparison between the output of the physiological and behavioral system requires a procedure which assures a more uniform temperature over the whole skin including hands and feet. This can be achieved in a well stirred water bath, in which water and skin temperature are nearly identical and where only very small differences in temperature of various areas are possible.

Methods

The subjects were placed in supine position totally immersed in a water bath (volume 1200 l). The water was stirred by a circulating pump. The temperature of the water was regulated by inflowing cold (10° C) or warm (55° C) water (60 l/min). A pedalling device installed in the bath was connected by a toothed belt with an eddy-current brake outside the water. The methods of recording deep-esophageal temperature, respiration, O_2-uptake, CO_2-loss and heart rate were the same as in recent experiments (Kitzing *et al.*, 1972). The water temperature was measured by a *Pt*-resistance thermometer. Our main subjects were 2 highly trained male persons (racings cyclist, see Table 1) whose thermoregulatory reactions under various conditions were studied in 350 experiments. In addition to the 77 experiments performed on these subjects, we carried out 10 control experiments on 5 untrained male persons.

Experimental Procedure

First the subject was totally submerged in the bath (35° C) for 5 min. Then he was dried and weighed (Potter bed balance 33 B, accuracy $\pm$ 5 g). After that the subject rested in the bath for 15 min. Throughout this period the water temperature was regulated automatically at 35 $\pm$ 0.1° C. During the remaining time until the end of the experiment the subject had to regulate the water temperature according to his thermal comfort sensation. By switching on either the cold or warm water inflow he adjusted the water temperature so that he neither felt warm nor cold. When he had to exercise he simultaneously started pedalling and regulating the

Table 1. Anthropometric data and maximal oxygen uptake for the subjects

Subject	Sex	Age (Years)	Weight (kg)	Height (cm)
J. S.	M	26	80	186
H. G. R.	M	26	71	178

Subject	Sex	Body surface (m^2)	$\dot{V}O_{2max}$[a] (l/min), STPD
J. S.	M	2.04	4.6
H. G. R.	M	1.88	4.5

[a] Estimated according to Astrand and Saltin (1961).

water temperature. In a few experiments the subject also had to regulate the water temperature in the first 15 min of the experimental period. Work load and pedalling rate (60 rpm, acoustic pacemaker) were constant over the whole exercise period (35 min). After a following recovery period (20 min) the subject was dried and weighed again.

Sweat loss was calculated from weight loss. Allowance was made for weight loss due to evaporation through respiration and for the difference in weight of exchanged gases (O_2 and CO_2). By means of control experiments in water of low temperature (32° C) we checked a possible error caused by soaking of the skin. No such error could be detected. An occasional increase of weight up to 50 g might have been caused by swallowing small amounts of water.

Results

1. Fig. 1 shows the time-temperature diagram of a typical experiment. At the start of the exercise esophageal temperature T_{oe} rises. At the same time the subject starts to lower the water temperature. During most of the experiments a steady state is achieved within 15—20 min. During the recovery period T_{oe} falls and the subject raises the water temperature.

2. During steady state, adjusted water temperature is inversely correlated to esophageal temperature. Taking into account our experimental conditions (fast water movement) water temperature may be considered as nearly identical with skin temperature. Fig. 2 shows the relationship between skin (i.e. water) temperature and esophageal temperature during steady state (large symbols). In both subjects esophageal temperature increases with oxygen uptake as an index of work load. Consequently, water temperature is reduced by the subject. Fig. 2 shows a higher correlation between T_{oe} and T_s in case of J. S. ($r = 0.96$) than in case of H. G. R. ($r = 0.69$). The small symbols, connected by an interrupted line, represent values during transient periods (first 15 min of exercise and recovery period). During the rising phase of esophageal temperature the ratio T_{oe}/T_s is of the same order as during steady state

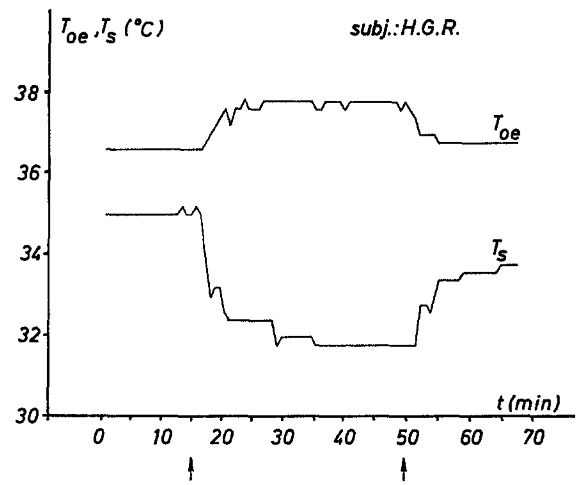

Fig. 1. Time-temperature diagram of a typical experiment. Beginning and end of exercise (2.77 l/min O_2-uptake) marked by arrows. Water temperature was regulated by the subject from the 15th minute to the end of the experiment

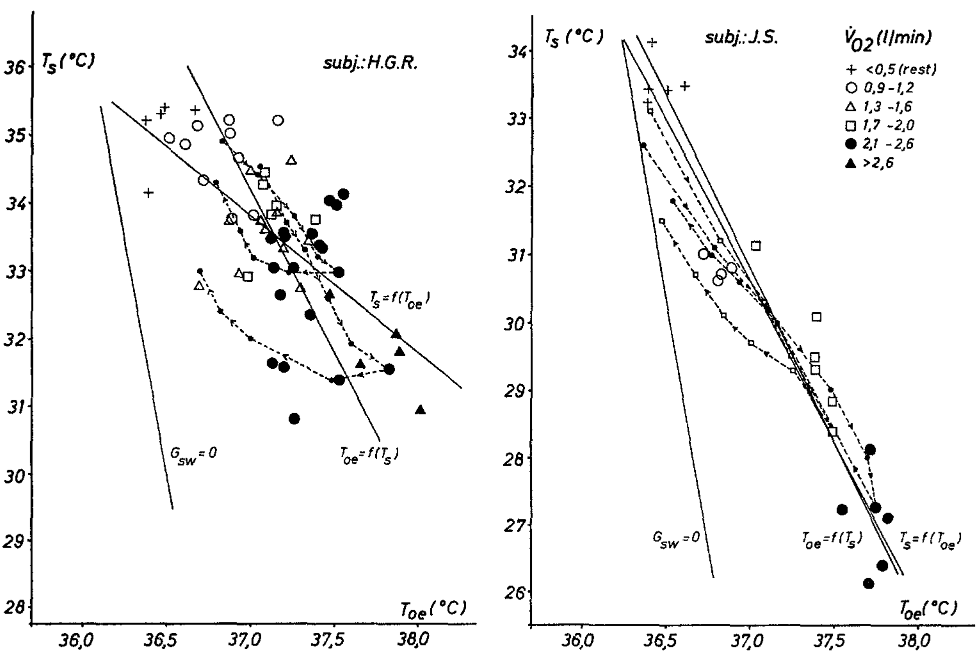

Fig. 2. Relationship of skin temperature T_s to esophageal temperature T_{oe} at thermal comfort during rest and exercise. For further explanations see text

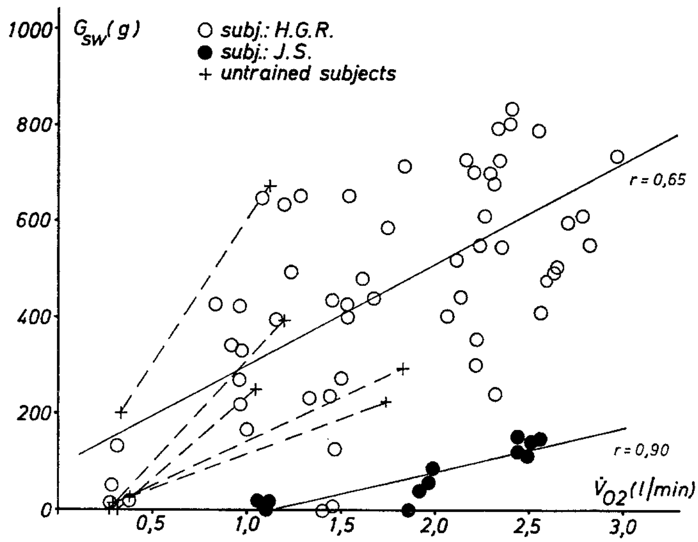

Fig. 3. Relationship of sweat loss G_{sw} to O_2-uptake at thermal comfort conditions during rest and exercise. Data taken from all experiments. Symbols connected by interrupted lines are values taken from the same untrained subject

whereas during the falling phase of esophageal temperature the ratio is somewhat greater (especially in case of H.G.R.).

3. In all subjects including the untrained ones sweat loss increases with work load. In Fig. 3 sweat loss is plotted against oxygen uptake. At rest, sweat loss is nearly zero.

4. Heat conductance k[1] also increases with oxygen uptake (Fig. 4). At rest the heat conductance of J. S. nearly reaches its lowest value, whereas in the case of H. G. R. it is considerably greater than the minimum (about 14 Watt/°C m² for both subjects).

5. The relationship between oxygen uptake and esophageal temperature as shown in Fig. 5 results from values obtained from 2 different sets of experiments. The correlation is remarkable high ($r = 0.92$). The large symbols indicate steady-state values taken from the experiments described here; the small symbols indicate steady-state values of pure physiological regulation. These data were obtained from experiments carried out within that range of ambient temperature, in which deep-body temperature remains nearly constant at a given work load (see M. Nielsen, 1938).

1 Heat conductance k is calculated as $\dot{Q}/(T_{oe} - T_s)$. ($\dot{Q}$ = heat flow from core to skin). Under steady state conditions the heat content of the body is constant. Therefore $\dot{Q}$ is proportional to oxygen uptake $\dot{V}_{O_2}$ and $k = \dot{V}_{O_2} \cdot c/(T_{oe} - T_s)$.

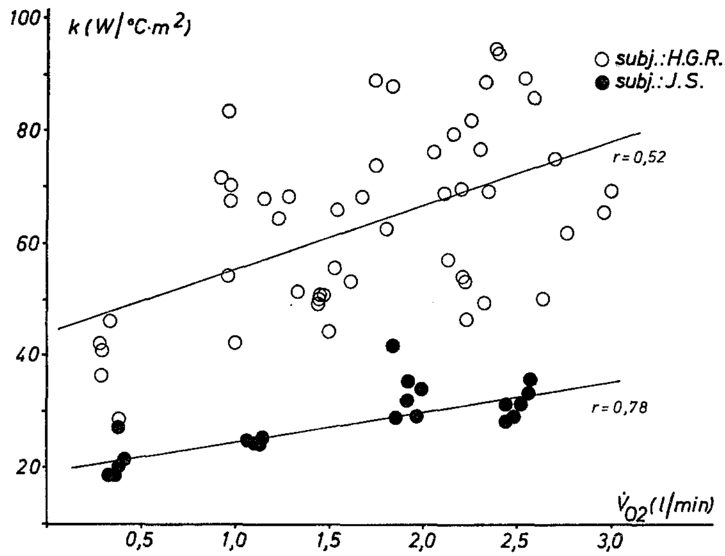

Fig. 4. Heat conductance k at thermal comfort conditions during rest and exercise plotted against O_2-uptake

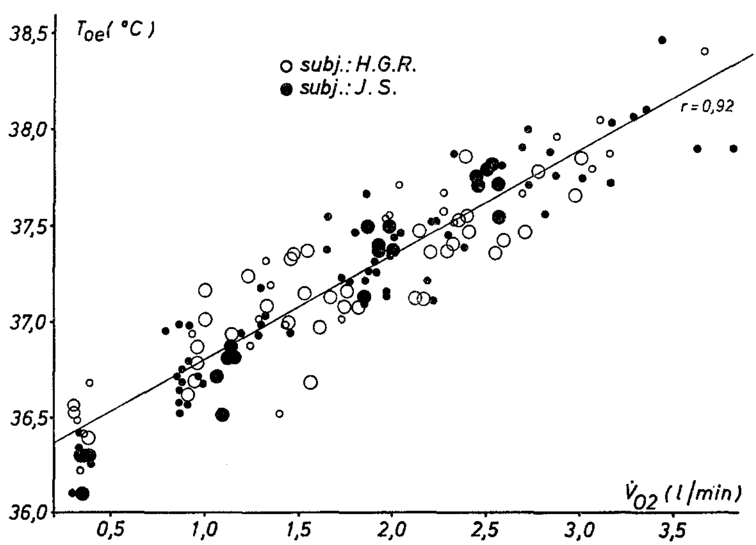

Fig. 5. Steady-state esophageal temperature as function of O_2-uptake. Data from experiments described here (large symbols) and from experiments on physiological regulation (small symbols, see Kitzing *et al.*, 1972). For further explanations see text

Discussion

Our results confirm well-known findings (see Fanger, 1970): man is in thermal comfort during rest under thermoneutral conditions. During exercise thermal comfort is achieved under thermal conditions which cause an increase in sweat loss and heat conductance as a function of O_2-uptake (see Figs. 3 and 4), i.e. during exercise physiological thermoregulation of man is active within the range of thermal comfort. This is not only true for highly trained athlets accustomed to internal heat stress during heavy exercise, but also for untrained subjects. Our results do not agree with the findings of Stitt *et al.* (1971) on a squirrel monkey. In these experiments, comfort temperature was identical with the thermoneutral temperature of the physiological system, even when hypothalamus temperature was changed by means of a thermode. The different results are probably due to the differences of the species.

The discrepancy between physiological and behavioral thermoregulation in man might be explained in terms of a changed set-point in the system of thermoregulatory behavior during exercise. This hypothesis cannot be discarded on the basis of our experimental findings, but, considering the input-output correlation of the system, in accordance with Cabanac *et al.* (1971) a non-thermal input in the system of behavioral thermoregulation seems unlikely. The data of Fig. 2 indicate the condition during which no further behavioral regulation is required; consequently during thermal comfort the output of the system is zero. In its simplest form the correlation equation between input and output for thermoregulatory behavior reads:

$$\text{Behavioral output} = 0 = a_o + a_1 T_{oe} + a_2 T_s \,. \qquad (1)$$

The regression line for this equation was calculated as $T_s = f(T_{oe})$ as well as $T_{oe} = f(T_s)$ (see Fig. 2). In Table 2 the coefficients a_i, calculated by means of the least square method, are compared with the coefficients of the system of physiological thermoregulation. From Table 2 one can derive the relative effectiveness of mean skin and deep-body temperature in driving the controller. In behavioral thermoregulation the ratio $a_1 : a_2$ is about 4, in physiological thermoregulation it is about 5 for heat conductance and about 14 for sweat rate[2].

The straight lines $G_{sw} = 0$ in Fig. 2 are the result of the equation $G_{sw} = a_o + a_1 T_{oe} + a_2 T_s$ (if sweat rate = 0) (see Behling *et al.*, 1972).

2 With increasing deep-body temperature the ratio $a_1 : a_2$ for behavioral regulation is the same as found for steady-state conditions. During the recovery period the ratio is somewhat smaller. This deviation may be caused by adaption of the thermoreceptors of the skin.

Table 2. Correlations of thermoregulatory responses with esophageal and mean skin temperature

Subject	Response	n	$a_0 \pm \sigma$	$a_1 \pm \sigma$	$a_2 \pm \sigma$	a_1/a_2	r
J. S.	Behavior I	21	200.3 ± 0.8	−4.58 ± 0.02	−1	4.6	−0.96
	Behavior II	21	43.0 ± 0.1	−1	−0.196 ± 0.004	5.1	
	Sweat rate[a]	106	−9745.0 ± 90	252.8 ± 1.8	17.0 ± 0.2	14.9	0.93
	Conductance[a]	100	−601.0 ± 23	14.7 ± 0.6	3.01 ± 0.09	4.9	0.76
H. G. R.	Behavior I	56	109.0 ± 0.7	−2.03 ± 0.02	−1	2.0	−0.69
	Behavior II	56	44.1 ± 0.2	−1	−0.207 ± 0.006	4.8	
	Sweat rate[a]	62	−7615.0 ± 102	195.6 ± 2.6	15.6 ± 0.4	12.5	0.83
	Conductance[a]	66	−954.0 ± 32	22.9 ± 0.8	4.38 ± 0.11	5.2	0.60

Remarks: Response $= a_0 + a_1 T_{oe} + a_2 T_s$. In case of "behavior" the regression is calculated as $T_s = a_0 + a_1 T_{oe}$ (I) and $T_{oe} = a_0 + a_2 T_s$ (II). Dimensions: Sweat rate (Evaporation) [W/m²]. Conductance [W/m^2 °C]. n = Number of experiments; σ = standard deviation; r = multiple correlation coefficient.

[a] See Behling *et al.* (1972). The correlation equation for conductance was calculated using only T_{oe} and T_s instead of T_{oe}, T_s, T_s^2 and T_s^3 as in the original paper.

This line determines the upper limit of the thermoneutral zone of physiological thermoregulation. One can easily see that this line is steeper than those which are characteristic for the steady-state values of thermoregulatory behavior. The lines for both responses approach each other in the range of low deep-body temperature and high skin temperature, i.e. under rest conditions. In this range, sweat rate is zero or almost zero during the behavioral experiments.

Despite the quantitative differences in the system of thermoregulation as a whole, there is a remarkable agreement in deep-body temperature in relation to oxygen uptake for both subjects under the different conditions of our two sets of experiments (compare Fig. 5). Values of esophageal temperature obtained in experiments in the climatic chamber are shown together with values obtained in the water bath. According to Saltin and Hermannsen (1966), one may expect this result in the climatic chamber, because both subjects have nearly the same maximal oxygen uptake (see Table 1). A question may arise from the fact that esophageal temperature is determined only by oxygen uptake, despite the completely different experimental conditions. In a warm environment, deep-body temperature is only regulated by changes of skin blood flow—indicated by heat conductance—regardless of the kind of heat flow from skin to environment. This heat flow is equal $k \cdot (T_{oe} - T_s)$. The water (i.e. skin) temperatures adjusted by the subjects, as well as the skin temperatures attained in the climatic chamber during the experiments mentioned here both scatter within that large range of skin temperature in which variations of $T_{oe} - T_s$ are counteracted by changes of heat conductance thus keeping heat flow nearly constant at a given heat production. Consequently, deep-body temperature as a function of oxygen uptake attains the same values in both sets of experiments.

A remarkable feature of the thermoregulatory behavior of our two subjects is the difference in the scattering of the experimental data. In general a large scattering of data may be expected in complex biological systems. This is true for the subject H. G. R. The subject J. S., however, shows exceptionally low scattering of the data. Apart from individual differences the main reason for this may be the fact, that J. S. was examined for only about 6 weeks, whereas H. G. R. was at our disposal for more than one year. During this time, variations in training activity and physical fitness might have led to a different responsiveness to thermal signals.

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