

Thermoregulatory Behavior in Infant Norway Rats (*Rattus norvegicus*) and Syrian Golden Hamsters (*Mesocricetus auratus*): Arousal, Orientation, and Locomotion

Greta Sokoloff, Mark S. Blumberg, Elizabeth A. Boline, Eric D. Johnson, and Necole M. Streeper
University of Iowa

The responses of 2- and 8-day-old rats (*Rattus norvegicus*) and hamsters (*Mesocricetus auratus*) to thermal stimulation were assessed in 4 experiments. In Experiment 1, the surface underlying the pup was cooled, and the latency to escape to a region of warmth was measured. Experiment 2 required pups to locomote farther to gain access to warmth. Experiment 3 was similar to Experiment 1 except the underlying surface was heated. Finally, in Experiment 4, locomotor behavior was assessed during isothermal cooling in which there was no possibility for escape. In general, hamsters exhibited more rapid and robust responses to thermal stimulation than rats. A framework for interpreting these results is presented emphasizing how differences in locomotor and thermogenic capabilities influence thermoregulatory behavior under different task conditions.

The thermoregulatory capabilities of infant mammals, especially altricial infants whose relatively limited ability to retain heat often compromises their ability to maintain thermal homeostasis, have been scrutinized for many decades (Blumberg, 2001; Brück & Hinckel, 1996; D. Hull, 1973; Leon, 1986; Satinoff, 1996). In general, investigators have focused primarily on behavioral capabilities or physiological capabilities, but rarely on both simultaneously. Because there are numerous ways in which behavioral and physiological capabilities can support and interfere with one another, it is important to understand the interrelations between these two dimensions of thermal homeostasis. As a first step toward this goal, the present study adopts a comparative approach to examine orientation and locomotor responses in the infants of two species that differ in their ability to produce heat endogenously.

Infant Syrian golden hamsters cannot produce heat endogenously until the end of the 2nd week postpartum (Blumberg, 1997; Hissa, 1968). These infants appear to compensate for this lack of endothermy with profound behavioral responses to thermal stimuli (Leonard, 1974, 1982). These behavioral responses have

been demonstrated repeatedly using a variety of tasks. For example, when placed on the cold end of a thermal gradient—an apparatus in which one end of a metal surface is heated and the other cooled, resulting in a continuous gradient of temperatures—infant hamsters, especially newborns, move rapidly toward the warm region of the gradient (Leonard, 1978).

In contrast to hamsters, infant Norway rats are capable of producing heat using brown adipose tissue (BAT) within a few hours after birth (Conklin & Heggeness, 1971; Spiers & Adair, 1986). Also in contrast to hamsters, infant rats perform poorly in many classic behavioral thermoregulation tasks (Fowler & Kellogg, 1975; Kleitman & Satinoff, 1982). For example, Kleitman and Satinoff (1982) showed that 1- to 6-day-old rats placed on the cold end of a thermal gradient required more than 60 min to move 3 cm. Interestingly, however, Shurtleff and Tobach (1979) demonstrated that infant rats are able to move rapidly off of a cold but small surface.

Although it is widely accepted that infant rats are behaviorally inferior to infant hamsters with regard to thermoregulation, no one has directly compared the two species using identical tasks and methods. In performing such a comparison between species, it is important to choose a task that can accurately and reliably reveal the orientation responses of infants without placing a disproportionate emphasis on locomotor performance; thermal gradients often require infants to locomote many inches or feet from a start location, a requirement that may obscure the abilities of these infants to orient toward a thermal stimulus. In addition, in comparing thermoregulatory behavior across species, it is important that all subjects begin the experiment at similar body temperatures, preferably at temperatures close to those found in the nest.

The goal of the present study was to examine the thermoregulatory behavior of infant rats and hamsters using procedures that would allow for an assessment of the behavioral rules that guide their behavior. For these experiments, 2- and 8-day-old subjects were tested from both species. These ages were chosen to allow for comparisons with previous experiments as well as to control for

Greta Sokoloff, Mark S. Blumberg, Elizabeth A. Boline, Eric D. Johnson, and Necole M. Streeper, Program in Behavioral and Cognitive Neuroscience, Department of Psychology, University of Iowa.

Greta Sokoloff is now at the Department of Psychology, Indiana University Bloomington.

This work was supported by National Institute of Mental Health Grant MH50701 to Mark S. Blumberg. We thank Lloyd Frei and Keith Miller of the Judson S. Brown Instrumentation Shop in the Department of Psychology at the University of Iowa for their critical contributions to the design and construction of the diode apparatus and its accompanying control system.

Correspondence concerning this article should be addressed to Mark S. Blumberg, Program in Behavioral and Cognitive Neuroscience, Department of Psychology, University of Iowa, Iowa City, Iowa 52242. E-mail: mark-blumberg@uiowa.edu

postnatal and postconception ages (because the gestation length of hamsters is 6 days shorter than that of rats, 2-day-old rats and 8-day-old hamsters are the same postconception age). To assess thermoregulatory behavior in these infants, we designed and built a novel apparatus that would obviate many of the technical and interpretational problems of past experiments. In addition, infrared thermography was used to measure skin temperatures continuously and noninvasively.

General Method: Experiments 1–3

Subjects

We used 2- and 8-day-old Sprague-Dawley rats (*Rattus norvegicus*; PD2 and PD8 rats; $N = 168$) from 52 litters and 2- and 8-day-old Syrian golden hamsters (*Mesocricetus auratus*; PD2 and PD8 hamsters; $N = 168$) from 52 litters. Equal numbers of males and females were used in each condition. When littermates were used, they were always tested at different ages or assigned to different experimental conditions. Table 1 presents the body weights for each of the groups of infants in the present experiments. Pups were born to females in the animal colony at the University of Iowa. Litters and mothers were housed in standard laboratory cages ($48 \times 20 \times 26$ cm) where food and water were available ad libitum. Litters were culled to 8 pups within 3 days after birth (day of birth = Day 0). Rats were maintained on a 12-hr light–dark cycle (lights on at 0630), and hamsters were maintained on a 14:10-hr light–dark cycle (lights on at 0600).

Test Environment

Individual pups were tested on an apparatus consisting of an array of Peltier diodes (International Thermoelectrics, Chelmsford, MA). Each diode was a 4.0×4.4 -cm ceramic tile, and the array was 10 tiles long and 6 tiles wide. The top of the apparatus was open to room air. Independent delivery of current to each diode was controlled using a custom-designed circuit board. The delivery of current from multiple power supplies was controlled using a computer with a 24-bit input–output board. A customized software program controlled the magnitude and polarity of current delivered to each diode so that the temperature of the surface of each diode could be accurately controlled.

Infrared (IR) Thermography

An IR camera (Thermovision 900, FLIR Systems, Portland, OR) with a 20° lens was used to measure the emission of IR radiation from the skin surface of the pups and the surface of each diode. Image acquisition was controlled by a computer system (Tracer Plus, FLIR Systems). The system

provided on-line image analysis or image storage to hard disk for off-line analysis. The IR camera was mounted directly above the diode apparatus.

To measure the skin temperature and diode surface temperature using IR thermography, it was first necessary to derive calibration equations for each surface based on the emissivity of infant skin and diode surface. (*Emissivity* is the ratio of the radiant energy emitted by a surface to the energy emitted at the same temperature by a black body radiator.) The process of deriving these calibration equations has been described in detail elsewhere (Sokoloff & Blumberg, 2001). Briefly, calibration equations were derived by comparing skin and diode temperatures, measured with the IR system across a range of temperatures, with the known temperature values provided by a reference thermocouple. Finally, these equations were used to correct IR temperature data and thereby provide accurate measures of absolute temperature.

Procedure

Littermates were removed from the nest by an experimenter wearing latex gloves (to minimize conductive cooling) and quickly placed on the surface of the diode apparatus. During the initial acclimation period, the surface temperature of the tiles was maintained at approximately 38 to 39 °C; at this temperature, pups exhibit dorsal skin temperatures that are similar to those measured in the nest. All subjects were placed on the tiles within a small polyethylene mesh ring scaled in weight to the size of the infant; the ring was sized so as to confine the pup within a 4-tile central region on the surface of the apparatus. The median percentage of the weight of the ring relative to infant body weight was 32.9% for PD2 rats, 31.0% for PD8 rats, 37.6% for PD2 hamsters, and 34.8% for PD8 hamsters. Because infant mammals prefer contact with edges (i.e., *thigmotaxis*), the ring was used to inhibit movements off of the central region before the test began; moreover, during the test, the ring provided sufficient resistance to dampen random movements and thereby increased the likelihood that the pups' movements were evoked by thermal stimulation.

For each set of littermates, the 1st infant was placed in the center of the tile surface, and the other infants were placed in the corners of the apparatus where they could stay warm but would not interfere with the testing of a pup. A heavy ring of PVC tubing was placed on the top of each polyethylene ring to prevent the pups from moving prematurely. The 1st pup tested from each litter (and therefore all subsequent littermates) was acclimated on the warm surface for at least 15 min. One minute before the end of the acclimation period and before a trial began, the PVC ring was removed. The test began with the acquisition of a baseline IR image, at which time the computer controlling current delivery to the diodes was used to alter the surface temperatures of the diodes according to a preestablished program. IR images were recorded automatically to hard disk once every 10 s throughout the test. In addition, pup behavior, as visualized by the IR system, was continuously recorded to videotape. Air temperature

Table 1
Age and Mean Body Weight (\pm SEM) for the Subjects in Experiments (Exp.) 1, 2, 3, and 4

Postnatal age (days)	Postconception age (days)	Body weight (g)			
		Exp. 1	Exp. 2	Exp. 3	Exp. 4
Rat					
2	24	7.8 \pm 0.1	7.8 \pm 0.2	6.6 \pm 0.1	7.7 \pm 0.2
8	30	17.6 \pm 0.4	17.9 \pm 0.7	18.5 \pm 0.5	18.9 \pm 0.4
Hamster					
2	18	3.7 \pm 0.1	3.9 \pm 0.1	3.4 \pm 0.1	3.7 \pm 0.1
8	24	9.7 \pm 0.2	9.4 \pm 0.1	9.8 \pm 0.1	10.6 \pm 0.2

was recorded by hand onto a data sheet at the beginning and end of the test. The pup was able to move along the surface of the apparatus by pushing the ring with its snout or other parts of its body. The test ended either when the pup escaped from the centrally cooled or heated area or after 10 min had elapsed. Escape latency was defined as the time elapsed from the beginning of the test until the pup had moved its entire body off of the central area.

Data Analysis

Skin temperatures from IR images were obtained by determining the temperature values coded by pixels in the interscapular (T_{is}) and back (T_{back}) regions of the pup. For all three experiments, the escape latency was measured for each subject in each condition. Data were analyzed using a three-factor (species, age, condition) analysis of variance (ANOVA). Post hoc tests were performed when significant effects and interactions were obtained. Alpha was set at $p < .05$. All data are presented as mean \pm SEM.

Experiment 1

The aim of Experiment 1 was to compare the thermoregulatory behavior of infant rats and hamsters using identical test conditions. For this experiment, PD2 and PD8 rats and hamsters were acclimated on a warm tile surface (Figure 1A). After acclimation, the temperature of the tile surface was decreased 0 °C, 2 °C, 4 °C, or 8 °C (Figure 1B). To escape the cooling surface, the infant pushed the polyethylene ring toward the surrounding region of warmth (Figure 1C). In this experiment, the warm region was immediately adjacent to the cooling region and could therefore be easily detected with only a small amount of movement.

Method

Subjects. We used 64 PD2 and PD8 rats from 16 litters and 64 PD2 and PD8 hamsters from 16 litters ($n = 8$ in each group).

Procedure. Four littermates with visible milk bands were removed from their home cage and placed on the surface of the diode apparatus. Each pup was assigned, using a balanced design, to one of four conditions, defined according to whether the surface temperature of the 4-tile start area was decreased by 0 °C, 2 °C, 4 °C, or 8 °C. After a 15-min acclimation period, a baseline IR image was acquired, followed immediately by the predetermined change in tile temperature. Testing continued for each pup until it successfully escaped from the 4-tile area or a period of 10 min elapsed. When a test ended, the pup was removed from the apparatus and weighed before being returned to its home cage. The surface of the diodes was cleaned with alcohol, and the central 4 tiles were reheated to 38–39

°C. The 2nd pup was then moved to the 4-tile start area in the center of the apparatus and given at least 5 min to acclimate. (More acclimation time was allowed if an infant was not behaviorally quiescent 5 min after being moved to the central region of the apparatus.) This process was repeated until all 4 littermates had been tested. The data for 1 PD8 rat and 1 PD8 hamster were excluded because the infants climbed over the polyethylene ring.

Results and Discussion

After acclimation but before the test began, T_{is} and T_{back} were higher for infant rats than for infant hamsters. Specifically, for infant rats, T_{is} and T_{back} were 36.9 ± 0.1 °C and 36.3 ± 0.1 °C, respectively, whereas for infant hamsters, T_{is} and T_{back} were 35.2 ± 0.2 °C and 34.9 ± 0.2 °C, respectively (there were no significant age differences within species for any body temperature measure). The higher skin temperature of the infant rats reflects their higher metabolic rates (Sokoloff & Blumberg, 1998).

Figure 2 presents mean escape latency for each of the groups of infants in all four conditions. For all infants, as the magnitude of the cooling of the 4-tile area increased, the latency to escape the central 4-tile region decreased, $F(3, 110) = 43.2$, $p < .0001$. Specifically, infants exhibited shorter escape latencies in the 8 °C condition than in the 2 °C condition ($ps < .05$). Escape latency differed between rats and hamsters, $F(1, 110) = 71.0$, $p < .0001$, with infant hamsters escaping faster than rats. Even in the 2 °C condition, infant hamsters showed significantly shorter escape latencies than all other infants ($ps < .05$). In the 4 °C condition, PD8 hamsters showed shorter escape latencies than all other infants ($ps < .005$), and PD2 hamsters showed shorter escape latencies than both PD2 and PD8 rats ($ps < .005$).

Consistent with previous research (Kleitman & Satinoff, 1982; Leonard, 1974), these results indicate that infant hamsters can escape from a region of cold more quickly than infant rats. There are a number of ways, however, in which these results differ from those of previous investigators. For example, in her study of thermoregulatory behavior in infant hamsters, Leonard (1974) reported a weakening of thermotaxic responses beginning at 8 days of age; contrary to this finding, however, PD8 hamsters were as fast as or faster than PD2 hamsters in each of the three cooling conditions. Furthermore, although Kleitman and Satinoff (1982) found that PD2 rats were virtually immobile when placed on the

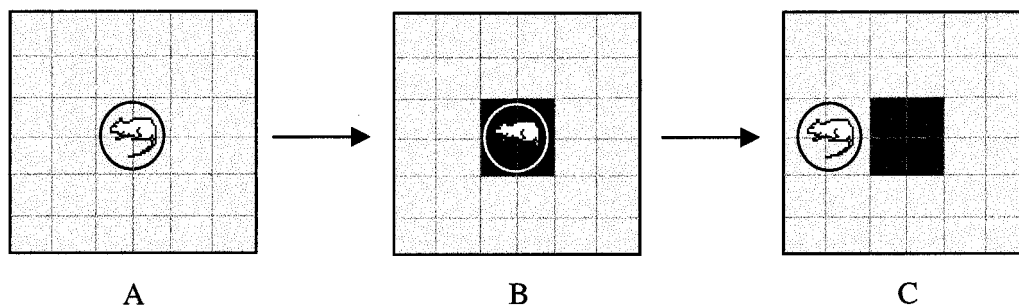


Figure 1. The experimental paradigm used in Experiment 1. The test started after an infant rat or hamster acclimated on the warm surface of the tiles (A). After the acclimation period, the temperature of the 4-tile start area was decreased by 0 °C, 2 °C, 4 °C, or 8 °C (B). The rat or hamster was observed until it escaped the start area (C) or until a period of 10 min had elapsed.

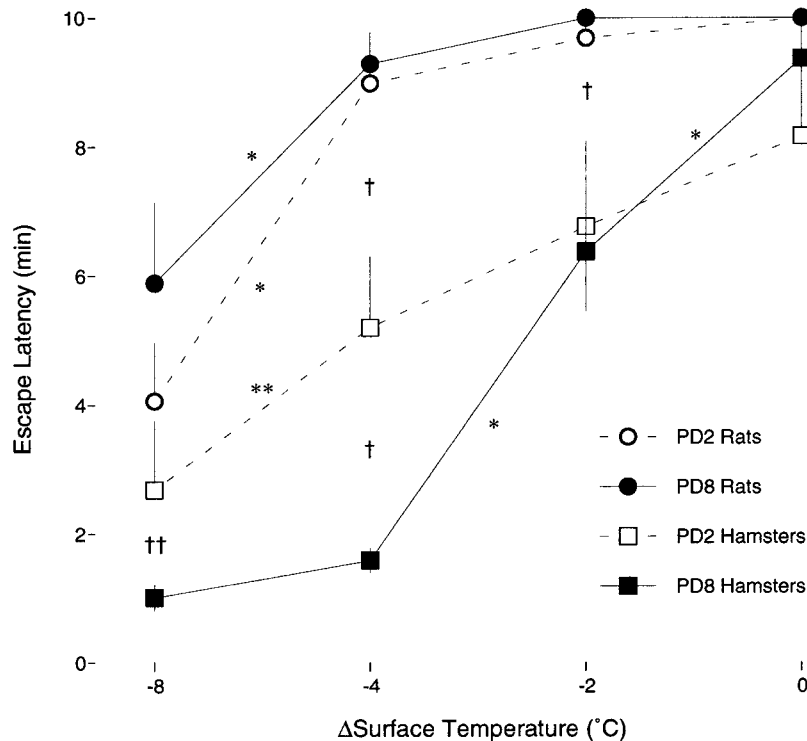


Figure 2. Mean (\pm SEM) escape latency for infants in the four cooling conditions in Experiment 1. Although escape latency decreased with cooling for both infant rats and hamsters, infant hamsters showed significantly shorter escape latencies than infant rats in all conditions. Postnatal Day 8 (PD8) hamsters consistently showed the shortest escape latencies. * = significantly different from adjacent points; ** = significantly different from 0 °C and -2 °C conditions only; † = significant difference between rats and hamsters on both sides of the symbol; †† = significantly different from Postnatal Day 2 (PD2) and PD8 rats.

cold end of a thermal gradient, the latencies found here indicate that these infants, although slower than infant hamsters, are capable of escaping from the cold in less than 10 min. Similarly, Fowler and Kellogg (1975) found that rat pups younger than 5 days of age were unable to move toward a warm compartment. These differences between the present and previous results highlight the sensitivity of thermoregulatory behavior to the demands of the task. For example, the immobility of newborn rats reported by Kleitman and Satinoff may have resulted from rapid bodily cooling at the beginning of the experiment coupled with the use of an apparatus in which the thermal gradient was too shallow to provide sufficient thermal orientation cues.

Experiment 2

In Experiment 1, any movement by the infant was sufficient to provide access to the warm surrounding region. Therefore, that experiment cannot be used to distinguish between directed and undirected movements, or *taxes* and *kineses*, respectively (Fraenkel & Gunn, 1940/1961). Thermal gradient alleyways and many other tasks that have been used previously are also of limited utility for distinguishing taxes from kineses (nonetheless, it has become commonplace to refer to infant thermoregulatory behavior as *thermotaxis*). Drawing this distinction between taxes and kineses requires that the infants be tested under conditions in which the

thermal cues to warmth are not adjacent to the animal's starting location, thereby providing an opportunity to assess the dependence of the animal on proximal thermal cues as a guide to behavior. Therefore, in the present experiment, infants were again acclimated on a warm tile surface (Figure 3A and 3C), at which time they experienced 8 °C cooling of a 4-tile region (Figure 3B) or a 16-tile region (Figure 3D). If an infant relies on proximal thermal cues for orientation and locomotion toward warmth, then the absence of such cues should slow or prevent the infant's escape from the central 4 tiles in the 16-tile condition.

Method

Subjects. We used 40 PD2 and PD8 rats from 20 litters and 40 PD2 and PD8 hamsters from 20 litters ($n = 10$ in each group).

Procedure. Two littermates with visible milk bands were removed from their home cage and placed on the surface of the diode apparatus. Each pup was assigned to one of two conditions, defined according to whether an 8 °C decrease in surface temperature was isolated to the 4-tile start area (4-tile condition) or to a 16-tile area that included the start area (16-tile condition); the order of testing was counterbalanced. As in Experiment 1, after a 15-min acclimation period, a baseline IR image was acquired, followed immediately by the change in tile temperature. Testing continued for each pup for a period of 10 min. When the test ended, the pup was removed from the apparatus and weighed before being returned to its home cage. The surface of the diodes was cleaned with alcohol, and the

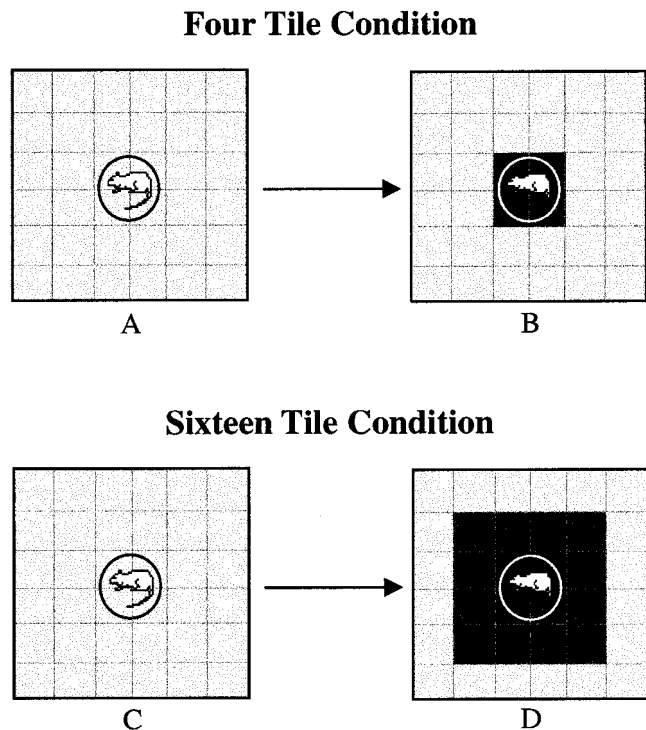


Figure 3. The experimental paradigm used in Experiment 2. In the 4-tile condition, after infants acclimated on the warm diode surface (A), the temperature of the 4-tile start area was decreased by 8 °C (B). In the 16-tile condition, after acclimation (C), the temperature of 16 tiles, including the start area, was decreased by 8 °C (D). Each infant was allowed 10 min to escape the cold surface.

temperature of the 4 or 16 tiles was reheated to 38–39 °C. The 2nd pup was then moved to the 4-tile start area in the center of the apparatus and given at least 5 min to acclimate. (More acclimation time was allowed if an infant was not behaviorally quiescent 5 min after being moved to the central region of the apparatus.) Five PD8 hamsters climbed up and over the ring; in these instances, littermates were used in their place.

Results and Discussion

After acclimation but before the test began, T_{is} and T_{back} for the infant rats were 36.8 ± 0.2 °C and 36.1 ± 0.2 °C, respectively, and, for the infant hamsters, these values were 35.3 ± 0.2 °C and 35.1 ± 0.2 °C, respectively. These values are similar to those in Experiment 1.

Figure 4 presents the mean escape latency for the subjects in the 4-tile and 16-tile conditions. There were significant effects of both species and condition, $F(1, 72) > 32.6$, $ps < .0001$, with hamsters escaping to warmth more quickly than rats, regardless of condition. In addition to showing the escape latencies to warmth, Figure 4 shows the latencies to escape the central 4 tiles in the two experimental conditions. Recall that in the 4-tile condition, escaping the central 4 tiles is equivalent to gaining access to warmth, but in the 16-tile condition, moving off of the central 4 tiles does not improve the infant's thermal situation (see Figure 3). It can be seen that PD2 hamsters escaped from the central 4 tiles with the same latency regardless of condition (and, indeed, also escaped the

16-tile area with nearly the same latency). In contrast, PD8 hamsters required significantly more time to escape the central 4 tiles, as did the rats at both ages ($ps < .05$).

The increased latency to escape the central 4 tiles in the 16-tile condition may reflect a reliance in the PD2 rats and PD8 rats and hamsters on proximal thermal cues for movement away from the central 4 tiles. In other words, these infants may have been moving toward warmth as much as they were moving away from cold. This is most clear for the infant rats who, in the 16-tile condition, were virtually fixed within the central 4 tiles. In contrast, the PD2 hamsters were unaffected by the differing thermal cues in the two conditions, perhaps reflecting their heightened sensitivity to the 8 °C temperature decrease used here.

It is important to acknowledge the role that different locomotor patterns could have played in shaping some of these results, especially those concerning the different abilities of PD2 and PD8 hamsters to escape the 16-tile area despite the clear arousal produced at both ages by the cooling of the surface. Specifically, whereas PD2 hamsters locomote using a distinctive creeping motion in which all four limbs move synchronously and the infant moves in a linear trajectory, PD8 hamsters no longer creep and, instead, exhibit a locomotor pattern more similar to infant rats; this latter pattern, called *punting*, is characterized by a circular pattern of motion that is generated by the forelimbs using the hind limbs as a pivot. Thus, it is possible that the PD2 and PD8 hamsters were similarly aroused by cooling, but the linear, creeping locomotor behavior of the PD2 hamsters was more effective for escaping the cold under these experimental conditions. On the other hand, differences in locomotor behavior appear less able to explain the increased time required by the PD8 hamsters to escape from the 4-tile region in the 16-tile condition.

Experiment 3

Warm and cold stimuli are not equivalent in their effects on infant behavior and development. In general, it is assumed that the maintenance of a warm developmental environment is essential for rapid, normal growth, a view that is based in part on the assumption that avoiding cold prevents the diversion of limited energy resources away from growth and toward heat production (Leon, 1986; Satinoff, 1996). In support of this view, warm stimuli are generally attractive to young animals and can be effective reinforcers (Alberts & May, 1984; Blumberg & Sokoloff, 1998; Flory, Langley, Pfister, & Alberts, 1997; Johanson & Hall, 1980; Wasserman, 1973). On the basis of these observations, it is not surprising that previous work with infant rats and hamsters has shown that these infants do not respond symmetrically to hot and cold stimuli (Kleitman & Satinoff, 1982; Leonard, 1974). Therefore, in the present experiment, we observed infant behavior in response to the heating of the 4-tile start area to assess differences in responses to hot thermal stimuli and to compare them to the results from Experiment 1.

Method

Subjects. We used 64 PD2 and PD8 rats from 16 litters and 64 PD2 and PD8 hamsters from 16 litters ($n = 8$ in each group).

Procedure. Four littermates with visible milk bands were removed from their home cage and placed on the surface of the diode apparatus. Each pup was assigned, using a balanced design, to one of four conditions,

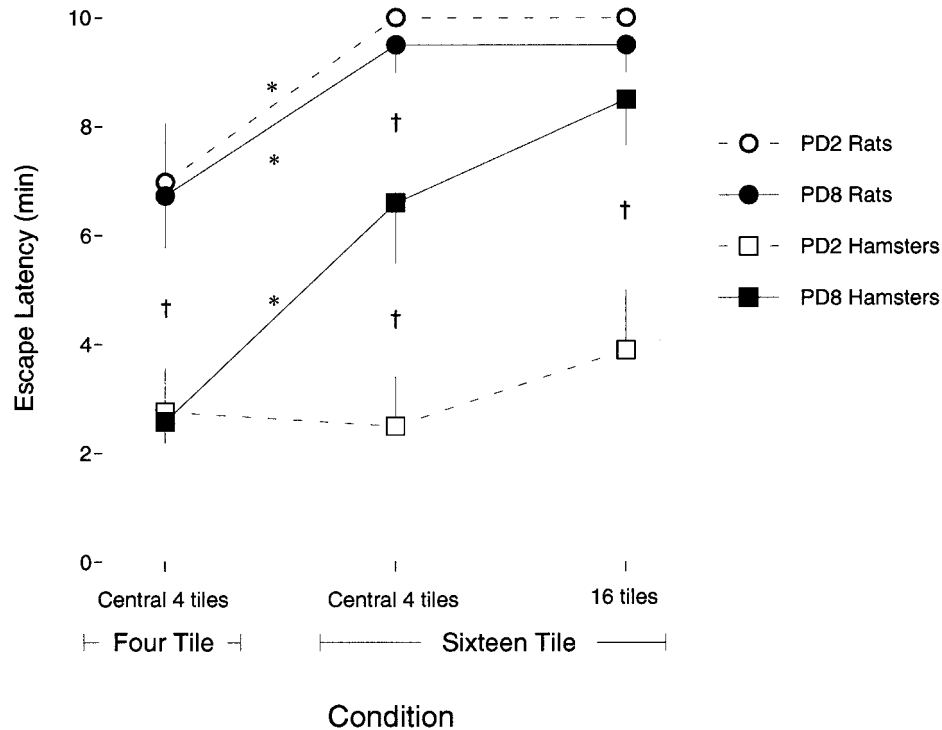


Figure 4. Mean (\pm SEM) escape latency for infants in Experiment 2. There was no difference in escape latency for Postnatal Day 2 (PD2) hamsters in the 4- and 16-tile conditions. In contrast, infant rats and Postnatal Day 8 (PD8) hamsters required more time to escape the central 4 tiles, suggesting that these infants used proximal thermal cues to escape from the cold surface. * = significant difference between adjacent points; † = significant difference between rats and hamsters on both sides of the symbol.

defined according to whether the surface temperature of the 4-tile start area was increased by 0 °C, 4 °C, 8 °C, or 12 °C. As in Experiment 1, after a 15-min acclimation period, a baseline IR image was acquired, followed immediately by a predetermined change in surface temperature. Testing continued for each pup until it successfully escaped from the 4-tile area or a period of 10 min elapsed. When a test ended, the pup was removed from the apparatus and weighed before being returned to its home cage. The surface of the diodes was cleaned with alcohol, and the temperature of the central 4 tiles was returned to 38–39 °C. The 2nd pup was then moved to the 4-tile start area in the center of the apparatus and given at least 5 min to acclimate. (More acclimation time was allowed if an infant was not behaviorally quiescent 5 min after being moved to the central region of the apparatus.) This process was repeated until all 4 pups had been tested. The data for 2 PD8 rats were excluded because the infants climbed up on the ring. The data for 1 PD2 and 1 PD8 hamster were excluded because of experimenter error.

Results and Discussion

After acclimation, T_{is} and T_{back} for the infant rats were 35.5 ± 0.2 °C and 35.0 ± 0.2 °C, respectively, and for the infant hamsters these values were 33.8 ± 0.2 °C and 33.9 ± 0.2 °C, respectively. As in Experiments 1 and 2, skin temperatures of the infant rats were higher than the skin temperatures of the infant hamsters. The temperatures of all pups in this experiment were approximately 1 to 1.5 °C lower than in the two previous experiments, however, which was due in part to lower room temperatures as well as to lower baseline diode surface temperatures.

Figure 5 presents mean escape latency for each of the groups of infants in all four conditions. There was a significant effect of condition, $F(3, 108) = 31.1$, $p < .0001$, and a significant interaction between condition, species, and age, $F(3, 108) = 5.4$, $p < .05$. Infant rats, and especially the PD8 hamsters, showed shorter escape latencies in the 12 °C condition ($ps < .01$). In contrast, the mean escape latency of PD2 hamsters did not change over the four temperature conditions.

Figure 6 combines the mean escape latency data from the present experiment with those of Experiment 1. The top row of plots shows the mean escape latency for infant rats. There is little difference between heating and cooling for either the 0 °C or the 4 °C conditions, whereas for the 8 °C condition, escape latency was much shorter when the tiles were cooled. When the temperature of the tiles was increased by 12 °C, PD8 rats escaped with a similar latency as those that were on tiles that were cooled by 8 °C. The bottom row of plots shows the mean escape latency for infant hamsters. For both the 4 °C and 8 °C conditions, cooling of the tiles had a substantially greater effect on escape latency than did heating. In addition, as stated above, increasing the temperature of the tiles by 12 °C was insufficient to affect the behavior of PD2 hamsters.

These results seem to reinforce the notion that infants respond asymmetrically to heating and cooling, perhaps reflecting the higher prevalence of cold challenge during early development. It should be stressed, however, that there are asymmetries inherent in

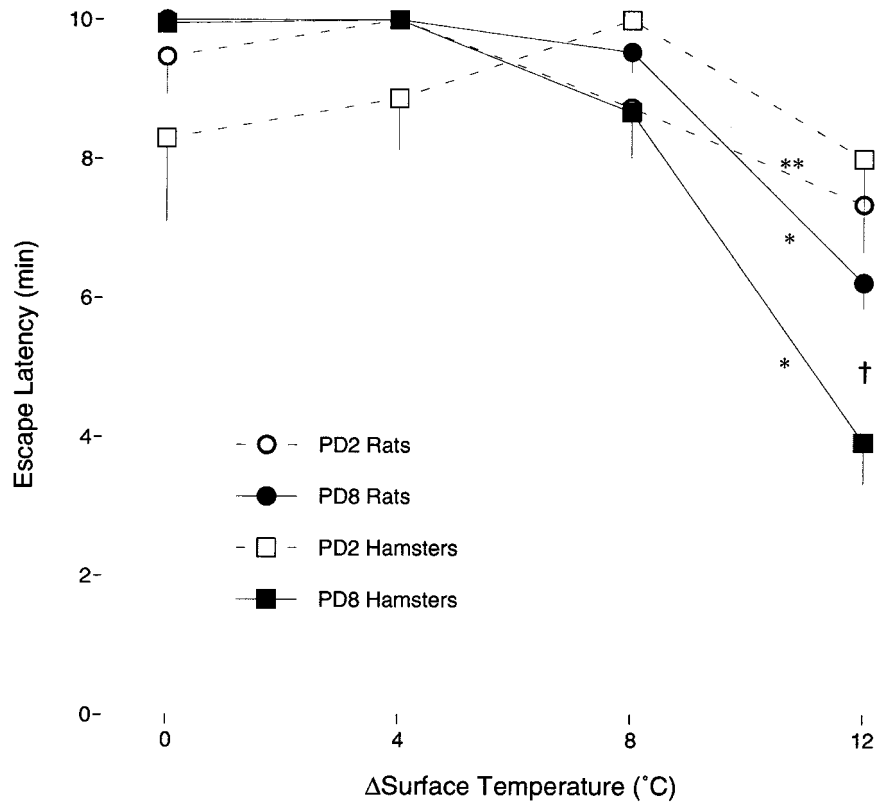


Figure 5. Mean (\pm SEM) escape latency for infants in the four heating conditions in Experiment 3. Escape latency decreased significantly only in the 12 °C condition. Once again, Postnatal Day 8 (PD8) hamsters consistently showed the shortest escape latencies, whereas Postnatal Day 2 (PD2) hamsters showed no change in escape latency for any of the four conditions. * = significantly different from all other conditions; ** = significantly different from 0 °C and 4 °C conditions only; † = significant difference between rats and hamsters on both sides of the symbol.

the design of this experiment that may have influenced these results. Specifically, because the air temperature in the room was approximately 24 °C, the cooling protocol brings the diode surface temperature closer to room temperature, whereas the heating protocol moves the diode surface temperature away from room temperature. Therefore, for us to more accurately assess the symmetry in infants' responding to heat and cold, pups should be acclimated to an air temperature and diode surface temperature of approximately 37 °C, and the diode surface temperature should then be increased or decreased in equal increments. Nonetheless, it is noteworthy that infants from both species, regardless of body size, insulation, and endothermic capabilities, exhibited negligible responses to heating relative to their responses to cooling.

Experiment 4

In Experiments 1–3, escape latency was used to assess the behavioral capabilities of infants during thermal stimulation. Escape latency is a composite measure that is influenced by the infant's ability to become aroused, orient toward a target stimulus, and locomote toward that stimulus. In some cases, it is not clear whether orientation is involved. It is also not clear how the motor activity of infants changes during a cooling episode. Therefore, to

simplify our task of understanding the behavioral differences between our subjects during thermal stimulation, infant rats and hamsters were tested on a 16.0- × 17.6-cm surface in which the entire floor was cooled simultaneously and thermal cues to warmth were not provided. The aim of using this isothermal cooling procedure was to assess the most fundamental locomotor behaviors of infant rats and hamsters so as to gain insight into their behavioral capabilities in more complex thermal environments.

Method

Subjects. We used 48 PD2 and PD8 rats from 33 litters and 48 PD2 and PD8 hamsters from 21 litters ($n = 24$ in each group). Equal numbers of males and females were used in each condition. When littermates were used, they were always tested at different ages or assigned to different experimental conditions. Table 1 presents the body weights for each of the groups of infants in this experiment. All subjects were housed and raised as in Experiments 1 through 3.

Procedure. A pup with a visible milk band was removed from its home cage, weighed, and placed on the diode surface. (Unlike the previous three experiments, at no time were polyethylene rings used to constrain the pups' behavior.) During acclimation and testing, each pup was confined to a 16-tile area (16.0 × 17.6 cm) inside a black Plexiglas box. In addition to the IR camera, a microcamera was positioned above the diode apparatus for

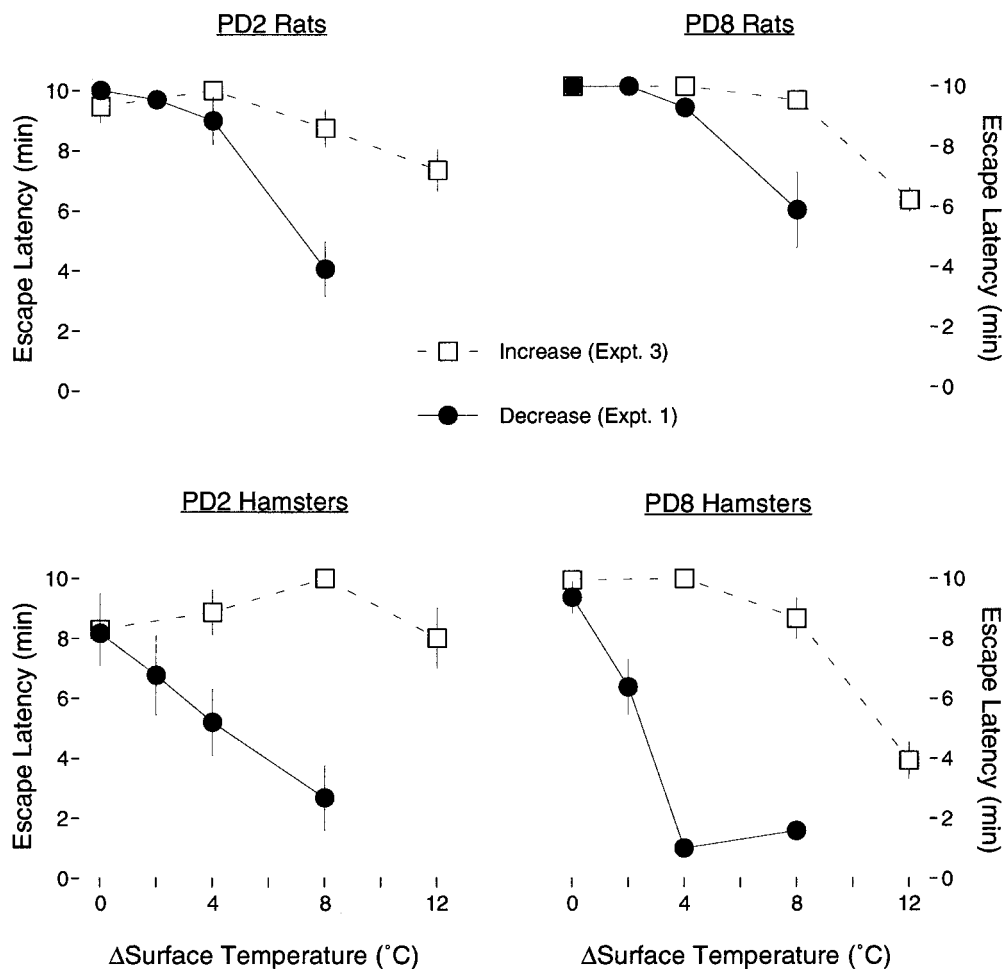


Figure 6. Mean (\pm SEM) escape latency for infants in the cooling and heating conditions in Experiments 1 and 3, respectively. For all infants, increases in the surface temperature resulted in substantially longer escape latencies than decreases in the surface temperature. PD2 = Postnatal Day 2; PD8 = Postnatal Day 8; Expt. = experiment.

recording of infant behavior to videotape. During a 45-min acclimation period, the diode surface temperature was maintained at approximately 38 to 39 $^{\circ}$ C.

Pups were assigned, using a balanced design, to one of three conditions. In the first condition (0 $^{\circ}$ C), the temperature of the diodes remained unchanged at the acclimation temperature for the entire 120-min test. In the second condition (4 $^{\circ}$ C), the temperature of all 16 diodes was decreased by 4 $^{\circ}$ C at 0, 30, 60, and 90 min of the test, resulting in a total temperature decrease of 16 $^{\circ}$ C during the 120-min test. In the third condition (8 $^{\circ}$ C), the temperature of all 16 diodes was decreased by 8 $^{\circ}$ C at 0 and 60 min of the test, also resulting in a total decrease of 16 $^{\circ}$ C during the 120-min test. IR images were stored to disk every minute throughout the test. The diode surface was cleaned with a mild bleach and water solution between each testing session to remove any odor cues. After the testing period was completed, the pup was returned to its home cage.

Data analysis. Behavioral data were analyzed from videotape using an automated video-tracking system (EthoVision, Noldus, Sterling, VA). Using this system, it was possible to track the location of the pup continuously within the testing area. Once a pup's behavior was tracked and recorded to disk, the software was used to calculate the absolute distance traveled by the pup during each 15-min interval. These data were analyzed using a

three-factor (species, age, condition) repeated measures ANOVA. Post hoc tests were performed when significant main effects and interactions were obtained.

As described for Experiments 1 through 3, skin temperatures from IR images were obtained by determining the temperature values coded by pixels in the interscapular and back regions of the pup. For pups at each age and species, mean changes in T_{back} (ΔT_{back}) for each 5-min interval were regressed against mean distance traveled over the same 5-min interval to assess the relationship between cooling rates and locomotor behavior.

For all tests, alpha was set at $p < .05$. All data are presented as mean \pm SEM.

Results and Discussion

Table 2 presents, for all groups of infants, T_{back} at 0, 60, and 120 min of the test and $T_{\text{is}} - T_{\text{back}}$ at 120 min. As in the previous experiments, infant rats exhibited higher values of T_{back} than infant hamsters. Consistent with higher values of T_{back} , infant rats in the 4 $^{\circ}$ C and 8 $^{\circ}$ C conditions also showed larger values of $T_{\text{is}} - T_{\text{back}}$ ($p < .005$), indicative of BAT thermogenesis (Blumberg &

Table 2

T_{back} at Min 0, 60, and 120 and $T_{is} - T_{back}$ at Min 120 in the 0 °C, 4 °C, and 8 °C Conditions in Experiment 4

Species and age	T_{back}			$T_{is} - T_{back}$
	0 min	60 min	120 min	120 min
0 °C				
Rat				
PD2	36.5 ± 0.4	36.8 ± 0.4	37.1 ± 0.4	0.4 ± 0.2
PD8	35.8 ± 0.2	36.0 ± 0.3	36.4 ± 0.3	0.4 ± 0.2
Hamster				
PD2	34.8 ± 0.4	35.2 ± 0.4	35.4 ± 0.6	0.2 ± 0.1
PD8	34.7 ± 0.4	35.1 ± 0.4	35.1 ± 0.5	0.4 ± 0.1
4 °C				
Rat				
PD2	36.2 ± 0.4	30.2 ± 0.5	23.8 ± 0.7	1.4 ± 0.2
PD8	36.0 ± 0.5	31.8 ± 0.7	26.2 ± 1.0	1.7 ± 0.3
Hamster				
PD2	34.9 ± 0.6	28.2 ± 0.7	22.2 ± 0.8	0.1 ± 0.1
PD8	34.8 ± 0.2	29.5 ± 0.2	23.2 ± 0.1	0.2 ± 0.1
8 °C				
Rat				
PD2	36.6 ± 0.4	31.2 ± 0.5	24.5 ± 0.6	1.4 ± 0.2
PD8	36.2 ± 0.5	32.3 ± 0.8	27.0 ± 1.4	1.9 ± 0.1
Hamster				
PD2	35.1 ± 0.4	28.7 ± 0.3	23.5 ± 0.5	0.0 ± 0.0
PD8	34.6 ± 0.4	29.2 ± 0.4	23.3 ± 0.8	0.1 ± 0.0

Note. T_{is} = temperature values ($M \pm SEM$) coded by pixels in the interscapular region of the pup; T_{back} = temperature values ($M \pm SEM$) coded by pixels in the back region of the pup; PD = postnatal day.

Stolba, 1996). Finally, PD8 rats exhibited significantly higher values of T_{back} and $T_{is} - T_{back}$ than all other infants at the 120-min time point in both the 4 °C and 8 °C conditions ($ps < .05$).

Figure 7 presents the total distance traveled over the surface of the apparatus for each 15-min period of the test in the 0 °C, 4 °C, and 8 °C conditions. In general, overall distance traveled increased as the magnitude of the change in surface temperature increased, $F(2, 82) = 17.1, p < .0001$. Furthermore, for the conditions in which the surface temperature of the apparatus decreased (i.e., the 4 °C and 8 °C conditions), the distance traveled varied with time over the 120-min test period, $F(14, 574) = 1.8, p < .05$. Specifically, with the exception of the PD2 rats, the activity of the infants increased significantly within those 15-min periods when surface temperature was decreasing ($ps < .05$).

During the first two cooling episodes in the 4 °C condition, PD8 hamsters traveled farther on the surface of the apparatus than all other infants ($ps < .05$). By the third cooling episode, PD2 hamsters had increased their activity so that hamsters of both ages were traveling farther than the infant rats ($ps < .05$). These results are consistent with the results found in Experiment 1, where PD8 hamsters showed the shortest escape latencies to changes in surface temperature, whereas PD2 hamsters, although faster than infant rats, did not match the speed of the PD8 hamsters until the surface temperature was decreased by 8 °C. This increase in motor activity shown by the PD2 hamsters is striking given the fact that

they are moving more as their body temperature decreases substantially during the test (see Table 2).

During the first episode of cooling in the 8 °C condition, PD8 hamsters traveled farther on the surface of the apparatus than all other infants ($ps < .005$), and PD2 hamsters traveled farther than PD2 rats ($p < .05$; the difference between PD8 and PD2 rats was nearly significant, $p = .05$). During the second episode of cooling, however, PD2 and PD8 hamsters and PD8 rats did not differ in their motor activity, and all traveled farther than PD2 rats ($ps < .05$). Interestingly, the second episode of cooling in this condition resulted in a large increase in activity by PD8 rats, indicating that these infants can respond quickly and robustly when the thermal stimulation is sufficiently strong.

Finally, Figure 8 shows the relationship between the distance traveled and ΔT_{back} for each 5-min period throughout the 120-min test. ΔT_{back} accounted for 46% and 74% of the variance in distance traveled for PD2 and PD8 hamsters, respectively (right-hand plots). In contrast, ΔT_{back} accounted for much less of the variance in distance traveled for infant rats (left-hand plots). The results of the present experiment combined with the results of the previous experiments suggest that infant hamsters are much more sensitive to thermal stimulation than infant rats. This finding implies a relationship between locomotor activation during thermal stimulation and rapid and successful thermoregulatory behavior.

General Discussion

The ability of infants to navigate novel environments and locate regions of warmth has been investigated in a variety of species, including rats, mice, gerbils, hamsters, kittens, and rabbits (Eedy & Ogilvie, 1970; Fowler & Kellogg, 1975; Freeman & Rosenblatt, 1978; J. Hull & Hull, 1982; Johanson, 1979; Kleitman & Satinoff, 1982; Leonard, 1974; Ogilvie & Stinson, 1966). These studies have played a valuable role in highlighting the importance of behavioral thermoregulation to altricial infants for the maintenance of a warm microenvironment and, in turn, to the promotion of normal growth and development. On the other hand, it is still unclear what the sensory mechanisms and behavioral rules are that underlie these thermoregulatory adjustments to thermal stimuli and how these mechanisms and rules differ across species and change during development. Significantly, comparisons between species and across ages have often been made without sufficient regard to methodological issues that can influence the interpretation of results.

Under the testing conditions used in Experiment 1, both infant rats and hamsters were capable of escaping from a rapidly cooling region, with hamsters escaping more quickly than rats. We did not see evidence of a diminished capacity for behavioral thermoregulation in PD8 hamsters or a nearly nonexistent capacity in PD2 rats as suggested by other investigators using different methods (Fowler & Kellogg, 1975; Kleitman & Satinoff, 1982; Leonard, 1974). Experiment 2 was designed to assess the thermal information required to evoke the escape responses by manipulating the availability of proximal thermal cues. Whereas PD2 rats and PD8 rats and hamsters were affected by the loss of these proximal cues, PD2 hamsters were not, a result that highlights the heightened thermal sensitivity and surprising locomotor capabilities of newborn hamsters.

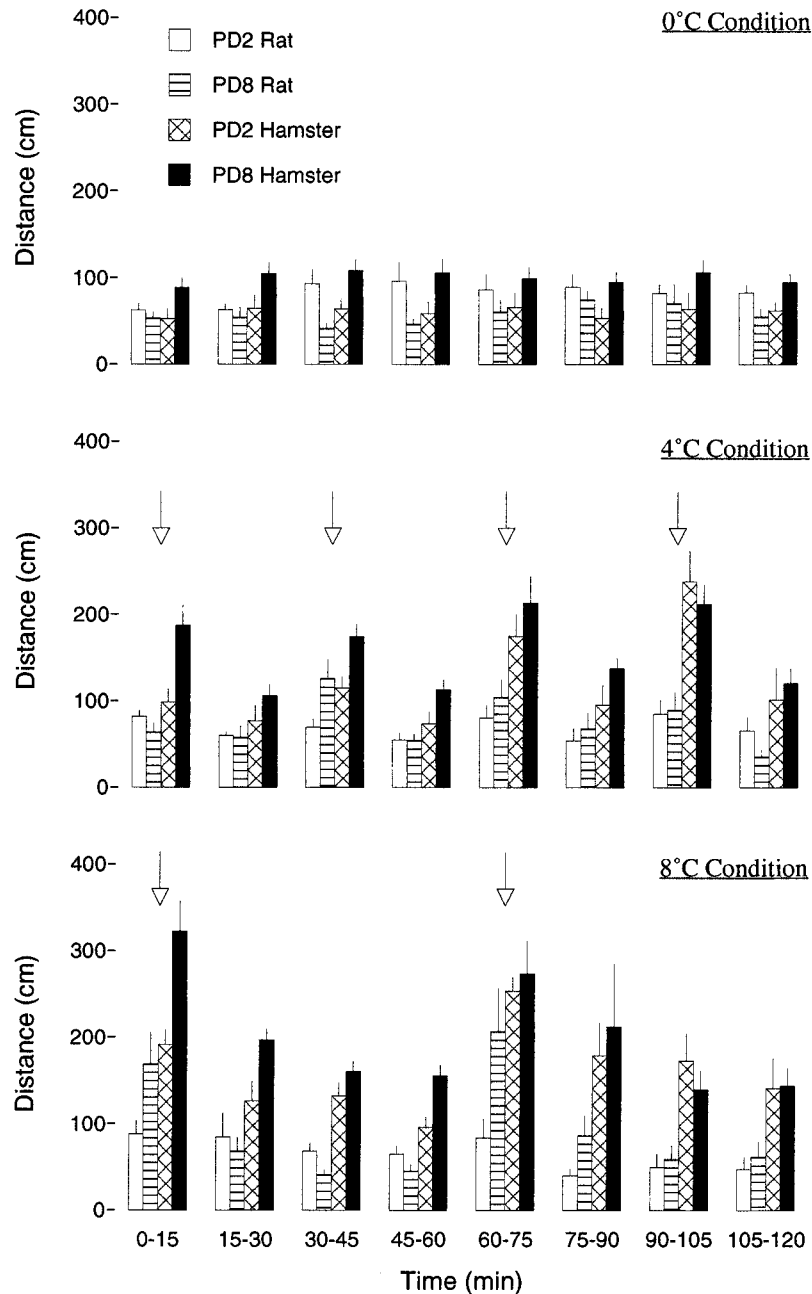


Figure 7. Mean cumulative distance traveled for each 15-min period for infants in the three experimental conditions in Experiment 4. Arrows indicate that diode surface temperature was decreased at Min 0, 30, 60, and 90 in the 4 °C condition and at Min 0 and 60 in the 8 °C condition.

Experiment 3 examined the ability of heating, rather than cooling, to evoke escape behavior. The results indicate a profound asymmetry in responding to heat and cold, although, as discussed earlier, this asymmetry may be due in part to methodological asymmetries. Nonetheless, the differences, especially for the newborn rats and hamsters, are striking, and these results are consistent with Kleitman and Satinoff's (1982) and Leonard's (1974) findings that newborns are limited in their ability to move away from heat.

Finally, Experiment 4 was designed to assess the locomotor underpinnings of thermoregulatory behavior in infant rats and hamsters. Once again, infant hamsters were generally more activated by cooling than infant rats and, in contrast to Leonard's (1974) observations, PD8 hamsters were the most active during cooling. These results help to explain why infant hamsters were better able to escape the cold in Experiments 1 and 2: Their sensitivity to cooling evokes increased locomotion that can bring them into contact with thermal cues to which they can orient and approach.

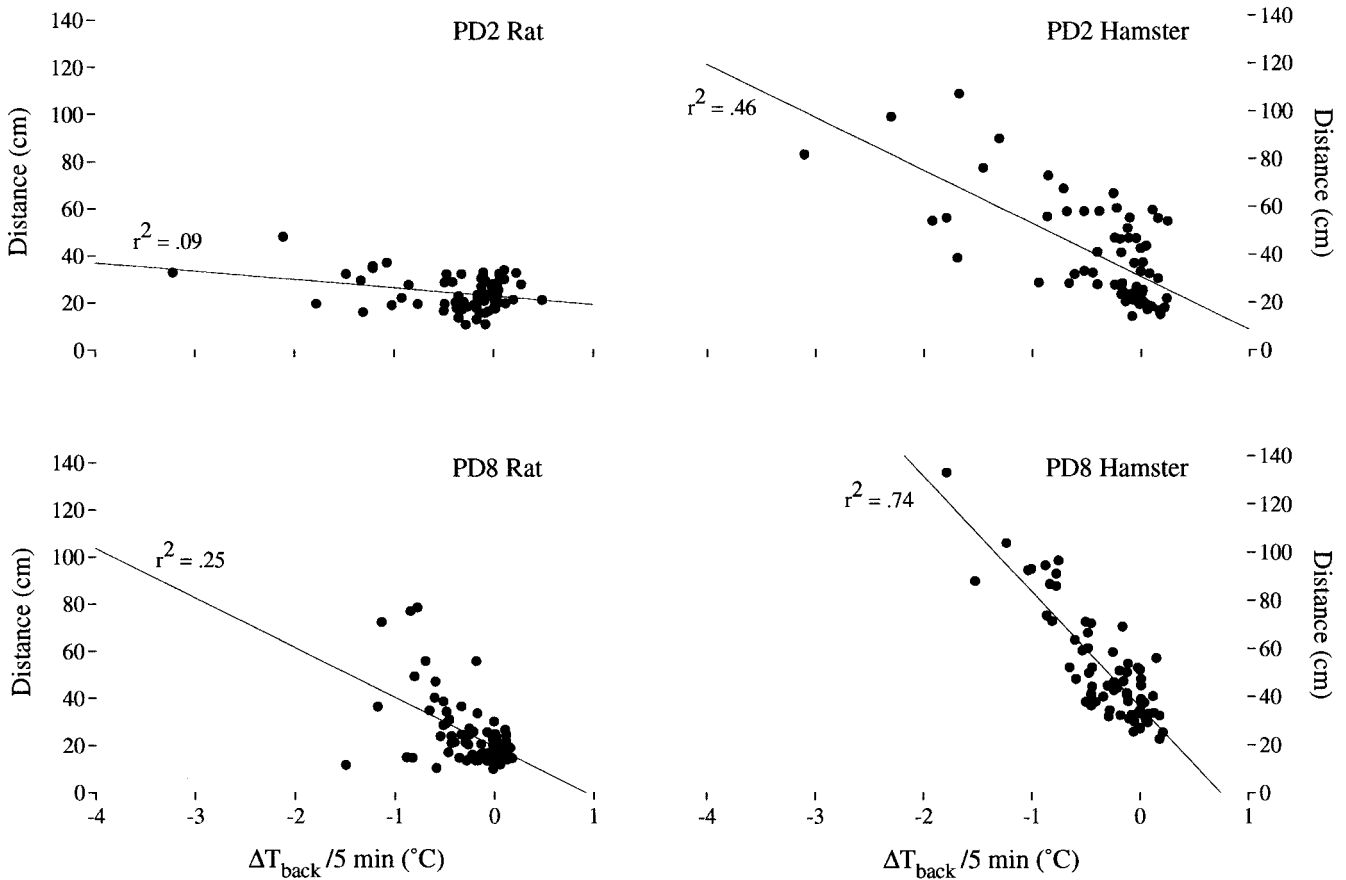


Figure 8. Mean distance traveled versus mean change in back temperature (ΔT_{back}) for each 5-min period for infants in Experiment 4. Plots are depicted separately for each age and species. PD2 = Postnatal Day 2; PD8 = Postnatal Day 8.

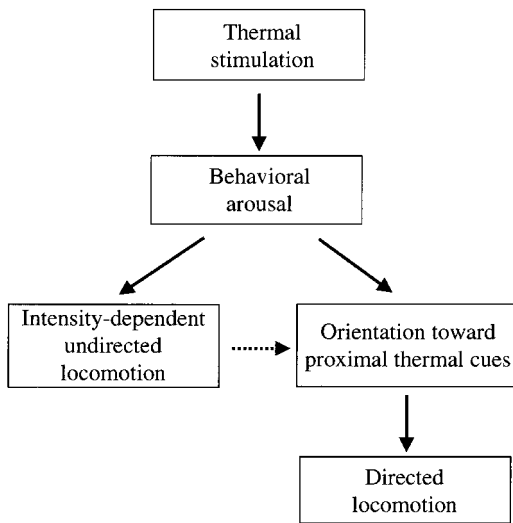


Figure 9. Flow chart depicting a working hypothesis for the cascade of processes involved in infant thermoregulatory behavior.

Figure 9 presents a working hypothesis of the processes that may lead to successful thermoregulatory behavior in infants. First, thermal stimulation must be sufficient to produce behavioral arousal. Once aroused, the infant can respond by exhibiting undirected motor behavior or by orienting to proximal thermal cues in the environment (if they are available); in turn, behavioral orientation provides the foundation for directed movement. When proximal thermal cues are unavailable, undirected movements can serendipitously bring the infant into contact with proximal thermal cues, which can then evoke orientation and directed locomotion. Thus, according to this perspective, undirected and directed motor responses can both contribute to thermoregulatory behavior depending on the magnitude of the thermal stimulation and the behavioral task that confronts the infant.

The endothermy of infant rats and the lack of endothermy in infant hamsters provide a useful basis for comparing the role of endothermy in the modulation of a variety of physiological and behavioral responses to cold (Blumberg & Sokoloff, 1998; Sokoloff & Blumberg, 1998; Sokoloff, Blumberg, & Adams, 2000). The present findings provide further support for the view that the presence or absence of endothermy is a fundamental, defining feature of altricial infants. Endothermic infants, such as rats, invest energy in heat production during cold exposure, and it may be energetically advantageous to minimize movement so as to

permit centralization of blood and heat within the thoracic cavity; locomotion necessarily entails increased blood flow to the limbs and, consequently, increased heat loss. In contrast, nonendothermic infants, such as hamsters, have little to lose by increasing locomotion in the cold. Thus, it appears that infant rats and hamsters illustrate two evolutionary strategies linking physiological and behavioral thermoregulation. The degree to which these species-specific characteristics are malleable, however, is unclear: Specifically, it is possible that the presence of endothermy blunts the infant rat's perception of thermal stimulation. Addressing this question will require experiments in which behavioral responses of infant rats are tested when endogenous heat production is blocked pharmacologically.

Toward the end of their review of orientation behaviors in animals, Fraenkel and Gunn (1940/1961) stated that "kineses and taxes are of very slight importance at most in the behaviour of mammals" (p. 303). This view was influenced in part by their recognition that learning processes, rather than behaviors typically designated as instinctive, play a greater role in mammalian behavior than in the invertebrates that were the focus of the earliest work on orientation. Fraenkel and Gunn, however, do not appear to have considered the role that unlearned orientation mechanisms may play in infant mammals as building blocks for the learning processes that they identify. Clearly, we have much to learn about the contributions of learned and unlearned components of behavioral thermoregulation in infants, including the sensory and neural bases of behavioral thermoregulation and their integration into the increasingly complex behavioral repertoires of developing infants.

References

- Alberts, J. R., & May, B. (1984). Nonnutritive, thermotactile induction of filial huddling in rat pups. *Developmental Psychobiology*, *17*, 161–181.
- Blumberg, M. S. (1997). Ontogeny of cardiac rate regulation and brown fat thermogenesis in golden hamsters (*Mesocricetus auratus*). *Journal of Comparative Physiology B*, *167*, 552–557.
- Blumberg, M. S. (2001). The developmental context of thermal homeostasis. In E. M. Blass (Ed.), *The handbook of behavioral neurobiology: Vol. 13. Developmental psychobiology, developmental neurobiology and behavioral ecology: Mechanisms and early principles* (pp. 209–238). New York: Plenum.
- Blumberg, M. S., & Sokoloff, G. (1998). Thermoregulatory competence and behavioral expression in the young of altricial species—Revisited. *Developmental Psychobiology*, *33*, 107–123.
- Blumberg, M. S., & Stolba, M. A. (1996). Thermogenesis, myoclonic twitching, and ultrasonic vocalization in neonatal rats during moderate and extreme cold exposure. *Behavioral Neuroscience*, *110*, 305–314.
- Brück, K., & Hinckel, P. (1996). Ontogenetic and adaptive adjustments in the thermoregulatory system. In M. J. Fregly & C. M. Blatteis (Eds.), *Handbook of physiology* (pp. 597–611). Oxford, England: Oxford University Press.
- Conklin, P., & Heggeness, F. W. (1971). Maturation of temperature homeostasis in the rat. *American Journal of Physiology*, *220*, 333–336.
- Eedy, J. W., & Ogilvie, D. M. (1970). The effect of age on the thermal preference of white mice (*Mus musculus*) and gerbils (*Meriones unguiculatus*). *Canadian Journal of Zoology*, *48*, 1303–1306.
- Flory, G. S., Langley, C. M., Pfister, J. F., & Alberts, J. R. (1997). Instrumental learning for a thermal reinforcer in 1-day-old rats. *Developmental Psychobiology*, *30*, 41–47.
- Fowler, S. J., & Kellogg, C. (1975). Ontogeny of thermoregulatory mechanisms in the rat. *Journal of Comparative and Physiological Psychology*, *89*, 738–746.
- Fraenkel, G. S., & Gunn, D. L. (1961). *The orientation of animals*. New York: Dover. (Original work published 1940)
- Freeman, N. C. G., & Rosenblatt, J. S. (1978). The interrelationship between thermal and olfactory stimulation in the development of home orientation in newborn kittens. *Developmental Psychobiology*, *11*, 437–457.
- Hissa, R. (1968). Postnatal development of thermoregulation in the Norwegian lemming and the golden hamster. *Annales Zoologici Fennici*, *5*, 345–383.
- Hull, D. (1973). Thermoregulation in young mammals. In G. C. Whitrow (Ed.), *Comparative physiology of temperature regulation: Special aspects of thermoregulation* (Vol. 3, pp. 167–200). New York: Academic Press.
- Hull, J., & Hull, D. (1982). Behavioral thermoregulation in newborn rabbits. *Journal of Comparative and Physiological Psychology*, *96*, 143–147.
- Johanson, I. B. (1979). Thermotaxis in neonatal rat pups. *Physiology and Behavior*, *23*, 871–874.
- Johanson, I. B., & Hall, W. G. (1980). The ontogeny of feeding in rats: III. Thermal determinants of early ingestive responding. *Journal of Comparative and Physiological Psychology*, *94*, 977–992.
- Kleitman, N., & Satinoff, E. (1982). Thermoregulatory behavior in rat pups from birth to weaning. *Physiology and Behavior*, *29*, 537–541.
- Leon, M. (1986). Development of thermoregulation. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology: Vol. 8. Developmental psychobiology and developmental neurobiology* (pp. 297–322). New York: Plenum.
- Leonard, C. M. (1974). Thermotaxis in golden hamster pups. *Journal of Comparative and Physiological Psychology*, *86*, 458–469.
- Leonard, C. M. (1978). Maturation loss of thermotaxis prevented by olfactory lesions in golden hamster pups. *Journal of Comparative and Physiological Psychology*, *92*, 1084–1094.
- Leonard, C. M. (1982). Shifting strategies for behavioral thermoregulation in developing golden hamsters. *Journal of Comparative and Physiological Psychology*, *96*, 234–243.
- Ogilvie, D. M., & Stinson, R. H. (1966). The effect of age on temperature selection by laboratory mice (*Mus musculus*). *Canadian Journal of Zoology*, *44*, 511–517.
- Satinoff, E. (1996). Behavioral thermoregulation in the cold. In M. J. Fregly & C. M. Blatteis (Eds.), *Handbook of physiology* (pp. 481–505). Oxford, England: Oxford University Press.
- Shurtleff, D., & Tobach, E. (1979). Neonatal rat pups' (Long-Evans DAB) behavioral responses to thermal stimuli. *Bulletin of the Psychonomic Society*, *13*, 75–77.
- Sokoloff, G., & Blumberg, M. S. (1998). Active sleep in cold-exposed infant Norway rats and Syrian golden hamsters: The role of brown adipose tissue thermogenesis. *Behavioral Neuroscience*, *112*, 695–706.
- Sokoloff, G., & Blumberg, M. S. (2001). Competition and cooperation among huddling infant rats. *Developmental Psychobiology*, *39*, 1–9.
- Sokoloff, G., Blumberg, M. S., & Adams, M. M. (2000). A comparative analysis of huddling in infant Norway rats and Syrian golden hamsters: Does endothermy modulate behavior? *Behavioral Neuroscience*, *114*, 585–593.
- Spiers, D. E., & Adair, E. R. (1986). Ontogeny of homeothermy in the immature rat: Metabolic and thermal responses. *Journal of Applied Physiology*, *60*, 1190–1197.
- Wasserman, E. A. (1973, August 31). Pavlovian conditioning with heat reinforcement produces stimulus-directed pecking in chicks. *Science*, *181*, 875–877.

Received July 2, 2001

Revision received November 1, 2001

Accepted November 8, 2001 ■