Body Temperature Regulation in Rats during Exercise of Various Intensities at Different Ambient Temperatures

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Abstract We examined the relationship between body temperature, tail vasomotor response, and work intensity at different ambient temperatures in rats, using a treadmill and continuously measuring oxygen uptake during exercise. At an ambient temperature (T_a) of 24°C, rectal temperature (T_{re}) at the beginning of tail vasodilation during exercise increased in proportion to work intensity. After tail vasodilation T_{re} remained steady, and at the end of 30 min exercise T_{re} level was proportional to work intensity. At T_a of 14°C, T_{re} at the end of exercise was slightly higher than at 24°C, and was higher at higher work intensities. At T_a of 4°C, T_{re} rose slower during exercise than at higher T_a s and even dropped at relatively low work intensities. Tail vasodilation did not occur in most cases. At T_a of 34°C, T_{re} rose continuously during exercise. These data indicate that body temperature of rats during exercise rises in proportion to work intensity, but the extent of body temperature rises differs according to T_a .

Key words: rectal temperature, tail vasomotor response, work intensity, ambient temperature, rat.

Deep body temperature in man rises during exercise in proportion to work intensity, irrespective of ambient temperature (T_a) of 5 to 25°C (NIELSEN, 1938). The physiological mechanism of this exercise-induced hyperthermia is not clear. Although man has been given detailed attention in many studies, methodological limitations have necessitated animal studies as well.

The rat, extensively used as an experimental animal in acute and chronic studies, has made a great contribution to elucidate central nervous mechanism for thermoregulation. Since the rat, however, does not sweat or pant (ADOLF, 1947), and moreover cannot spread saliva effectively during exercise, how is body temperature of the rats during exercise influenced by work intensity and T_a ? Although some reports have investigated the relationship between work intensity

and deep body temperature at a given T_a (THOMPSON and STEVENSON, 1965; GOLLNICK and IANUZZO, 1968; WILSON *et al.*, 1978; SONNE and GALBO, 1980; HARRI *et al.*, 1982), the relationship remains obscure. Since treadmill speed has been used to indicate work intensity in most studies, individual differences among the animals may have been responsible for discrepancies in results. Core temperature during exercise in man was set according to the relative work load of the individual and not to the absolute work load performed (SALTIN and HERMANSEN, 1966). A similar consideration should be applied to exercising rats. A relationship between deep body temperature during exercise and T_a has also been reported (HART and JANSKY, 1963), but how work intensity might influence this relation is unclear.

The purpose of this study was to clarify the relationships among work intensity, tail vasomotor response, and deep body temperature in rats during treadmill running. We also investigated the influence of T_a on this relation.

MATERIALS AND METHODS

Experimental apparatus. A motor-driven treadmill could operate at any speed between 2 and 50 m/min in a stable manner. The belt speed could be kept consistent because a direct-current motor was connected directly to the driving wheel and was controlled by a servomechanism. The treadmill itself was situated inside an acrylic metabolic chamber (inside dimensions, $35 \times 8 \times 18$ cm), but the motor lay outside.

Oxygen uptake ($\dot{V}_{O_2}$) was measured by an open-circuit system. Atmospheric air was led into the box at the rear of the treadmill. Outgoing air passed through an absorption pump and a flow meter. When flow rate was adjusted to 5 l/min (ATPS) in preliminary work, no air inside the chamber leaked out and measurements were stable. One hundred ml/min of this flow was passed through an oxygen analyzer (Toray, LC-700E). $\dot{V}_{O_2}$ was calculated by determining the relation between difference of $O_2\%$ (inlet $O_2\%$ – outlet $O_2\%$) and air flow. The response time of the system following injection of a marker gas was 50 s. This delay of O_2 measurement was corrected after the end of each experiment.

Evaporative water loss (EWL) was assessed by measuring absolute humidity (AH) with a hygrometer (Sibaura, SM-360) in the metabolic chamber. EWL was calculated according to change in AH and air flow.

Rectal (T_{re}) and tail skin (T_{tail}) temperatures were measured by Cu-Co thermocouples. T_{re} and T_{tail} were continuously recorded by a chart recorder.

Animals, training, and $\dot{V}_{O_{2\max}}$ test. Experiments were performed on male Wistar rats with initial body weights of approximately 100 g. These rats were housed in a cage maintained at an air temperature of 25°C and had free access to food and water. Lighting was controlled automatically for a 0600–1800 h light cycle.

The rats were trained to get accustomed to the treadmill running in a climatic room at a T_a of 24°C. Rats were induced to run by mild electrical stimulation. If the rat stopped running and its feet touched an electrified grid at the rear of the treadmill, the rat received an electrical shock as long as the feet remained in contact

with the grid. Training consisted of 2 days/week for 6 weeks. The rats ran initially for 10 min/day at 10 m/min. Thereafter, duration and running speed of the exercise was increased gradually and they ran continuously for 30 min at 15 m/min.

$\dot{V}_{O_{2\max}}$ was examined twice, before and after a series of experiments, in each rat that could run stably in the above training. Prior to each $\dot{V}_{O_{2\max}}$ test, the rat was weighed and then placed in the treadmill chamber. The rat first exercised for 5–10 min at 10 m/min, rested 3 min, and then exercised at 15 m/min. The running speed was increased 2.5 m/min every 3 min until the rat could no longer maintain pace with the treadmill. The highest $\dot{V}_{O_2}$ recorded during the final 30 s of every 3 min running period was taken as $\dot{V}_{O_{2\max}}$.

Experimental conditions.

1. Procedure 1: We measured T_{re} , T_{tail} , $\dot{V}_{O_2}$, and EWL at one steady state during running for 30 min with T_a at 24°C. At the start of each experiment, thermocouple probes for measuring T_{re} and T_{tail} were attached. T_{re} was measured with a thermocouple inserted 6 cm into the anus. T_{tail} was measured with a thermocouple taped to the dorsal surface of the tail about 6 cm distal to its base. The rat was placed in the treadmill chamber, set in a climatic room at T_a of 24°C with relative humidity at $54 \pm 4\%$. Thirty min later, $\dot{V}_{O_2}$, T_{re} , T_{tail} , and AH were measured for 10 min and then the rat ran for 30 min at running speed of 3 to 30 m/min. Average $\dot{V}_{O_2}$ during exercise was calculated from the 10th to the 30th min of the treadmill run, and we estimated the relative work intensity for each run on the basis of this average $\dot{V}_{O_2}$. After the 30 min of running, further measurements were taken over a 30 min recovery period. The ordering of the running speed was randomized and each rat was tested 5–8 times. All experiments were performed between 1:00 and 6:00 p.m.

2. Procedure 2: This experimental series, to examine the effect of T_a , was performed at T_a s of 4, 14, and 34°C, with relative humidity at 50–70%. The experimental procedure was otherwise the same as in Procedure 1. The rats experienced T_a s of 4 and 14°C in random order and lastly 34°C.

Statistics. Statistical evaluation of the result was performed by linear regression and analysis of variance, with further analysis by a paired Student's *t*-test where appropriate. Data were considered statistically significant if $p < 0.05$. The results are expressed as mean value $\pm$ S.D.

RESULTS

Of 20 rats undergoing the treadmill running training, 13 exhibited stable running at a speed of 15 m/min for 30 min. Since the other 7 frequently received electrical shocks while running, they were excluded from the experiments. Mean body weight at the $\dot{V}_{O_{2\max}}$ test was 302 ± 16 g and mean $\dot{V}_{O_{2\max}}$ was 69.5 ± 4.3 ml/(min · kg) in 13 rats. $\dot{V}_{O_{2\max}}$ for each rat was the same in two tests.

Fig. 1. Rectal temperature (T_{re}), tail skin temperature (T_{tail}), oxygen uptake ($\dot{V}_{O_2}$), and absolute humidity (AH) at rest, during exercise for 30 min, and in recovery, at an ambient temperature of 24°C.

Running at 24°C

In Procedure 1 five rats performed 34 trials. Figure 1 shows a typical result. At rest, T_{re} was 37.4°C and T_{tail} was only a little higher than T_a . T_{re} decreased a little just after running began, and then it began to rise. When T_{re} reached 39.0°C, T_{tail} began to rise gradually. At nearly the same time, T_{re} rose less rapidly, eventually attaining a steady level. AH rose during exercise. After the exercise, T_{tail} rose still more and T_{re} dropped gradually.

Figure 2A shows the relation between T_{re} and relative work intensity ($\dot{V}_{O_{2max}}\%$) at the time T_{tail} began to rise. Mean T_{re} (broken line) at rest before exercise was $37.5 \pm 0.4^\circ\text{C}$ and mean $\dot{V}_{O_2}$ at rest was $24.7 \pm 3.3 \text{ ml}/(\text{min} \cdot \text{kg})$. T_{re} at the beginning of T_{tail} rise in 34 trials increased in proportion to work intensity, reaching 39.3°C at 75% $\dot{V}_{O_{2max}}$ and leveling off at higher work intensities. The regression line in the range from 45 to 75% $\dot{V}_{O_{2max}}$ was $Y = 35.77 + 0.048X$ ($r = 0.83$). Degree of the T_{tail} rise, however, was independent of work intensity. Figure 2B shows how T_{re} related to work intensity at the end of 30 min of exercise. The T_{re} , as at the beginning of T_{tail} rise, was proportional to work intensity, reaching a maximum at 75% $\dot{V}_{O_{2max}}$. The regression line for this relation in the range of 45–75% $\dot{V}_{O_{2max}}$ was $Y = 35.22 + 0.048X$ ($r = 0.73$). EWL, calculated from change in AH over the 30 min exercise period, is plotted against work intensity in Fig. 3. Mean EWL at rest was $24.3 \pm 7.8 \text{ mg}/(\text{min} \cdot \text{kg})$. During 30 min of exercise EWL increased in proportion to work intensity.

Running at 4, 14, and 34°C

Eight rats were used for Procedure 2. Thirty-eight trials were performed at a T_a

Fig. 2. Relation of rectal temperature (T_{re}) at the beginning of tail skin temperature (T_{tail}) rise (A), and at the end of 30 min exercise (B) to oxygen uptake ($\dot{V}O_2$), normalized to individual maximal oxygen uptake ($\dot{V}O_{2max}$), at an ambient temperature of 24°C . Each symbol indicates the same rat. Broken lines indicate mean T_{re} just before exercise.

Fig. 3. Relation of evaporative water loss during 30 min exercise to oxygen uptake ($\dot{V}O_2$), normalized to individual maximal oxygen uptake ($\dot{V}O_{2max}$), at an ambient temperature of 24°C .

of 4°C . Mean T_{re} at rest before exercise was $37.7 \pm 0.3^\circ\text{C}$ and the mean $\dot{V}O_2$ was $32.3 \pm 4.1 \text{ ml}/(\text{min} \cdot \text{kg})$. T_{tail} did not rise during exercise in most cases. Rate of T_{re} rise with exercise was lower than at other ambient temperatures. In fact, T_{re} even decreased during running at low work intensities. Figure 4 shows a typical example in which T_{re} dropped during exercise. Although $\dot{V}O_2$ increased a little during running from the resting value, T_{re} dropped continuously at a rate of $0.02^\circ\text{C}/\text{min}$, reaching 36.9°C ($\Delta T_{re} = -0.7^\circ\text{C}$) by the end of 30 min of exercise. After the exercise, T_{re} began to rise and reached 37.4°C in 10 min.

Fig. 4. Rectal temperature (T_{re}), tail skin temperature (T_{tail}), oxygen uptake ($\dot{V}O_2$), and absolute humidity (AH) at rest, during exercise, and during recovery, at an ambient temperature of 4°C.

Fig. 5. Relation of rectal temperature (T_{re}) at the end of 30 min exercise to oxygen uptake ($\dot{V}O_2$), normalized to individual maximal oxygen uptake ($\dot{V}O_{2max}$), at an ambient temperature of 4°C. The broken line indicates mean T_{re} just before exercise. Open circles mean that T_{tail} did not rise during the 30 min of running.

Figure 5 shows the relation of T_{re} to work intensity at the end of exercise. T_{re} was higher at higher work intensities with a regression line of $Y = 36.36 + 0.017X$ ($r = 0.46$). Compared to T_{re} at rest (broken line), however, T_{re} during exercise was seen to be dropping at work intensities below 70% $\dot{V}O_{2max}$.

At a T_a of 14°C, 35 trials were performed. Mean T_{re} at rest before exercise was 38.0 ± 0.4 °C and the mean $\dot{V}O_2$ was 25.9 ± 4.0 ml/(min · kg). As the rat ran, T_{tail} rose in some instances but remained at the pre-exercise level in others. In either case, T_{re} maintained a steady level in the latter half of the exercise period. The relation of T_{re} to work intensity at the time T_{tail} began to rise is presented in Fig. 6A. T_{re} rose in

Fig. 6. Relation of rectal temperature (T_{re}) to oxygen uptake ($\dot{V}O_2$) at the beginning of tail skin temperature (T_{tail}) rise (A), and at the end of 30 min exercise (B), normalized to individual maximal oxygen uptake ($\dot{V}O_{2max}$), at an ambient temperature of 14°C. Broken lines indicate mean T_{re} just before exercise. Open circles mean that T_{tail} did not rise during the 30 min of running.

Fig. 7. Relation of rectal temperature (T_{re}) at the end of 30 min exercise to oxygen uptake ($\dot{V}O_2$), normalized to individual maximal oxygen uptake ($\dot{V}O_{2max}$), at an ambient temperature of 34°C. The broken line indicates mean T_{re} just before exercise. Open triangles indicate T_{re} at the cessation of exercise in rats that could not run the entire 30 min.

proportion to work intensity, with a regression line of $Y = 36.59 + 0.041X$ ($r = 0.80$). This line was significantly different from the line at T_a of 24°C ($p < 0.01$). Figure 6B shows the relation of T_{re} to work intensity at the end of 30 min exercise. The cases of T_{tail} rise (closed circles) and no T_{tail} rise (open circles) form distinguishable clusters. At the end of exercise at a given work intensity, T_{re} was higher in rats showing no T_{tail} rise than in rats whose T_{tail} rose. In rats exhibiting a rise in T_{tail} the regression

line was $Y = 37.04 + 0.026X$ ($r = 0.61$); otherwise the equation was $Y = 37.98 + 0.018X$ ($r = 0.53$).

Fifteen trials were performed at a T_a of 34°C . Mean T_{re} just before the beginning of exercise was $38.8 \pm 0.4^\circ\text{C}$. T_{tail} already exceeded 37°C at rest. In the 15 trials, rats could run for the entire 30 min in 11 cases. The experiments were prematurely discontinued in the remaining 4 trials, because the rats did not run even when they received continuous electrical shocks on the feet during the exercise periods. Figure 7 shows how T_{re} at the end of exercise was related to work intensity. T_{re} in rats that stopped running early (open triangles) exceeded 40.9°C in every instance, whereas rats that ran for the entire 30 min showed continual rises in T_{re} that never leveled off.

DISCUSSION

To study the mechanism of body temperature regulation during exercise, we tried to use the rat as the model. Although the rat has been used extensively in exercise studies, regulation of body temperature during exercise in this species remains a puzzling topic for work physiologists. Earlier studies have reported the relations between work intensity and physiological variables such as deep body temperature or tail vasomotor response, but the resulting picture remains fuzzy. We decided to approach this problem by using $\dot{V}_{O_2}$ at a neutral T_a as a standard for estimating work intensity.

During exercise for 30 min at a T_a of 24°C , tail vasodilation, observed as rise in T_{tail} , was seen in every trial. T_{re} at the beginning of this tail vasodilation was proportional to work intensity and reached a maximum (39.3°C) at approximately 75% $\dot{V}_{O_{2max}}$. WILSON *et al.* (1978) reported that the tail became warmer during exercise at a threshold deep body temperature of 39°C and was independent of work intensity. T_{tail} at rest before exercise was about 6°C higher than T_a in their study. In our study, however, the T_{tail} was only a little higher than T_a , indicating relative vasoconstriction. This difference of T_{tail} before exercise may have been effected.

T_{tail} at the end of exercise at a T_a of 24°C was $30\text{--}32^\circ\text{C}$, regardless of work intensity. After the exercise, T_{tail} continued to rise at higher work intensities (ΔT_{tail} about 2°C). This indicates that tail blood vessels were not fully dilated during the exercise. Previous studies in our laboratory on human subjects demonstrated that during light work in which the effects of forced evaporation and sweating were ruled out, increase in work intensities caused a proportional fall in skin temperature in larger surface area (NAKAYAMA *et al.*, 1977, 1981). The cause of this vasoconstriction is unknown, but is regarded to be due to non-thermal factors related to exercise. The rise in core temperature during work could be explained by decreased heat loss due to persistent vasoconstrictor tone. Thus, skin temperature during exercise depended on thermoregulatory vasodilation produced by elevated body temperature and the non-thermally induced vasoconstriction. As shown in Fig. 2A, T_{re} at the beginning of T_{tail} rise was higher, the higher the exercise intensity. This

result can be explained by non-thermal factors. Similarly, the fact that T_{tail} continued to rise after exercise should be considered a removal of the vasoconstrictor tone.

After tail vasodilation, T_{re} decreased and then remained at a steady level. Heat loss through the tail skin after vasodilation is equivalent to as much as 20% of all the heat produced in the body (RAND *et al.*, 1965). Vasodilation in the foot occurs at practically the same time as vasodilation in the tail (THOMPSON and STEVENSON, 1965). EWL, assessed by measuring AH, increased in proportion to work intensity. Since rats do not sweat, enhancement of EWL during exercise is considered dependent mainly on ventilatory evaporation increasing due to more frequent ventilation. The possibility of cutaneous evaporation increasing with vasodilation has also been suggested (CONLEY, 1985). However, we cannot attribute all of this EWL to heat loss, because the change of AH in this experiment includes evaporative water from excrement and urine. During exercise at a T_a of 24°C, rats can maintain thermal balance through the above-mentioned heat loss showing a proportional relationship between work intensity and internal temperature. The absolute value of deep body temperature at the end of exercise, especially if work intensity exceeded 75% $\dot{V}_{\text{O}_{2\text{max}}}$, tended to be lower than in a previous study (WILSON *et al.*, 1978). This may be attributable to such factors as duration of exercise, deep body temperature level before the start of exercise, and degree of training.

In our investigation on the relation between body temperature and T_a at various work intensities, T_{tail} did not rise during exercise in most cases at a T_a of 4°C. At a T_a of 14°C, T_{tail} rose during exercise in some cases but not in others. In those cases in which T_{tail} rose, T_{re} at the onset of T_{tail} rise was about 0.4°C higher than at a T_a of 24°C. In our previous study, threshold temperature to tail vasodilation induced by locally warming the preoptic area and anterior hypothalamus was affected by T_a (TANAKA *et al.*, 1986). The results of the present study suggest that threshold T_{re} to tail vasodilation during exercise is likewise affected by T_a .

T_{re} stabilized during exercise at a T_a of 14°C as well as 24°C. T_{re} at the end of exercise was higher at a T_a of 14°C than 24°C. This would be due to the suppression of the heat loss from the tail, because threshold T_{re} for T_{tail} rise became higher at a T_a of 14°C than 24°C at the same work intensity, and because the animals without T_{tail} rise during 30 min session of exercise attained higher T_{re} than those with T_{tail} rise. On the other hand, under extreme environmental conditions such as 4 and 34°C, rats could not maintain thermal balance during exercise. At a T_a of 4°C, T_{re} during exercise decreased at lower work intensities. During exercise $\dot{V}_{\text{O}_2}$, an indicator of thermogenesis, either remained at the resting level or increased. Thus, the drop in T_{re} during exercise would indicate that body heat was being lost at a greater rate than at rest. This would be due to the increase of dry heat-loss, because posture during exercise was different from that at rest. When T_a was at 34°C, T_{re} continued to rise throughout the 30 min running period, even though work intensity was only 40–50% $\dot{V}_{\text{O}_{2\text{max}}}$. Even at rest in such a hot environment in the present study, the

rat's tail blood vessels were already dilating and the rat displayed heat-loss behavior, such as grooming or body extension, enabling T_{re} to stay around 39°C. Since heat-loss behavior is incompatible with running, autonomic heat loss must have increased in such a situation. Rats, however, do not sweat. Nor can a rat be expected to be able to control body temperature solely by respiratory evaporative water loss.

In summary, these results show that deep body temperature of rats during exercise rises in proportion to work intensity, but the extent of deep body temperature rises differs according to T_a . If the rat is used as a model for studying thermoregulation in exercise, the study must carefully take T_a into account.

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