Showering as a Coolant for Rats Exposed to Heat

Abstract. *Rats exposed to heat learn to take showers and thus defend themselves against hyperthermia; thereafter the rate of showering is a direct function of ambient temperature. The showering effectively replaces spreading of saliva as the major defense against heat in desalivate rats, and appears to be highly preferred to the use of saliva by the intact animal. Since rats will work to obtain heat when cold, it is now clear that learned behavior is effective and physiologically appropriate for thermoregulation at temperatures both above and below the neutral range.*

Rats and other small mammals that neither sweat nor pant in the heat employ saliva as their major coolant. They groom themselves actively while excreting copious amounts of saliva, thus wetting their fur and skin and losing heat by evaporation. In the domestic rat, spreading of saliva begins at moderately high ambient temperatures (32°C for males, 36°C for females) and becomes excessive during severe heat. When saliva-spreading fails because of dehydration or desalivation (*1*), the rat cannot defend itself and suffers rapid and lethal hyperthermia at ambient temperatures above 36°C (*2*).

Since rats work for heat when cold (*3*), the demonstration that the evaporation of surface water (saliva) is their major coolant predicts that they will do the converse; that is, they should take showers in the heat.

They did so in our experiments by depressing a bar that opened a compressed-air line to a water aspirator (De Vilbiss No. 15) whose nozzle was positioned 25 cm directly above the bar; a press sprayed minute water droplets over the rat's face, head, upper back, and paws. The shower stall was a cylindrical wire-mesh cage (22.5 cm in diameter and 30 cm high) inside a 0.7-m^3 chamber controlled as to temperature within 1.0°C. A Gerbrands bar was fixed to the wall of the stall 5 cm above the floor. The nozzle of the aspirator was positioned just outside a small hole in the sheet-aluminum roof of the stall, and water reached it by hydrostatic pressure from a graduated cylinder within the chamber. Both the water and compressed-air lines were interrupted by solenoid valves that opened simultaneously on depression of the bar and delivered the shower. The duration (and volume) of the shower was controlled by an operations timer that delivered 0.5 second of spray (0.2 to 0.3 ml of water) for each of all presses of the bar occurring $\geq$ 0.5 second apart. Presses and showers were recorded separately on a Gerbrands recorder: presses operated the cumulative pen; showers (reinforcements), the event marker. Deep colonic temperatures were measured by a thermistor probe inserted at least 5 cm beyond the anal orifice both before and after test and training sessions. Water was available from a metal drinking spout attached to an inverted graduated cylinder fixed to the wall of the stall opposite the bar. Relative humidity within the chamber ranged from 20 to 50 percent—usually on the low side. When not under study, the adult male Sprague-Dawley rats (300 to 400 g) were housed individually at room temperature, with Purina pellets and tap water freely available. In the earliest experiments the rats were hand-shaped at 44°C. Currently the animals discover the shower and train themselves adventitiously when left in the shower stall overnight at 36°C. Six normal animals trained themselves overnight, with an average latency to the first 50 presses (1.25 cm of cumulative excursion) of 5 hours 51 minutes (range, 1 to 15 hours). After training, the rats were tested only once daily.

Once learned, showering begins promptly when the animal is reintroduced to heat, and the rate of showering (milliliters of water per hour) is a direct function of ambient temperature. Figure 1 (inset, left) shows the cumulative record of bar-pressing for showers of a single experienced rat exposed successively to 1 hour each of 42°, 36°, and 40°C. Showering begins within 5 minutes after the animal enters the heat (shown by the single deflection of the base line), and its overall rate is clearly a function of ambient temperature. The record also shows the episodic nature of the showering. The animals wet themselves in discrete bouts and groom or lie prostrate when not pressing the bar. With the shower overhead the animal characteristically stands erect over the bar while showering and manipulates the bar by applying weight with abdomen or forepaws; when the shower be-

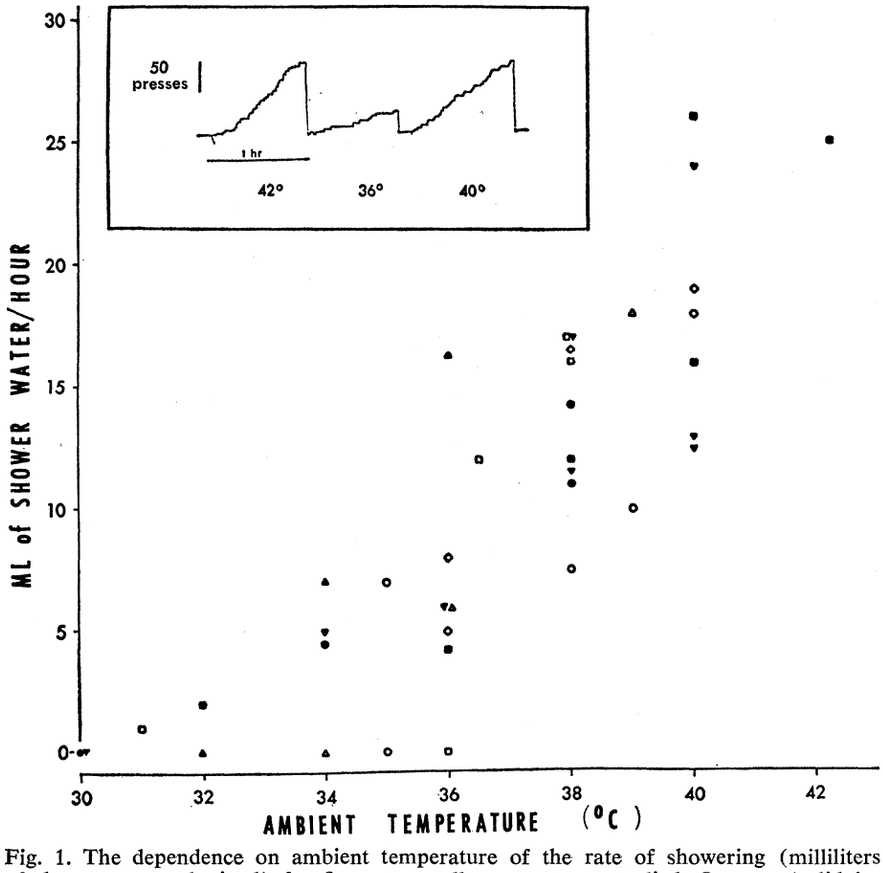

Fig. 1. The dependence on ambient temperature of the rate of showering (milliliters of shower water obtained) for five rats at all temperatures studied. One rat (solid inverted triangles) was not desalivated, three (circles, squares, and upright triangles) were tested both before and after desalivation, and the fifth (hollow diamonds) was trained and tested only after desalivation. Inset: cumulative record of bar-pressing for showers by a single rat at three different ambient temperatures during one session.

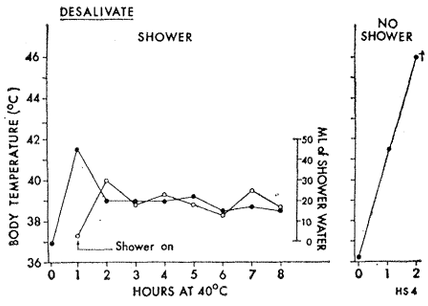

Fig. 2. Prevention by showering of lethal hyperthermia in a 40°C atmosphere by an experienced desalivate rat. Note that core temperature (solid circles) rapidly reaches 39°C and is maintained at that level when the shower is employed.

gins, it stretches upward, pointing its nose into the spray with its mouth and eyes closed.

The direct and apparently linear relation between rate of showering and increasing ambient temperature for both intact and desalivate male rats is shown (Fig. 1) for five rats tested over the range 30° to 42°C. The volume of shower water obtained during the last hour of a 1.5-hour test is shown for each animal at all temperatures tested. A solid symbol represents an intact animal; when hollow, the symbol represents the same animal after desalivation. Desalivation was by ligation and transection of all six major salivary ducts under ether anesthesia; it was confirmed by the development of prandial drinking and polydipsia in the home cage (*4*).

Note that showering begins between 30° and 32°C, the temperature at which spreading of saliva is first conspicuous in the male rat (*5*). The volume of shower water then increases for all rats with increasing temperature; the rats soak themselves at the highest temperatures, thoroughly wetting the hair of the head and neck despite the fact that some water is wasted on the bar and the floor and walls of the stall. Repeated testing of the same rat at the same temperature on different days yields comparable results (Fig. 1, especially at 38° and 40°C). Figure 1 also shows that data for animals with and without saliva overlap. Moreover, normal and desalivate core temperatures were not different when the sessions ended. These facts suggest that even when saliva is available, as in the intact rat, the animals choose the option of showers, utilize them at optimum rates, and thus swamp the contribution of endogenous water. The effectiveness of the shower for defense against heat is shown in two ways:

1) Four experienced intact rats were run for 1.5 hours at 40°C with the shower available, and then on a subsequent day without the shower. Before the tests, colonic temperatures averaged 37.8°C (range, 37.0° to 38.5°C) on the day without shower, and 37.6°C (range, 37.0° to 38.3°) on the day of the shower test. The mean core temperature at the end of the exposures to 40°C ambient was 40.4°C (range, 40.1° to 40.8°C) without the shower but only 39.1°C (range, 38.4° to 40.0°C) with the shower available. By showering, the animals maintained their core temperatures just above normal levels, and the regulated hyperthermia, seen when spreading of saliva is the only defense, was clearly reduced.

2) An experienced desalivate rat rapidly reduced its rising core temperature when the shower was made available 1 hour after exposure to 40°C (Fig. 2); thereafter it maintained itself at 39°C by taking approximately 15 ml of shower per hour. During the next test without shower the animal's core temperature rose uncontrolled in the heat and exceeded the lethal limit within 2 hours. This experiment was repeated with three other experienced desalivates; all did well when showering but became behaviorally incompetent within 2 hours when the shower was withdrawn. Clearly the shower is an effective substitute for spreading of saliva.

Drinking water was available during all these tests. Some animals did not drink while showering; others did, either from the reservoir or by consuming the shower water that condensed on the bar or the walls of the stall. Measured intakes varied widely (0.0 to 9.5 ml/1.5 hour), were inconsistent between animals, and were unrelated to increase in ambient temperature. Thirst and water reinforcement were therefore irrelevant to the behavior we discuss.

Thus rats acquire an operant with remarkable ease and effectiveness to provide themselves with exogenous water to effect loss of heat by surface evaporation. Typically they learn to take showers within 4 hours of exposure to moderate heat (36°C), and at higher temperatures they use the shower to reduce hyperthermia. Moreover, showering is an effective life-saving substitute for spreading of saliva in the desalivate rat, and it appears to be preferred by the intact rat that can either employ saliva in grooming or work for exogenous water. Our results, earlier studies (*3*) demonstrating that cold rats will work to obtain heat, and recent reports (*6*) of bar-pressing for cold air during exposure to heat emphasize the flexibility and physiological appropriateness of learned behavior for defense against extremes of ambient temperature.

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References and Notes

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Dorsal Root Potentials after C-Fiber Stimulation

Abstract. *A pure volley from C-fibers, set up by electrical stimulation of a cutaneous nerve and subsequent selective blocking of the A-fibers, generates in the cat spinal cord a dorsal root potential (C-DRP). Its polarity is the same as that of the dorsal root potential elicited by stimulation of the A-fibers (A-DRP), thus probably providing presynaptic inhibition of primary afferents. The size of the C-DRP increases in proportion to the size of the C-volley. A preceding A-DRP reduces the C-DRP.*

The myelinated cutaneous afferents exert onto each other strong presynaptic depolarizations which are probably paralleled by inhibitory actions (*1*). The spinal organization of the primary afferent depolarization (PAD) of mechanoreceptor afferents points to the functional significance of this inhibitory interaction (*2*). Afferent C-fibers take part in the nervous transformation of many kinds of peripheral stimuli. I have studied, therefore, whether these fibers also generate PAD's by testing whether a C-volley reaching the spinal cord