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# Ontogenetic Adaptation and Learning: A Developmental Constraint in Learning for a Thermal Reinforcer

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**ABSTRACT:** Hoffman, Flory, and Alberts (1999) demonstrated that 1-, 5-, and 11-day-old rats in a cool environment (25°C) acquired an operant head-turning response when rewarded with a 20-s warming of the platform on which they lay. In the current experiment 5- and 11-day-old rats in a hot environment (40°C) acquired the head-turning response when rewarded with a 20-s cooling of the platform on which they lay, but 1-day-olds did not. The concept of ontogenetic adaptation helps us interpret these results: Neonatal thermotaxis constrains the 1-day-olds from learning a novel operant response for a cool reinforcer in a hot environment. Because the thermotaxis wanes from birth, it is not as strong in 5- and 11-day-old pups that are thus able to learn the operant for a cool reinforcer. © 1999 John Wiley & Sons, Inc. *Dev Psychobiol* 34: 73–86, 1999

**Keywords:** operant conditioning; rats; development; thermotaxis

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The research reported in the present article is part of a series of investigations of how infant rats' learning for thermal rewards changes during development. The theoretical basis for this investigation is rooted in the concept of ontogenetic adaptation and in an "ecological" perspective of developmental process. The concept of ontogenetic adaptation (Oppenheim, 1980, 1981) recognizes that development involves qualitative changes in body, brain, and behavior. These changes involve addition and deletion of features or capabilities (thus emphasizing that development is not uniformly progressive). Such qualitative changes dur-

ing ontogeny present themselves as adaptive changes when they help the developing organism better fit its immediate environment. The ecological perspective, which blends nicely with the concept of ontogenetic adaptation, characterizes development as a series of adaptive changes to a series of niches, each distinguished by the way in which the animal meets its needs by interacting with its environment (e.g., Alberts, 1987; Alberts & Cramer, 1988; Alberts & Gubernick, 1984; Galef, 1979; Johnston, 1984; West, King, & Arberg, 1988). An adaptive-evolutionary view of development supports these perspectives by noting that natural selection can operate at each point in development (e.g., Williams, 1966), not solely on the adult.

Broadly applied, the ecological perspective suggests that learning capabilities will change during development as behavior dynamically adapts to succes-

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sive niches. Unfortunately, there has been little exploration of the idea that learning capabilities undergo a coherent sequence of changes during development, as do myriad other aspects of the growing, differentiating, and functioning body. In short, we are interested in viewing the development of learning as the development of another adaptive system. We expect learning to be naturally suited (possibly by the action of natural selection) for challenges that are characteristic of the ontogenetic sequence of habitats that an organism encounters (e.g., Alberts, 1994).

Specifically, in the current studies we are interested in how the capabilities of the rat pup to learn for thermal reinforcement change as the pups' behavior toward thermal stimuli dynamically changes. We began our studies of learning for thermal rewards with an appreciation of the importance of heat for the developing rat and its sensitivity to thermal stimuli. Although sensory transduction of thermal cues develops early, often prenatally (Alberts, 1984), temperature cues have been little utilized in studies of early learning. But, in an initial study, 1-day-old rats in a cool environment (25°C) quickly acquired an operant response when rewarded with a 20-s warming of the platform (from 25°C to 36°C) on which they lay (Flory, Langley, Pfister, & Alberts, 1997). The operant response, turning the head to one side, was learned rapidly—within 30 min after the thermal contingency began. The operant response extinguished when turns to that side were no longer reinforced.

Subsequently, we reapplied the same operant methodology, replicating the original findings with 1-day-olds and demonstrating that 5- and 11-day-olds also acquired the same operant response (Hoffman et al., 1999). Hoffman and colleagues (1999) predicted and found an ontogenetic difference in learning for a warm reinforcer. One-, 5-, and 11-day-old pups all learned to turn their head to one side for a warm reinforcer in a cool environment within the first 30 min of training, but only the responses of 1-day-old pups extinguished when the reinforcer was later given for head turns in the opposite direction. A second experiment revealed that while the reinforcer remained on, 1-day-old pups responded significantly more to the side to which they had turned just prior to reinforcer onset than to the opposite side. Thus, in Experiment 1, on those occasions during the reversal period in which the 1-day-old's head swung to the side opposite that correct during training, the reinforcer turned on and the repetitive responses made to that side while the reinforcer remained on provided both practice of the new response as well as numerous reinforced responses to the newly correct side. The 5- and 11-day-old pups did not respond more to the correct side while the reinforcer was

on and did not begin to reverse their response when the contingency changed.

Hoffman et al. (1999) based their prediction of ontogenetic differences in learning for a warm reinforcer on behavioral observations that suggest that the value of warmth declines from infancy on. So dramatic is the newborn rat's attraction to warm stimuli that the term *thermotaxis* is appropriate for many of its responses. The term *thermotaxis* refers to movement of the organism toward a source of warmth (see Fraenkel & Gunn, 1942; Johanson, 1979; Leonard, 1974 for additional perspective on the term). We also use the term *thermotaxis* to refer to a stereotyped pattern of a stationary pup in turning its head toward heat because head-turning is the initial and predominant movement used by neonatal pups to sample the area around them and to initiate a continued trajectory or change in direction toward heat.

The strength of neonatal *thermotaxis* wanes over the 1st weeks after birth (see Hoffman et al., 1999 for more detail). When placed in contact with a surface temperature gradient (thermocline) young rat pups are more consistent than older pups in initially moving toward warmth (Pfister, 1990); they also move more effortfully toward warmth than do older pups (Johanson, 1979; Kleitman & Satinoff, 1982). Persistent head-turning while the warm reinforcer was on (a *thermotaxis* response) was observed for 1-day-olds, but not for 5- or 11-day-olds (Hoffman et al., 1999). Blumberg and Stolba (1994) describe the appearance of stretching and locomotion (both components of *thermotaxis*) in 2-day-old rats exposed to a drop in environmental temperature below that at which their body is generating maximal heat by means of brown adipose tissue (BAT) metabolism. In contrast, 7-day-olds responded to the temperature challenge with increased vocalization but unaltered locomotion, also suggesting a waning of the *thermotaxis* response.

The ontogenetic difference in learning for a warm reinforcer reported by Hoffman et al. (1999) can be interpreted using the ontogenetic adaptation concept (Oppenheim, 1980, 1981) and the ecological perspective of development (Alberts & Cramer, 1988). Neonatal *thermotaxis* can be adaptive because warmth is a stimulus that contributes to thermal homeostasis by guiding the pups to huddle (Alberts, 1978). Small newborn mammals can neither generate nor conserve sufficient body heat to survive independently and must stay in contact with the dam and littermates to maintain a stable, warm body temperature. The infant must also remain with the huddle to obtain maternal care and social stimulation necessary for survival and uses warmth as a cue to do so. In contrast, older pups can meet their need for a stable, warm body temperature

by physiologically generating and conserving heat, and can locate and maintain contact with the huddle using olfactory cues. Enhanced learning for a warm reinforcer can thus be viewed as an ontogenetic adaptation to the neonatal thermal niche in which it is critical that neonates be able to modify their behavior (learn) to obtain heat from sources of warmth in their environment. The enhanced learning disappears in older pups, which interact with their environment differently to meet their needs for thermal homeostasis and social contact.

The current experiments explore further the ontogeny of learning for thermal reinforcers. Specifically, we are interested in whether there is an ontogenetic difference in learning the head-turning operant for a cool reinforcer, as there was for the warm reinforcer. While the thermotactic behavior of neonates led us to predict that they would readily learn the operant response for a warm reinforcer, the same behavior leads us to predict that they will be constrained from learning for a cool reinforcer. Further, we predict an ontogenetic difference in learning for a cool reinforcer—even though neonates may not learn the operant, older pups will because the value of cool stimuli increases coincidentally with the waning of neonatal thermotaxis.

We predict that thermotactic neonates may fail to learn the operant response for the cool reinforcer, even though they readily learned it for a warm reinforcer, because neonates are less responsive to cool stimuli than to warm. Each time that a neonate moves from one location to a warmer one it is choosing warmth over cool. Thus, the very existence of the thermotaxis indicates that neonates value warmth over cool across a wide range of temperatures. Further, Hull and Hull (1982) describe the approach of neonatal rabbits toward warmth as much more vigorous than the approach toward cool. Infant rabbits placed on a cool thermocline location immediately began moving until they detected the temperature gradient, then moved directly to a warm area where they abruptly stopped, settled, and remained. In contrast, neonatal rabbits placed on a hot region remained for 3–5 min before gradually moving to a slightly cooler region, thus selecting a position similar to that selected by littermates that started at a cool location. Because neonates are more responsive to warm stimuli than to cool it would not be surprising if a warm reinforcer in a cool environment was more potent in reinforcing an operant than a cool reinforcer in a hot environment.

Further, we predict that older pups will learn the head-turning operant for a cool reinforcer more readily than neonates because the value of contacting a cool stimulus as a means of dissipating heat increases as physical changes improve the conservation of heat.

Rats of all ages will actively approach cooler temperatures when started at a hot location on a thermocline (Gordon, 1993; Kleitman & Satinoff, 1982). Cooling, like warming, is valuable to pups of all ages. The value of approaching cool stimuli as a means of behaviorally thermoregulating should, however, markedly increase as the pup grows and develops.

Growth (increased mass) decreases the surface: mass ratio of a body, thus decreasing the rate of heat loss from a warm body to a cooler environment. Growth is also accompanied by a change in body composition, water content decreases and protein and fat deposition increase (Hahn & Koldovsky, 1966). Such changes result in a doubling of the ability to conserve heat from 3 to 7 days of age alone (Takano, Mohri, & Nagasaka, 1979). Further, Spiers and Adair (1986) conclude that changes in thermal insulation and control of heat loss are primarily responsible for the major improvements in ability to maintain thermal stability evident from 5 to 19 days of age.

With multiple factors increasing their bodies' heat load, older pups are more liable than are neonates to utilize heat-dissipating mechanisms to maintain thermal homeostasis. Pfister and Alberts (1985) suggested that the pups' repertoire of heat-conserving responses develops earlier than does their repertoire of heat-dissipating responses. For example, saliva spreading, a response to heat challenge that affords protection from hyperthermia by promoting evaporative cooling (Hainsworth, 1967), is not effective until about Day 15, whereas a variety of other heat-conserving responses are evident much earlier in rat development (Pfister & Alberts, 1985). We believe that part of the development of behavioral mechanisms for thermoregulation involves changes in the *value* of cool stimuli—that older pups value contact with cool stimuli as a means of dissipating heat. Further, we believe that the increase in value of cool stimuli with age changes the likelihood that pups will learn an operant for a cool reinforcer.

To test convincingly and validly how cooling is (or is not) a reward for infant rats, it is crucial to select carefully thermal parameters that are equilibrated for rat pups at the various ages. It may be necessary to use different temperatures for pups at each age tested. Either way, it is necessary to have an independent measure to equilibrate stimuli across age groups and thus account for age-related variables, such as size, sensory maturation, and physiological responses that can affect the efficacy of the stimuli.

Phase 1 of the present study was conducted to establish temperature parameters (air temperature and reward temperature) that are behaviorally equivalent for rat pups, 1, 5, and 11 days of age. To do this we

utilized a thermocline and measured rat pups' preferred surface temperature in the presence of a challenging, hot air temperature. Infant rat pups demonstrate a form of behavioral temperature regulation in this sort of test (e.g., Pfister, 1990), so we sought to use their capabilities as a means of equilibrating our parameters across ages.

In Phase 2, we then challenged the pups with the same hot ambient air and gave them the opportunity to receive a reinforcer matching the temperature they selected on the thermocline in Phase 1 for a head-turn operant. Specifically, the reinforcement involved the delivery of a surface temperature under their ventrum equal to the preferred temperature for each age group, as established in Phase 1. We predict that the cool reinforcer will not be sufficient to support associative learning in thermotaxic 1-day-old pups, but that 5- and 11-day-olds will learn the operant for the cool reinforcer.

## PHASE 1: ESTABLISHING THERMAL PREFERENDA

In Phase 1 of the experiment, individual rat pups 1, 5, and 11 days old were placed on a surface temperature gradient in a hot (40°C) environment. The surface temperature of the 3.5 ft long copper floor varied nearly linearly from 26°C to 40°C. We measured time spent on various regions of the gradient to determine the preferred temperature for pups of each age group. These data were used to standardize and equilibrate reinforcer temperature in the operant conditioning procedure (Phase 2).

A cool temperature that is preferred by 11-day-olds might be cooler than that preferred by 1-day-olds, due to the physical and physiological differences between these age groups. If a reinforcer preferred by 11-day-olds is not preferred by 1-day-olds, then a finding that 1-day-olds do not learn the operant for that reinforcer would not indicate that they could not learn for a cool reinforcer—just that the temperature selected by 11-day-olds was not equally reinforcing for 1-day-olds. If, however, the 1-day-olds are presented with a cool reinforcer in Phase 2 that matches their preferred temperature in Phase 1 and they do not learn the operant response, then we can conclude that they are constrained from learning the novel head-turning behavior for a cool reinforcer in a hot environment.

## Method

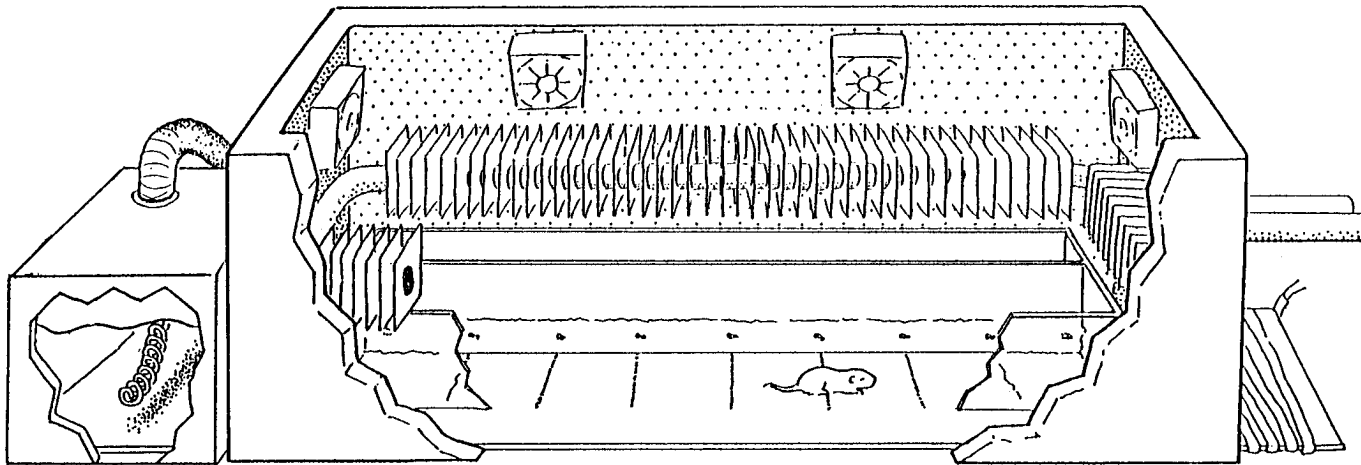
**Subjects.** Subjects were 24 Sprague-Dawley rat pups (*Rattus norvegicus*) bred and born in the Animal Be-

havior Laboratory at Indiana University. The original stock was obtained from Taconic Farms (Germantown, NY). Births were checked daily at 1700 hr (day of birth = Day 0). Litters were culled to 8 pups, 4 males and 4 females, on Day 3. All pups were housed with their mother and littermates in standard maternity cages (47 × 26 × 21 cm) and were maintained on a 12:12 hr light:dark cycle (2000 hr lights off/0800 hr lights on). Room temperature in the colony room ranged from 21°C to 23°C.

Eight pups of each age group (1, 5, and 11 days old) were tested in the experiment. Half of the pups in each age group were male and half were female. Each age group was derived from at least four different litters, usually with no more than 2 pups tested from a litter. No more than 3 pups in any age group were taken from a single litter.

**Apparatus.** The thermocline apparatus consisted of a 112 cm long sheet of 0.04 mm copper, 29 cm wide, that was cooled at one end and heated at the other. This copper sheet served as the floor of a 94 cm long × 12.7 cm wide test alley which varied in temperature from 26°C to 40°C. The thermocline was contained within a temperature-regulated enclosure maintained at 40°C (see Figure 1). The plywood walls of the enclosure were 1.3 cm thick and the interior measured 112 × 29 × 30 cm. The box was insulated on all sides with 3.8 cm thick Styrofoam and capped by a clear Plexiglas lid. The temperature inside the enclosure was controlled by circulating water through slant-fin tubing running around the perimeter of the enclosure. The slant-fin tubing connected to a temperature-regulated water circulator (Lauda RM6). Five small fans (8.3 × 8.3 × 2.5 cm) were mounted inside the enclosure to circulate the air and maintain an even ambient temperature throughout the enclosure. The fans were angled so that the heated air was directed down towards the floor. Experimental subjects were placed into and removed from the enclosure through a covered opening (35 × 25 cm) cut into the apparatus lid.

The thermal gradient was established by heating one end of the copper and chilling the other end. One end of the copper that extended beyond the enclosure (by 16.5 cm) was wrapped in 6 m of Glas-Col heating tape (Catalog Number AETO510, Terre Haute, IN) powered by a Variac (Model W10MT, Cambridge, MA). The opposite end of the copper that extended beyond the enclosure (by 30.5 cm) was encased in an insulated ice chest filled with antifreeze chilled to a temperature of -10°C by an immersion chiller (Model EK11, Haake, Saddle Brook, NJ) and mixed continuously by an immersion circulator (Catalog Number 69038, GCA/Precision Scientific).



**FIGURE 1** The floor of thermocline apparatus consisted of a sheet of copper heated at one end with heat tape and cooled at the opposite end with a chiller. The enclosure was maintained at 40°C by circulating heated water through slant-fin tubing. A pup is shown on the thermocline inside a Plexiglas lane that extended from 26°C to 40°C on the gradient. (Apparatus is not drawn to scale).

The locomotion of the pups over the thermal gradient was restricted by the confines of two Plexiglas alleys ( $94 \times 12.7 \times 30.5$  cm) that were placed on top of the thermal gradient. The alley walls were perforated by two rows of 1.3-cm holes to improve air circulation. To allow the experimenter to assess the pup's location on the thermal gradient, the length of the thermocline was divided into eight sections (10.8 cm wide) marked on the copper. The temperature of the copper was measured in nine locations along the thermocline: at the right edge of each of the eight sections and at the left edge of the last grid section. The surface temperature of each location was measured with an Omega Thermocouple Thermometer (Type E, Stamford, CT).

Ambient temperature was measured with a YSI Teletermometer (Model 43TA, Yellow Springs, OH) fitted with an air temperature probe. The air temperature probe was secured above the center grid line.

All experimental sessions were videophotographed. A Sony color video camera (Model DXC-151A) was mounted 1.1 m above the environmental enclosure. A wide-angle lens (8.5 mm) provided a view of the alleys. A Gyr Time-Lapse VCR (Model TLC1800, Anaheim, CA) recorded pups' behavior at a 1:6 record/playback ratio.

## Procedure

The behavior of 1-, 5-, and 11-day-old pups was observed on the thermocline for 2 hr in the 40°C ambient environment. The temperatures of the environment and thermal gradient were allowed to stabilize before subjects were tested by turning on the water bath that controlled ambient temperature and the heating tape, chiller, and circulator that controlled thermocline temperature 4 hr before an experimental test. The temperature of the thermocline was measured before and after each experimental session. The temperature of the thermocline remained quite stable over the experimental period, increasing an average of 0.34°C for each location measured. The surface temperature of the eight sections on the thermocline ranged from 26°C to 40°C: 26–29°C, 30–33°C, 34°C, 35°C, 35°C, 36°C, 37°C, and 38–40°C.

An individual 1-, 5-, or 11-day-old pup was removed from its home cage and taken to the experimental room. The pup was placed in the center of the fourth grid section at the start of the experimental session (Half of the pups of each age group were placed facing the cool end and half facing the warm end of the thermocline.) An experimental session lasted for 2 hr after which the pup was removed from the apparatus and returned to its home cage.

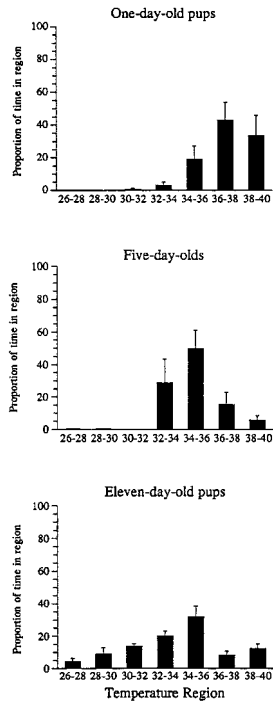
## Method of Analysis

An observer viewed the videotape of each 2-hr experimental session at six times normal speed and scored the amount of time each animal spent within each of the eight sections. An animal was determined to have selected a section along the thermocline if more than half of its body (tail excluded) was in contact with that section. The amount of time spent in each grid section was converted to the proportion of time spent in each location on the thermocline. Instead of presenting the proportion of time spent at a physical location on the thermocline, we present the proportion of time spent in each of the following temperature regions: 26°C–27°C, 28°C–29°C, 30°C–31°C, 32°C–33°C, 34°C–35°C, 36°C–37°C, and 38°C–40°C. We converted from proportion of time spent at a grid location to proportion spent at a temperature region individually for each pup (consulting the temperature measurements taken before and after each pup's experimental session). When the temperature range of a grid section overlapped several temperature regions we divided the proportion of time spent in the grid section evenly over the temperature selection regions. If, for example, a pup spent 40% of its time in Grid Section 1 (26–29°C) we recorded in our data that it spent 20% of its time in the 26–27°C temperature region and 20% of its time in the 28–29°C region.

To facilitate the comparison between proportion of time spent in temperature regions along the gradient, a weighted preference score was calculated for each pup. This preference score summarizes how the pup distributed its time over all seven regions. This score was calculated as the percentage of time spent in a particular region multiplied by the ordinal number of the region summed over all seven regions. The coolest region (26–27°C) was assigned the number 1, the next coolest region (28–29°C) the number 2, and so on. If a pup spent 20% of its time in Region 1, 20% in Region 2, and 60% in Region 3 the preference score was  $2.4 = (0.20 \times 1) + (0.20 \times 2) + (0.60 \times 3)$ . Low scores indicate a preference for cooler regions of the thermocline; a higher score indicates a preference for warmer regions.

## Results

One-day-old pups spent most of their time in the warmest regions of the thermocline 36–37°C and 38–40°C, while 5- and 11-day-old pups spent most of their time in relatively cooler 32–33°C and 34–35°C regions (see Figure 2). The mean weighted preference scores for each age group reflected the age-related difference in temperature preference. The mean prefer-



**FIGURE 2** Temperature preferences of 1-, 5-, and 11-day-old pups on a thermocline in a hot (40°C) environment.

ence scores ( $\pm$  standard error) for 1-, 5-, and 11-day-olds were  $6.03 \pm 0.21$ ,  $4.98 \pm 0.24$ , and  $4.41 \pm 0.27$ , respectively. An ANOVA revealed a significant overall difference for the three age groups,  $F(2, 21) = 11.58$ . Planned comparisons revealed that 1-day-old pups' scores were significantly higher than the scores of 5- and 11-day-old pups,  $F(1, 14) = 10.59$ ,  $22.60$ , respectively. The temperature preference scores of 5- and 11-day-old pups did not differ significantly,  $F(1, 14) = 2.52$ .

The preferred temperature region was 36–37°C for 1-day-old pups and 34–35°C for 5- and 11-day-old pups (see Figure 2). The percentage of time spent in the 36–37°C region for 1-, 5-, and 11-day-old pups was  $43.1\% \pm 10.7\%$ ,  $15.4\% \pm 7.4\%$ , and  $8.3\% \pm 2.4\%$ , respectively. The percentage of time spent in the 34–35°C region for 1-, 5-, and 11-day-old pups was  $19.0\% \pm 8.2\%$ ,  $49.9\% \pm 11.1\%$ , and  $32.1\% \pm 6.5\%$ , respectively. One-day-olds spent a significantly higher percentage of time in the 36–37°C region than did 5- or 11-day-olds,  $F(1, 14) = 4.56$  and  $10.05$ , respectively. Five-day-olds spent a significantly higher percentage of time in the 34–35°C region than did 1-day-old pups,  $F(1, 14) = 4.99$ . Five- and 11-day-olds did not differ in the percentage of time spent in the 34–35°C region,  $F(1, 14) = 1.91$ .

Because the locomotor abilities of 1-, 5-, and 11-day-old pups vary tremendously, we compared the

number of times that each pup moved from one grid to another during the 2-hr test as a way of assessing whether pups of all ages had sufficient locomotor abilities to sample different temperature regions. One-, 5-, and 11-day-old pups moved from one grid to another during the 2-hr experimental session  $15.5 \pm 1.45$ ,  $12.6 \pm 1.99$ , and  $16.38 \pm 2.28$  times, respectively. An ANOVA revealed no overall difference between the number of moves made by pups in the three age groups,  $F(2, 21) = 1.03$ .

Pups did differ, however, in the number of grid locations sampled during the experimental session. One-, 5-, and 11-day-old pups sampled  $4.75 \pm 0.31$ ,  $4.38 \pm 0.42$ ,  $6.25 \pm 0.37$  grid sections on the thermocline, respectively. An ANOVA revealed a significant difference in the number of grids sampled by the three age groups,  $F(2, 21) = 7.23$ . Planned comparisons revealed that 11-day-old pups sampled significantly more grid locations than did 1- or 5-day-old pups,  $F(1, 14) = 9.69$  and  $11.33$ , respectively. The number of grid locations sampled did not differ between 1- and 5-day-old pups,  $F(1, 14) = 0.51$ . The fact that 11-day-olds sampled more grid locations than the 1- and 5-day-olds pup may reflect their most sophisticated locomotory abilities of the 11-day-olds and an increased tendency to explore, and to approach novelty that occurs about this time in development.

Pups in the three age groups did differ in the amount of time they spent at the start location before moving to another grid. One-, 5-, and 11-day-old pups took 10:51 min, 23:26 min, and 20 s to leave the start location, respectively. Eleven-day-olds moved from the start location significantly more quickly than 1- or 5-day-old pups,  $F(1, 14) = 35.67$  and  $17.71$ , respectively. The 1-day-olds moved from the start location significantly more quickly than the 5-day-olds,  $F(1, 14) = 4.78$ . The fact that 11-day-olds moved from start much faster than the younger pups likely reflects the more-sophisticated ability to locomote of 11-day-olds relative to 1- and 5-day-old pups. The fact that 1-day-old pups, with less locomotory ability than 5-day-old pups, left the starting grid sooner than the 5-day-olds indicates that differences in locomotory ability alone cannot account for differences between age groups in time spent at the start. The 5-day-olds may have spent longer at the start location than the 1-day-olds because the temperature of the start location, 35°C, is close to the 5-day-olds' preferred temperature on the thermocline, but cooler than the 1-day-olds' preferred temperature. Although half of the pups in both age ranges were placed at the start location facing the cool end of the thermocline and half facing the warm end of the thermocline, fully 7 of 8 of the 1-day-olds moved first toward the warm end of the ther-

mocline, while only 5 of 8 of the 5-day-olds initially moved to a warmer location.

## Discussion

We found that 1-day-old pups preferred warmer regions on the thermocline than did 5- and 11-day-old pups. The preferred temperature region for 1-day-olds is 36–37°C and for 5- and 11-day-olds, 34–35°C. Although differences in locomotory abilities of our 1-, 5-, and 11-day-old pups influenced the number of grid locations sampled during the experiment, differences in locomotory abilities cannot alone account for the differences in preferred temperature. The fact that the number of times that each pup moved from one grid to another during the 2-hr test did not differ across age groups suggests that 1-, 5-, and 11-day-old pups were all capable of sampling the different temperature regions. Thus, we conclude that our choice of the thermocline task, as a way of assessing the temperature preferences of pups of different ages in the 40°C ambient, was appropriate.

Two experimental results support the view that the neonatal thermotaxis wanes during this period of development (discussed in the introduction) The 1-day-old pups began moving toward warmth 10 min earlier than the 5-day-old pups. The 1-day-olds also consistently moved in the direction of warmth when placed at 26°C on the thermocline, whereas the initial movement of the 5-day-olds was random with respect to temperature.

## PHASE 2: OPERANT RESPONDING FOR A COOL REINFORCER

In the second phase of the experiment 1-, 5-, and 11-day-old pups were tested to determine whether all age groups could acquire an operant head-turning response in a 40°C environment for a reinforcer consisting of cooling the platform on which it lay. The results of Phase 1 indicate that none of the three age groups spent the majority of their time in the 40°C region on the thermocline when the ambient temperature in that apparatus was maintained at 40°C. One-day-old pups prefer the 36–37°C temperature region and 5- and 11-day-old pups prefer the 34–35°C region. The surface temperature preferences measured at 40°C were incorporated into Phase 2: The reinforcing event that occurs after a correct operant response is rapid cooling of the platform temperature to that temperature preferred on the thermocline. For 1-day-old pups, the platform is cooled from 40°C to 36°C following a head

turn to the correct side. The platform is cooled from 40°C to 34°C following a head turn to the correct side for 5- and 11-day-olds.

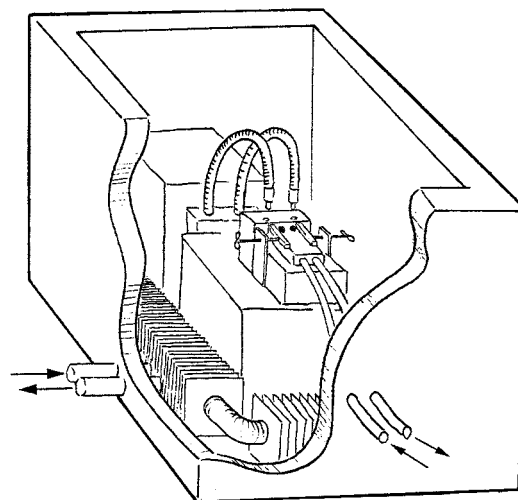
By using the reinforcers in operant training that match the age-related temperature preferences observed on the thermocline in Phase 1, we have an empirical basis for equating the value for pups in each age group of the platform cooling event that follows a correct head turn. If the older pups learn the operant and the younger pups do not, then we can conclude that the younger pups are constrained from learning for a cool reinforcer even though it is preferred and satisfies a homeostatic need.

## Method

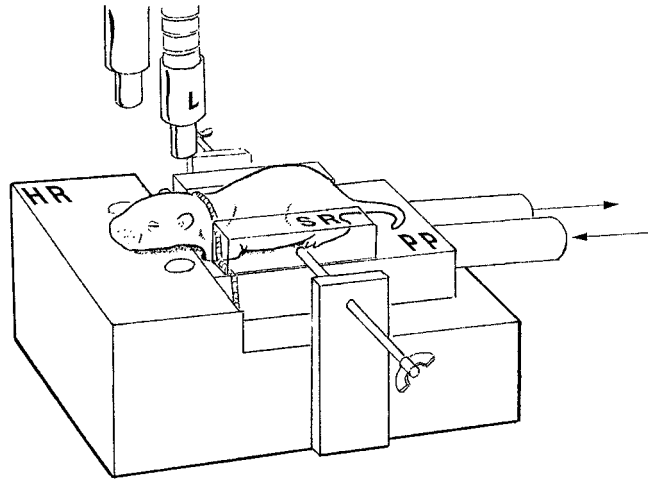
**Subjects.** Subject information is the same as in Phase 1.

### Apparatus.

**Overview:** The apparatus consisted of a temperature-controlled enclosure, maintained at 40°C (Figure 3), and the subject platform on which pups were restrained during the experiment (Figure 4). The pup



**FIGURE 3** The experimental apparatus for operant conditioning consisted of a platform, on which the pup was positioned, in a temperature-controlled enclosure. Water circulated through slant-fin tubing maintained the environment at 40°C. The surface temperature of the pup platform was maintained at 40°C, and decreased to either 36°C (for 1-day-old pups) or to 34°C (for 5- and 11-day-old pups) when the reinforcer was on, by circulating water from one of two temperature-controlled water baths. A lamp with two gooseneck extensions provided a directed source of light above the photocells.



**FIGURE 4** A 5-day-old pup is shown restrained on the pup platform (PP) by a string placed over the interscapular area and siderails (SR). A tissue-tape strap (not shown here) was also positioned over the pup's back. Two gooseneck extensions of a lamp (L) provided a source of light directed at the left and right photocells mounted below the pup's headrest (HR).

could completely cover one of two photocells by turning its head left or right. The temperature of the pup platform was controlled by circulating hot (40°C) or cool (34 or 36°C) water through it. When the pup turned its head in the direction designated as correct by the experimenter, the response was reinforced by warming the platform from 40°C to 34°C or 36°C for 20 s.

**Testing Environment.** Pups were tested in an enclosure (79 × 51 × 35 cm) in which ambient temperature was maintained at 40°C (see Figure 3). The enclosure, a galvanized metal box, was insulated on all sides and on the bottom with 3.8 cm thick Styrofoam. The top was covered by a double layer of Plexiglas lids. The temperature inside the enclosure was controlled by circulating water through slant-fin tubing around the inside perimeter of the enclosure. The slant-fin tubing connected to a heating water circulator (VWR Scientific, Model 1160A). Although it was unavoidable that the temperature inside the enclosure was perturbed when a pup was placed in the enclosure, temperature fluctuation was minimized by incorporating sliding Plexiglas doors into the design of the lids.

**Testing Platform.** The subject platform consisted of a restraining platform and a pup platform which rested on top of the restraining platform (see Figure 4). While the pup platform was constructed differently for the three age groups, the restraining platform was the same for all pups. The restraining platform (20 × 17 × 6 cm) was constructed of 0.32 cm thick

stainless steel. Two types of restraints held the pups in place: a piece of string tied snugly over the pup's interscapular area and Plexiglas siderails. The Plexiglas siderails (4.4 × 0.6 × 1.3 cm) were adjusted by moving threaded bolts mounted on the restraining platform. The siderails were adjusted so that each pup was held in place at the midline of the subject platform. Two slits (6 × 0.32 cm) were punched in the top restraining platform, one on either side of the midline beneath which two photocells were mounted. Left and right photocells were positioned 10 mm from midline for 1-day-old pups, 15 mm from midline for 5-day-olds, and 21 mm from midline for 11-day-olds.

The pup platform included a headrest and temperature-controlled copper platform. The black Plexiglas headrest and pup platforms were scaled to accommodate the variation in body sizes. The headrest for 1-day-old pups (10.2 × 2.5 × 3.5) was constructed of 0.32 cm thick black Plexiglas on all sides and on top. The headrest was constructed of black Plexiglas to prevent light other than that from the overhead lamp from influencing photocell activity. Two holes (0.95 cm diameter) were cut in the top of headrest above the positions of the photocells for the 1-day-old pups (10 mm to the left of the midline and 10 mm to the right of the midline). The holes were less than 0.2 cm from the subject platform. The headrests were constructed similarly for the 5- and 11-day old pups. The headrest for the 5-day-olds pups measured 11.4 × 2.9 × 3.8 cm and the holes in the top of the black Plexiglas were 15 mm from the midline. The headrest for the 11-day-olds pups measured 10.2 × 3.2 × 3.8 cm and the holes

in the top of the black Plexiglas were each 21 mm from the midline. A piece of clear Plexiglas ( $10.2 \times 2.5 \times 0.32$  cm) was glued to the top of the headrests so that the pup, turning its head left or right, could not detect the location of the holes in the headrest.

The temperature-controlled copper platform was a cubic rectangle fashioned of 0.08 cm thick copper through which independent streams of 40°C, 34°C, or 36°C water was circulated (see Figure 4). Two pup platforms were constructed; one for 1-day-olds and another for 5- and 11-day-olds. The platforms were designed so that the pup's front legs extended down from the surface (decreasing the likelihood of the pup escaping from the restraints and assuring complete contact of the pup's ventrum with the platform), as depicted in Figure 2. The 1-day-olds' platform ( $6.7 \times 4.8 \times 1.3$  cm) was constructed so that the pup's front legs extended down into a 0.7 cm space between the copper platform and the Plexiglas headrest. While the bottom of the platform measured  $6.0 \times 4.8$  cm, the top was  $6.7 \times 4.8$  cm. The top of the platform was attached to the sides and bottom to create the 0.7 cm that formed an overhang into which two holes (0.5 cm in diameter) were punched for the pup's front legs. The top and bottom surfaces of the pup platform ( $8.3 \times 4.8 \times 1.3$  cm) designed for the two older groups was punched with two 0.95 cm diameter holes through which two copper pipes (0.95 external diameter) were soldered, creating a small well for each forelimb. The front edge of the pipe was 0.95 cm from the front edge of the subject platform.

A system of electronically controlled valves directed one of two independent streams of temperature-controlled water through the subject platform during the experiment. At all times when the reinforcer was not on, 40°C water was circulated through the subject platform. When the reinforcer was turned on, 34°C or 36°C water was circulated through the pup platform. Temperature flux was rapid; the platform surface temperature changed from 40°C to 34°C or 36°C in 3–4 s. The temperature of the two water streams was regulated independently by two heating/refrigerating water circulators (Haake, Model D1-G). A diagram of the water circulators, solenoid valves, passive T-connectors, and tubing is available upon request.

A head-turning response was recorded, once a pup was restrained on the platform, whenever light from the double gooseneck fiber optic lamp directed at the photocells was blocked. Each arm of the lamp (Reichert, Model 1177, Buffalo, NY) was positioned approximately 3.2 cm above the surface of the headrest.

All experimental events, including recording subject responses and delivery of reinforcers, were con-

trolled by an IBM 486 PC. Software controlling experimental events was written in BASIC by C. M. Hoffman.

## Procedure

An individual 1-, 5-, or 11-day-old rat pup was removed from its home cage and taken to the experimental room. The restraint and pup platforms were removed from the temperature-controlled environment and the pup restrained on the platform. Side restraints were adjusted so that the pup was positioned on the midline. A single piece of string, threaded through the holes on the restraint platform, was placed snugly over the pup's interscapular area. A tissue-tape strap (1.3 cm wide) attached to the left and right siderails was placed over the pup's back. If restraints were too snug the pups became inactive, therefore the experimenter attempted to adjust the restraints only as tight as was necessary to prevent the pup from escaping. Once the pup was restrained it was observed for several minutes before the platform and pup were placed in the experimental environment. If the pup escaped from restraints during observation it was restrained more snugly, then observed, then placed in the experimental environment.

In the initial phase of the experiment each pup's responses were recorded for 30 min, during which time no reinforcement was given. Number of responses to the left and to the right were recorded throughout baseline. In order for successive responses to be recorded, the pup had to clear a photocell before breaking it again, thus assuring that each response was independent. All pups responded bilaterally during baseline (making no fewer than 20% of responses to one side). During training, the temperature-controlled platform was cooled from 40°C to 34°C or 36°C for 20 s when the photocell on the correct side was blocked by the pup's head. The platform temperature changed quickly at reinforcer onset—from 40°C to 34°C or 36°C in 3–4 s. Occlusion of the other photocell had no effect but was similarly recorded. Training lasted for 1 hr. The side that was designated correct was randomly assigned by the experimenter. Half of the pups in each age group were reinforced for head turns to the left and half for head turns to the right.

Each pup that increased the percent of head turns to the correct side by at least 25% during training from baseline performance then began a reversal phase. During reversal, the temperature-controlled platform was warmed from 40°C to 36°C or 34°C when the pup's head blocked the photocell on the side opposite that correct during training. Head turns to the side that

was correct during training had no effect but were similarly recorded. Reversal lasted 1 hr.

### Method of Analysis

Although the pups' responses were recorded during training and reversal while the reinforcer was off and during the 20-s periods when the reinforcer was on, we did not include all of the responses recorded in our analysis. To assess whether pups had learned the operant response–reinforcer contingency, we counted as part of our analysis the pup's first response during training and its first response each time the reinforcer turned off. If no correct responses were made during a 30-min period (and therefore no reinforcers received and no first responses after a reinforcer turned off) then only the first response of that period was included in the analysis. The number of first responses to both the correct and incorrect sides were totaled and the percent of head turns to the side reinforced during training calculated for all experimental periods.

### Results and Discussion

One-day-old pups did not learn to turn their heads to the side reinforced during training. In contrast, 5- and 11-day-old pups did significantly increase from baseline levels the percent of head turns to the reinforced side in training (Figure 5). Paired *t* tests compared the percent of head turns made during the first and second 30 min of training to the percent made during baseline. Tests with alpha levels less than .05 are reported as significant. As can be seen in Figure 5, the percentage of responses made by 1-day-olds to the correct side during the first,  $t(7) = 0.83$ , and second,  $t(7) = 0.74$ , 30-min periods during training did not differ from that during baseline. In the middle graph of Figure 5 it is clear that 5-day-old pups did, however, respond significantly more to the correct side during the first,  $t(7) = 4.01$ , and second,  $t(7) = 4.23$ , 30-min period of training than during baseline. Similarly, the rightmost graph shows that 11-day-olds responded significantly more to the correct side during the second 30-min period of training,  $t(7) = 5.42$ , even though first 30-min period of training,  $t(7) = 2.01$ , did not differ from baseline. Five- and 11-day-olds learned operant response–reinforcer contingency during 1 hr of training, but the 1-day-old pups did not.

Five- and 11-day-old pups significantly reduced the percentage of head turns during reversal to the side reinforced during training (Figure 5). The percent of head turns to the side reinforced during training was significantly lower for 5-day-olds during the first and

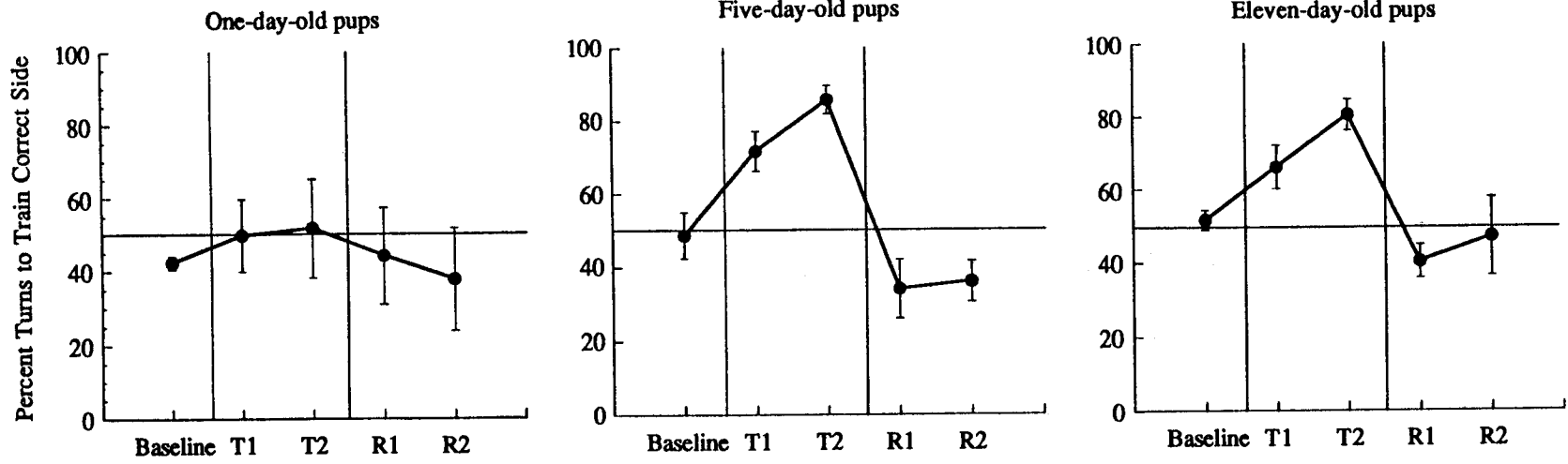
second 30 min of reversal from that recorded in the last 30 min of training,  $t(7) = 6.01$ , and the first 30 min of reversal did not differ from the second,  $t(7) = 0.21$ . The percent of head turns to the side reinforced during training was significantly lower for 11-day-olds during the first 30 min of reversal than in the last 30 min of training,  $t(7) = 6.01$ , and the first and second 30 min of reversal did not differ,  $t(5) = 0.94$ . The lower number of degrees of freedom in this last test reflects the fact that two 11-day-old pups stopped responding during the last 30 min of reversal.

The head-turning behavior of 1-day-old pups was not affected by switching the side that was reinforced during the reversal phase. The percentage of head turns to the side reinforced during training did not differ significantly in the first or second 30 min of the reversal phase from the percentage of head turns recorded to that side during training,  $t(6) = 1.74$  and 2.25, respectively. Because one 1-day-old pup stopped responding during the first 30 min of the reversal phase, the *t* test comparing the last 30 min of reversal to the last 30 min of training includes data for only 7 pups. The fact that the behavior of 1-day-old pups was not affected by switching the reinforced side is not surprising. One-day-olds did not learn the head-turning operant for the cool reinforcer during training, nor did they learn to turn their head in the opposite direction for the cool reinforcer during reversal.

There is an ontogenetic difference in learning the head-turning operant for a cool reinforcer. One-day-old pups did not learn the head-turning operant response for a cool reinforcer in a hot environment, whereas 5- and 11-day-old rats did.

### GENERAL DISCUSSION

The results of the current studies demonstrate an ontogenetic change in the pups' capacity to learn for a cool reinforcer between postnatal Day 1 and Day 5. The results of Phase 1 provided clear, age-related thermal preferences for 1-, 5-, and 11-day-old pups, through a surface temperature selection test in a 40°C ambience. These preferences then became the precise thermal parameters used for Phase 2. The positively thermotactic 1-day-old pups did not learn a head-turn operant for a cool (36°C) reinforcer in a hot (40°C) environment, though they readily learned the same operant for a warm (36°C) reinforcer in a cool (25°C) environment (Hoffman et al., 1999). We conclude, therefore, that a warm reinforcer is much more potent than a cool reinforcer for neonates, as we had expected. Five- and 11-day-old pups did learn the



**FIGURE 5** Percent of head turns to the side correct during training during baseline, training (T1 and T2), and reversal (R1 and R2). Five- and 11-day-old pups learned the operant during training and extinguished the learned response during reversal. One-day-old pups did not learn to turn their head to one side to receive the cool reinforcer.

head-turn operant for a cool reinforcer in a hot environment, leading us to also conclude that the potency of the cool reinforcer increased between Day 1 and Day 5. Because we customized the temperature of the cool reinforcer to the preferred temperature of each age group on the thermocline, instead of using a single cool temperature for all groups, we conclude that the age-related difference in learning for the cool reinforcer was not due to a difference in the absolute value of cool preferred by pups of different ages. The age-related difference in learning exists because the thermotaxis 1-day-old pups are constrained from learning for a cool reinforcer.

Pups of all ages explored the hottest region of the thermocline and moved away from the heat toward the cool end until they arrived at a preferred intermediate temperature. This preferred cool temperature, capable of supporting an approach response, was not capable of supporting associative learning in 1-day-old pups. Why did the 1-day-olds display a preference for a cool temperature on the thermocline, but fail to learn the head-turning operant for contact with the same cool temperature? It is critical to grasp the difference between the thermocline and operant tasks. On the thermocline, once the pup has moved from the hot location to a cooler preferred region it can remain at that temperature without further effort. In contrast, the pup platform in the operant task returns to 40°C after the 20-s reinforcement period ends. To maintain contact with the cool reinforcer in the operant task the neonate must respond with the operant each time that the reinforcer shuts off. The cool reinforcer is sufficient to elicit settling and maintain the pups' generally passive presence on that region of the thermocline, but is not sufficiently potent to support learning and performing the head-turn operant.

Five- and 11-day-old pups, in contrast to the neonates, did learn the head-turn operant for a cool reinforcer in a hot environment. Five- and 11-day-olds pups also preferred a cooler temperature (34°C) on the thermocline in the hot ambient than did the neonates. These results support our suggestion that the value of cool stimuli increases coincidental with the waning of the neonatal thermotaxis. That is, as the pups grow and are better able to conserve body heat, they must also develop mechanisms of dissipating heat such as panting, saliva spreading, and approaching and maintaining contact with cool stimuli.

It is interesting to note that although warm and cool stimuli can both serve homeostatic needs of rats of all ages (as revealed by their thermoregulatory behavior on thermoclines, the ability to serve a homeostatic need is clearly not sufficient to make the stimuli equivalent as reinforcers in an operant task. The cool tem-

perature preferred on the thermocline by 1-day-old pups was attractive, we presume, because it served the homeostatic need of cooling down the hot neonate. The same cool temperature was not, however, capable of supporting associative learning in 1-day-old pups.

The ontogenetic difference in learning for a cool reinforcer reported herein can be interpreted using the ontogenetic adaptation concept (Oppenheim, 1980, 1981) and the ecological perspective of development (Alberts & Cramer, 1988). The fact that neonates cannot learn an operant response for a cool reinforcer can be related to the infants' thermal adaptations. While the infant rat is dependent for survival upon responding to warmth with a thermotaxis response, there is no clear benefit to be gained from learning a novel behavior that would lead the pup toward a cool stimulus—such an ability would make the pup susceptible to learning behaviors that would move it away from its mother and littermate siblings and places its life in jeopardy. In fact, the presence of the neonatal thermotaxis strongly suggests that warm stimuli have a privileged status, connecting to strong and salient behavioral responses (the thermotaxis). In these ways we view the pups' learning ability as part of its overall adaptive organization. With growth and maturation of the thermogenic and insulative systems, pups become more thermally independent. We have also seen the pups learning for thermal reinforcement alter accordingly. These studies encourage further study of learning in adaptive/ecological frameworks.

## NOTES

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