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Neonatal Thermotaxis Improves Reversal of a Thermally Reinforced Operant Response

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ABSTRACT: One-, 5-, and 11-day-old rats in a cool environment (25°C) acquired an operant response when rewarded with a 20-s-long warming of the platform (from 25 to 36°C) on which they lay. In Experiment 1, the head-turning response was learned by pups at all ages. When the contingency was reversed so that pups were reinforced for turning to the side opposite that correct during training, the original response extinguished for 1-day-olds, but not for 5- or 11-day-olds. In Experiment 2, the rewarded side was randomly selected for each trial. One-day-olds perseverated in turning to the side correct on that trial while the reinforcer remained on, but 5- and 11-day-old rat pups did not. We conclude that 1-day-old pups were more responsive to the change in experimental contingency in Experiment 1 due to this thermotactic behavior. © 1999 John Wiley & Sons, Inc. *Dev Psychobiol* 34: 87–99, 1999.

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A 1-day-old rat can be removed from its nest and immediately trained to make the operant response of turning its head to one side (Flory, Langley, Pfister, & Alberts, 1997). The rewarding stimulus was a 20-s pulse of warming, provided conductively through the platform on which the infant lay. The learning was rapid—within 30 min—and robust, with the newborns performing more than seven responses per minute.

Warmth is a potent reinforcer in mammals, especially in small and immature ones, but thermal cues have remained generally underutilized in the study of

the ontogeny of learning and memory (Alberts, 1984). The experiments reported herein explore further the head-turning operant for thermal reward.

In Experiment 1 we tested 1-, 5-, and 11-day-old rat pups, using the methods of Flory et al. (1997). We predicted that pups in all three age groups would acquire the head-turn operant with a 20-s warming of the platform (from 25 to 36°C) in a 25°C environment. Earlier reports were encouraging: Infant rats as young as 1 day and as old as 8 days learned to raise their heads and activate a warm airstream (30–35°C) that provided convective warming (Guenaire, Costa, & Delacour, 1982). Three- to 5-day-old pups in the Guenaire et al. (1982) study did not learn the operant, however, presumably due to competition between the operant and emerging locomotor behaviors. On the other hand, Pfister (1990) found that 1-, 3-, 7-, and 11-day-olds learned a head-turning operant for a 40°C

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airstream—suggesting that there is no competition between the head-turning operant chosen for our experiments and emerging locomotor behaviors.

Though we predicted learning by 1-, 5-, and 11-day-old pups tested in Experiment 1, we anticipated some ontogenetic differences in learning or memory for tasks involving thermal stimuli. For instance, there might be age-related differences in the speed with which pups acquire the operant or in their ability to reverse an operant learned for a warm reinforcer. Our prediction of ontogenetic differences in learning was based on parallel differences in the strength and the form of thermal responses in infant rats at these ages.

Specifically, we view the rat's early behavior as dominated by responses to thermal stimuli. So dramatic is the neonatal rat's attraction to warm stimuli that the term *thermotaxis* is appropriate for many responses. We use the term *thermotaxis* to refer to a reliable pattern of movement of the organism toward a source of warmth (see Johanson, 1979; Leonard, 1974 for examples in infant rodents, and consult Fraenkel & Gunn, 1942 for a detailed and more definitive discussion of the term *taxis*). Although very young rats cannot maintain an upright posture or support their own weight, they will propel themselves toward warmth with their limbs ("crawling" or "swimming") and also by repeatedly rolling over and righting themselves.

Thermotactic behavior by rat pups is strongest in newborns and wanes over the 1st weeks after birth. When placed in contact with a surface temperature gradient (thermocline) neonatal mammals demonstrate strong thermotaxis (Hull & Hull, 1982; Johanson, 1979; Ogilvie & Stinson, 1966; Pfister, 1990). Several criteria can be used to assess strength of a thermotaxis on a thermocline: the consistency with which the pup initially moves toward the warmth, the effortfulness of their move toward warmth, and the temperatures sampled.

Younger pups are more consistent than older pups in moving first in the direction of warmth, instead of cool, on a thermocline. Pfister (1990), for example, found that 5-day-olds placed in contact with a 26°C zone on a linear gradient ranging from 19°C to 45°C consistently moved toward a warmer zone whereas 10-day-olds initially moved nonsystematically in relation to temperature.

Younger pups move more effortfully toward sources of warmth than do older pups. Johanson (1979) found that food- and social-contact-deprived 3-day-olds moved farther along a heat gradient than did similarly treated 6-day-olds. Pups of both ages moved away from cool zones of the thermocline, but the 3-day-olds moved further up the gradient, even after fre-

quent pauses and turns. Kleitman and Satinoff (1982) found that some of the youngest pups moved furthest on a thermocline during a 2-hr test. In the 20°C Start Group, two 1-day-old pups moved 15 cm toward the heat source while only two other pups under the age of 6 days moved as far.

Thermotactic infant mammals do not sample cold stimuli that older animals will sample under similar conditions. The range of temperatures that rat pups will sample on a thermocline remains stable and high (25–42°C) from birth to 15 days of age and only widens to include cooler regions during the 3rd postnatal week (Pfister, 1990). Hull and Hull (1982) observed that after moving from a cold starting location to a warm region, neonatal rabbits settle and remain at that location. In contrast, 9-day-old rabbits will occasionally move away from the preferred warm location to explore a cooler region and then return.

Rat pups show other response patterns indicative of diminishing thermotaxis. Huddling behavior by 5-day-old rat pups is profoundly affected by warmth to the exclusion of other perceptible stimuli whereas huddling by 15-day-olds is demonstrably affected by non-thermal stimuli—specifically, by olfactory cues of its own species (Alberts, 1978a; Alberts & Brunjes, 1978). Blumberg and Stolba (1996) describe the behavior of rat pups exposed to a drop in environmental temperature below that at which their body generated maximal heat by means of brown adipose tissue (BAT) metabolism. The drop in temperature caused sleeping 2-day-old and 7- to 8-day-old pups to wake. Upon waking, the 2-day-olds began stretching and locomoting. In contrast, 7- to 8-day-olds responded to the temperature challenge with increased vocalization but unaltered locomotion, suggesting a waning of the thermotactic response.

Evidence of waning thermotaxis suggests that the value of warmth as a reinforcer might also decline with age. We, therefore, anticipate ontogenetic differences in learning the thermally reinforced operant. Although the literature reviewed above indicates that the neonatal thermotaxis wanes over the entire first 3 weeks after birth, we tested pups in the 1st week and a half after birth with the knowledge that thermotaxis wanes dramatically during this period of development.

EXPERIMENT 1

Experiment 1 was designed to determine whether 5- and 11-day-olds pups would acquire the operant response for a warm reinforcer. One-, 5-, and 11-day-old pups were tested for a half-hour baseline during which no reinforcers were given. They were then

tested for an hour during which head-turning responses to one side were reinforced with warmth. During the final hour of testing all three age groups of pups were reinforced with warmth for turning to the side opposite that correct during training.

Method

Subjects. Subjects were 24 Sprague-Dawley rat pups (*Rattus norvegicus*) bred and born in the Animal Behavior 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 ($47 \times 26 \times 21$ 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. Pups from each age group were taken from four different litters (usually 2 pups from each litter, no more than 3 pups from any one litter).

Apparatus.

Overview: The apparatus consisted of a temperature-controlled enclosure, maintained at 25°C (Figure 1), and the subject platform on which pups were restrained during the experiment (Figure 2). The pup could completely cover one of two photocells by turning its head left or right. The temperature of the pup platform was controlled by circulating cool (25°C) or warm (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 25°C to 36°C for 20 s.

Testing Environment. Pups were tested in an enclosure ($79 \times 51 \times 35$ cm) in which ambient temperature was maintained at 25°C (see Figure 1). 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,

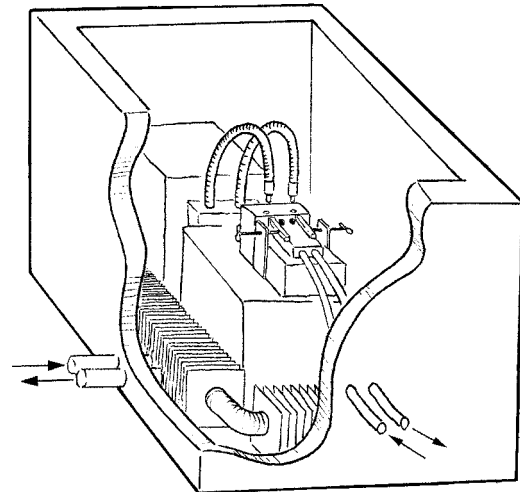


FIGURE 1 The experimental apparatus consisted of a pup platform, on which the pup was positioned, in a temperature-controlled enclosure. Water circulated through slant-fin tubing maintained the environment at a constant 25°C. The temperature of the copper pup platform was maintained at 25°C and increased to 36°C while the reinforcer was on by circulating water from one of two temperature-controlled water baths. A lamp with two gooseneck extension provided a directed source of light above the left and right photocells that sensed the position of the pup's head.

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 2). While the pup platform was constructed differently for the three age groups, the restraining platform was the same for all pups. The restraining platform ($20 \times 17 \times 6$ 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 ($4.4 \times 0.6 \times 1.3$ 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 accommo-

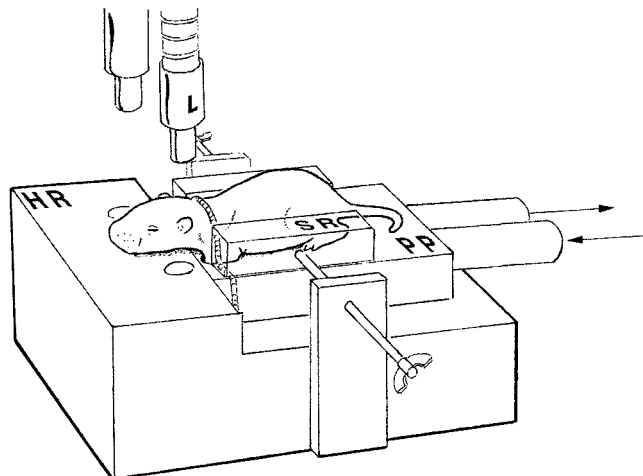


FIGURE 2 A 5-day-old pup is shown restrained on the pup platform (PP) by a string placed over the interscapular area and siderails (SR). A tissue-tape strap (not shown here) was also positioned over the pup's back. Two gooseneck extensions of a lamp (L) provided a directed source of light at the left and right photocells mounted below the pup's headrest (HR).

date the variation in body sizes. The headrest for 1-day-old pups ($10.2 \times 2.5 \times 3.5$) 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-old pups measured $11.4 \times 2.9 \times 3.8$ cm and the holes in the top of the black Plexiglas were 15 mm from the midline. The headrest for the 11-day-old pups measured $10.2 \times 3.2 \times 3.8$ 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 headrest 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 25°C or 36°C water were circulated (see Figure 2). 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' pup 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. The bottom of the platform measured 6.0×4.8 cm, and the top was 6.7×4.8 cm. The top of the platform was attached to the sides and bottom to create the 0.7 cm 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 were 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, 25°C water was circulated through the subject platform. When the reinforcer was turned on, 36°C water was circulated through the pup platform. Temperature flux was rapid; the platform surface temperature changed from 25°C to 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 ap-

proximately 3.2 cm above the surface of the head-rest.

All experimental events, including recording subject responses and delivery of reinforcers, were controlled 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 warmed from 25°C to 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 25°C to 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 25–36°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 in our analysis. To assess whether pups had learned the operant response–reinforcer contingency, we counted the pup's first response during training and its first response each time the reinforcer turned off. If no correct responses were made in 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 was calculated for all periods.

Results

One-, 5-, and 11-day-old pups learned to turn their heads to the side reinforced during training, significantly increasing from baseline the percent of head turns to the reinforced side (Figure 3). 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. One-, 5-, and 11-day-old pups made a significantly higher percent of responses to the correct side during the first, $t(7) = 3.81, 3.17, 8.05$, and second, $t(7) = 4.28, 3.60, 8.69$, 30-min periods during training. Thus, all three age groups selectively increased responses to the side designated correct by the experimenter. This selective increase in turns to the correct side indicates that the pups learned the operant response–reinforcer contingency.

In the reversal phase, 1-day-old pups significantly reduced the percent of head turns to the side reinforced during training whereas 5- and 11-day-old pups did not (Figure 3). Paired *t* tests compared the percent of head turns made during the first 30 min of reversal to the percent made during the last 30 min of training and compared the first to the second 30 min of reversal. During the first 30 min of reversal, 1-day-old pups significantly decreased the percent of responses to the side that had been reinforced during training, $t(7) = 2.49$. The percent of head turns to the side reinforced during training did not differ significantly between the

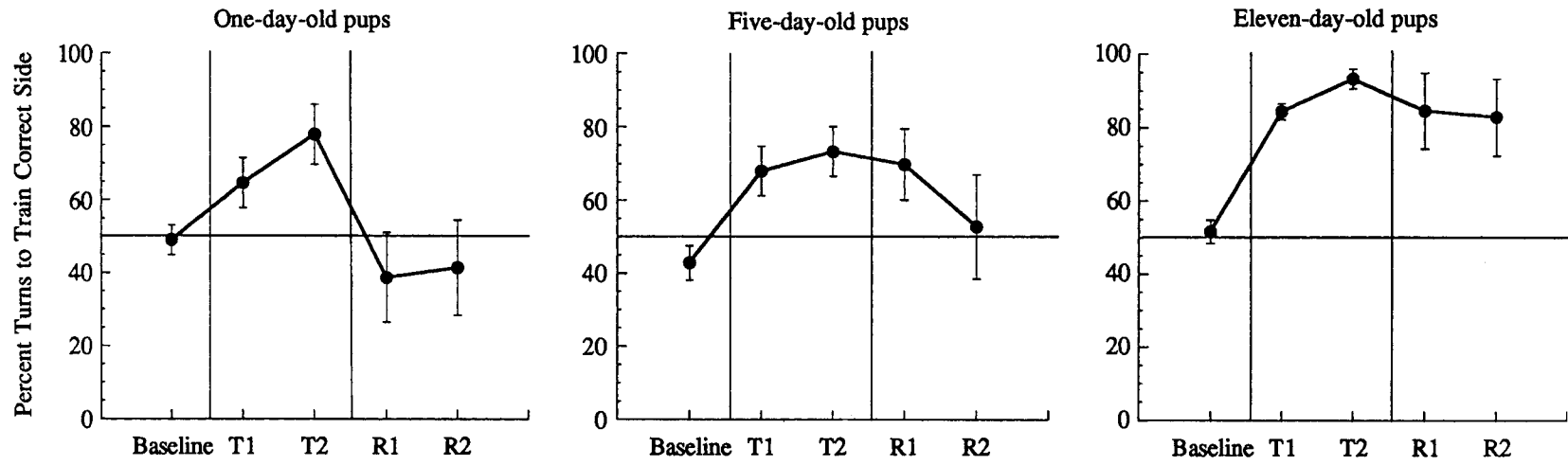


FIGURE 3 One-, 5-, and 11-day-old pups all increased the percent of head-turn to the correct side during training, relative to baseline, but only the 1-day-old pups began to reverse the operant response when responses to the side opposite that correct in training were later reinforced.

first and second 30 min of reversal, $t(6) = 0.66$ (The t test comparing the second 30 min of reversal to training includes data from only 7 pups because one 1-day-old pup stopped responding after the first 30 min of reversal. This cessation in responding is best explained not by response fatigue, but in terms of frustration that occurs when the reinforcement contingency is reversed—see Flory et al., 1997 for an extended discussion.)

Neither 5- nor 11-day-old pups significantly reduced the percent of head turns to the side reinforced during training when turns to that side were no longer reinforced (Figure 3). Only six 5-day-old pups were tested in the reversal condition because only 6 pups increased their percent of head turns to the correct side by at least 25% during training from baseline performance. The t -test comparing the first 30 min of reversal to training includes data for these six 5-day-old pups. One additional 5-day-old pup stopped responding after the first 30 min of reversal and the t test comparing the first and second 30 min of reversal therefore includes data for only five 5-day-old pups. The percent of head turns to the side reinforced during training did not differ between the last 30 min of training and the first 30 min of reversal for 5- or 11-day-old pups, $t(5) = 1.02$ and $t(7) = 0.80$, respectively. The percent of head turns to the side reinforced during training did not differ between the first and second 30 min of reversal for 5- or 11-day-old pups, $t(4) = 1.53$ and $t(7) = 2.56$, respectively. While low subject number may have influenced the lack of significant difference between training and reversal in the case of the 5-day-olds, this cannot account for the lack of a significant decline in responding to the side correct in training for the 11-day-olds because the t tests for these pups include all 8 subjects. Thus, there is no evidence of extinction of the operant response–reinforcer association during the hour after the response–reinforcer contingency was reversed for 5- and 11-day-old pups.

One possible explanation for why the 1-day-old pups extinguish but the 5- and 11-day-olds pups did not might be that the 1-day-old pups did not acquire the operant association as well as the older pups. But an ANOVA comparing the percent of head turns to the correct side during the second 30 min of training did not reveal a significant difference between age groups, $F(2, 21) = 2.74$. Single-degree-of-freedom comparisons between 1- and 5-day-olds and 1- and 11-day-olds during the second 30 min of training also did not reveal a significant difference in performance, $F(1, 14) = 0.18$ and 3.20 , respectively. All measures indicate that the 1-day-olds acquired the operant response as well as the 5- or 11-day-olds.

Discussion

One-, 5-, and 11-day-old rat pups acquired an operant head-turning response within 30 min of training during which head turns to an experimenter-designated correct side were reinforced by warming the platform on which they lay. After 1 hr of training, the 1-day-old pups' operant response extinguished when reinforcers were no longer presented for turns to the side correct during training, whereas 5- and 11-day-old pups continued to respond to the side correct during training.

We considered the possibility that the age-related difference in reversal of the learned operant could be because the 1-day-olds learned the operant less well than did the 5- and 11-day-old pups. We ruled out this explanation because 1-, 5-, and 11-day-old pups all performed the operant at equivalent levels during the final 30 min of training.

An alternative explanation for the age-related difference in reversal is that 1-day-old pups are dramatically thermotactic and therefore more responsive to the change in experimental contingencies for earning access to warmth than 5- or 11-day-olds. We test this hypothesis in Experiment 2.

EXPERIMENT 2

Experiment 2 was conducted to determine if there is a difference in thermotactic behavior toward the warm reinforcer for 1-, 5-, and 11-day-old rat pups that could account for the difference in the ability of 1-day-olds versus 5- and 11-day-olds to begin to reverse during Experiment 1. Evidence of a heightened responsiveness toward warmth in 1-day-olds was noted during preliminary data analyses for Experiment 1. As noted earlier in the method of analysis section (for Experiment 1), we included only the first response during each 30-min period and the first response emitted each time the reinforcer turned off (as an indication of whether the pup had learned which response would turn the reinforcer back on). We did, however, examine the percent of responses made to the correct and incorrect sides while the reinforcer was on in preliminary analyses. It seemed that 1-day-old pups were more likely to make head turns to the correct side during the 20 s that the warm reinforcer was on than were 5- and 11-day-olds.

We reasoned that an ontogenetic difference in thermotaxis while the reinforcer was on might account for the fact that 1-day-old pups were more responsive to the reversal in experimental contingencies than the 5- and 11-day-old pups. The 1-day-olds might have

turned “toward warmth” during the delivery of the reinforcer because they had a tendency to continue to turn toward the side that they had turned to immediately before reinforcer onset. We regard a stereotyped pattern of head turning toward heat as taxic. Our interpretation is that head turning is the initial and predominant movement used by neonates to sample the area around them and to initiate a continued trajectory or change in direction toward heat. Thus, a stereotyped pattern of head turning toward heat is an expression of thermotaxis. If 1-day-olds made thermotactic responses during the reversal period to the newly correct side while the reinforcer remained on, such responses might serve as practice that would make them likely to begin to reverse the operant learned during the first hour. After making many responses to the newly correct side while the reinforcer was on, 1-day-old pups would be more likely to turn their heads to that side when the reinforcer turned off, and less likely to turn in the direction that had been correct during training. If 5- and 11-day-old pups did not make as many responses to the correct side while the reinforcer was on they did not practice and the new response therefore, perhaps, did not begin to reverse the learned operant.

In Experiment 1, pups were reinforced for turning to one side for as many trials as occurred in an hour. This procedure does not enable determination of whether the pups turned to the correct side while the reinforcer was on (a) because that response was reinforced throughout training, or (b) because they perseverated in making the response that immediately preceded reinforcer onset. If 1-day-olds turned, while the reinforcer was on, to the side correct during training because they had been consistently reinforced for that response, then they might continue turning to the side correct during training when the reinforcer was on during reversal. If this happened, then a tendency to turn to the correct side while the reinforcer was on during training would not explain why the 1-day-olds were distinctly responsive to the change in experimental contingency during reversal. If, however, thermotaxis led 1-day-olds to repeat the response that occurred immediately before reinforcer onset then they would turn, while the reinforcer was on, to the side correct in training during training and to the side correct in reversal when the contingency changed. Turns to the side correct during reversal while the reinforcer was on would provide 1-day-olds with practice making the new response and explain their responsiveness to the change in response–reinforcer contingency.

To experimentally test whether an age-related difference in thermotactic behavior could account for the ontogenetic difference in modifying the learned operant during the reversal period, we modified the pro-

cedure of Experiment 1. In Experiment 2 a left head turn was correct on half of the trials and a right head turn was correct on the remaining trials for all pups. The side that was correct was randomly chosen on each trial. Because pups could not know which side to turn for any single trial, we expected that the proportion of head turns to the left or right would not depart from baseline when we analyzed the first head turn made after the reinforcer turned off. If pups perseverated the response that they had made immediately before reinforcer onset on that trial, while the reinforcer was on, then the number of head turns to the side “correct for that trial” would be significantly above chance while the reinforcer was on. We predicted that 1-day-old pups would continue responses to the side that caused reinforcer onset while the reinforcer remained on, but that 5- and 11-day-old pups would not demonstrate as strong taxic behavior.

Method

Eight pups of each age group (1, 5, and 11 days old) were tested in the experiment. Subject and apparatus information are the same as for Experiment 1.

Each pup’s responses were recorded for a 30-min baseline period during which no reinforcement was given. During testing the temperature-controlled platform warmed from 25°C to 36°C for 20 s when the photocell on the side correct for that trial was blocked by the pup’s head. On half of the trials in each group of 10 trials, left was correct and on half right was correct. Whether left or right was correct on any given trial was randomized across trials. Responses were recorded while the reinforcer was on and while it was off.

Method of Analysis

Method of analysis is the same as for Experiment 1 with the exception that the proportions of responses to the correct side were analyzed while the reinforcer was on and for the first response that occurred after the reinforcer turned off.

Results

One-day-old pups demonstrated a robust thermotaxis, whereas 5- and 11-day-old pups did not (Figure 4). For 1-day-old pups, the proportion of head-turns to the side correct on that trial while the reward was on did not differ from baseline during the first 30 min, $t(7) = 1.19$, but did differ significantly from baseline for the second, third, and fourth 30-min periods, $t(7) = 2.6$, $t(6) = 2.89$, and $t(5) = 3.03$, respectively. For 5-day-

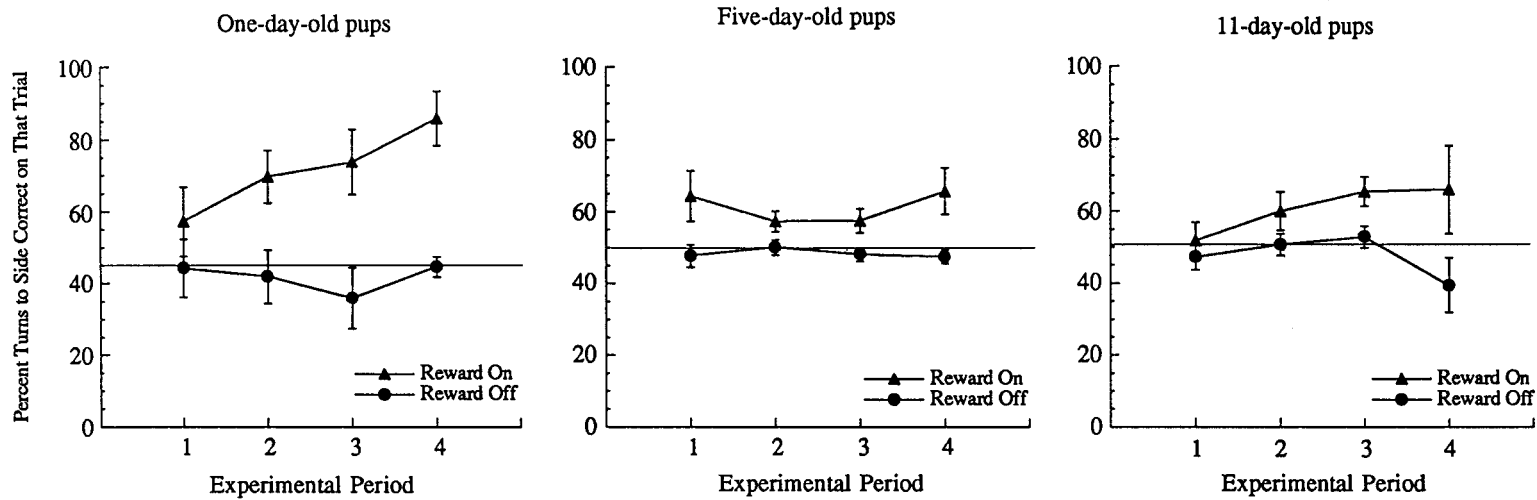


FIGURE 4 One-day-old pups perseverated in responding while the reinforcer was on to the side that they had turned immediately prior to reinforcer onset, but 5- or 11-day-old pups did not. Because the side that was correct on each trial was unpredictable, and left and right responses were correct equally often, the percent of responses to the side correct on that trial did not differ while the reward was off from the percent of responses to the left side during baseline (indicated by the solid line on each graph).

olds the proportion of head turns to the correct side while the reward was on did not differ from baseline for any period, $t(7) = 1.67, 1.60, 1.92, 2.37$. For 11-day-old pups the proportion of head turns to the side correct for that trial did not differ for the first, second, or fourth period, $t(7) = 0.08, t(7) = 1.11$, and $t(6) = 0.91$, respectively. The proportion of head turns to the correct side while the reward was on did differ for the third period for 11-day-olds, however, $t(6) = 2.98$.

Because head turns to the left and right were correct on an equal number of trials and the trials on which left or right was correct were randomized, we predicted that the number of first head turns made after the reinforcer was turned off would not depart from baseline and, in fact, it did not for any age group. The proportion of first head turns made after the reinforcer turned off did not depart from baseline for 1-day-old pups, $t(7) = 0.12, t(7) = 0.28, t(6) = 1.05$, and $t(5) = 0.66$; for 5-day-old pups, $t(7) = 0.46, 0.16, 0.31$, and 0.51 ; or for 11-day-old pups, $t(7) = 0.84, t(7) = 0.11, t(6) = 1.17$, and $t(6) = 1.40$.

Discussion

One-day-olds pups show a strong tendency to turn their head in the direction that was correct for that trial while the warm reinforcer is being delivered. During left-correct trials they turn their heads left while the reinforcer is on and during right-correct trials they turn their heads right while the reinforcer is on. Five-day-old and 11-day-old pups did not show robust thermal taxes. Although the 11-day-olds did turn in the correct direction for each trial while the reinforcer was on during the third 30-min period of testing, their responding was not significantly different from baseline during the first, second, or fourth periods.

GENERAL DISCUSSION

The results supported both our predictions, namely of acquisition of the head-turn operant for 1-, 5-, and 11-day-old pups, and of an ontogenetic difference in learning that correlates with age-related declines in the value of the warm reinforcer. One-, 5-, and 11-day-old pups learned to turn their head for a warm reinforcer in a cool environment within the first 30 min of a 1-hr training session, but only the responses of 1-day-old pups extinguished when reinforcement was later given for head turns in the opposite direction. An age-related difference in acquisition cannot account for the difference in extinction of the operant behavior because the three age groups performed the operant at the same high level at the end of training.

Experiment 2 revealed that 1-day-old pups, during the period that the warm reinforcer was on, responded significantly more to the side to which they had turned just prior to reinforcer onset than to the opposite side. In contrast, 5- and 11-day-old pups did not respond more to the side correct on that trial while the reinforcer was on. We interpret the 1-day-olds' persistent head turning as a direct reflection of their thermotaxis. That is, within the confines of testing situation, the pups' turning behavior reflected persistent movement in the direction of warmth.

We believe that an age-typical thermotaxis rendered 1-day-old pups distinctly responsive to changes in the operant response–reinforcer contingencies in Experiment 1. On those occasions during the reversal period in which a 1-day-old's head swung to the side opposite that correct during training, its thermotactic responses to heat created repetitive responses to the newly correct side, thus providing both practice of the new response as well as numerous reinforced responses to the newly correct side. Because 5- and 11-day-olds did not make as high a percentage of responses to the newly correct side while the reinforcer was on, they neither practiced as much nor did they experience as many reinforced responses. Therefore, the older pups did not begin to reverse the learned operant.

One-day-old pups are more thermotactic than 5- and 11-day-olds and more responsive to the change in experimental contingencies for earning access to warmth than the 5- and 11-day-old pups. We can gain insight into how the decline in thermotactic behavior relates to the decline in ability to respond to the change in response–reinforcer contingency in Experiment 1 by considering the concept of ontogenetic adaptation and an "ecological" perspective of developmental process. Oppenheim (1980, 1981) offered the concept of ontogenetic adaptation to denote features of the organism which appear—and often disappear—at a distinct point in development during which their appearance or disappearance serves some adaptive purpose. The ecological perspective, which integrates nicely with the concept of ontogenetic adaptation, characterizes development as a sequence 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, 1985; West, King, & Arberg, 1988).

We propose that the capability to learn for a thermal reinforcer changes during development as behavior towards thermal stimuli dynamically adapts to successive ontogenetic niches. That is, as thermotactic behavior wanes, the pup's capability to learn for a warm

reinforcer adapts. Why does the neonatal thermotaxis wane? There are two processes that may contribute.

First, waning of the neonatal thermotaxis over the 1st weeks after birth may reflect the development of the pup's ability to produce and conserve body heat over a range of environmental temperatures. Neonatal rats pups are exceptionally thermally vulnerable—they can neither produce nor conserve sufficient body heat to survive independently. At birth, a pup's body temperature drops from the intrauterine temperature of 37.5°C to that of the nest environment (25°C). Brown adipose tissue (BAT) thermogenesis is evident 30 min after birth (Alberts, Ronca, & Blumberg, 1992), but this initial thermogenic response is relatively meager. BAT thermogenesis improves dramatically over the 1st postnatal days: The maximum metabolic rate in response to cold challenge doubles from birth to 48 hr old (Taylor, 1960) and the BAT thermogenic response peaks at about 5 to 7 days of age (Hsieh, Emery, & Carlson, 1971; Takano, Mohri, & Nagasaka, 1979).

The ability to conserve body heat is as critical to maintaining thermal homeostasis as is the ability to physiologically generate heat. The ability to conserve heat doubles from 3 to 7 days of age alone (Takano et al., 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 5–19 days old. Growth (increased mass) tends to decrease 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). By 10 days of age a light coat of fur covers the rat pup's body, but, to our knowledge, its insulative value has not been studied. By Day 14, however, fur has a demonstrable value for maintaining body temperature (Hahn, 1956). Although neonates have no detectable vasoconstriction response to reduce heat loss, pups can effectively alter heat flow around 12 to 14 days of age (Conklin & Hegeness, 1971; Taylor, 1960). A final developmental step before achieving thermal independence is the appearance of shivering thermogenesis at or after Day 21 (Conklin & Hegeness, 1971; Taylor, 1960).

Second, the waning of the neonatal thermotaxis might reflect a change in the sensory cue that pups use to maintain contact with the huddle. Warmth is a stimulus that satisfies a homeostatic need for rats of all ages. For neonates, though, warmth is also a cue that guides them to the huddle. Neonates may respond thermotaxically to warmth because warmth is the signal for localizing the huddle and obtaining maternal care,

food, social stimulation, and protection from danger, as well as being a stimulus that allows the pup to maintain a stable, warm body temperature. Neonates displaced from the huddle orient and return even though sensory function is absent in some modalities (e.g., vision and audition) and severely limited in others (e.g., regional tactile sensitivity and olfaction). For the first 2 weeks after birth contact behavior is dominated by cues of warmth and contact comfort (Alberts, 1978b; Alberts & Brunjes, 1978; Cosnier, 1965; Jeddi, 1970; Rosenblatt, 1976). Contact comfort cannot be sensed until the pup is touching the target, but pups can sense and respond to the warmth of the mother and huddle from a short distance.

Over the 1st days after birth olfactory cues from the mother and siblings become established as incentives for a variety of behaviors, including huddling, because the odors are associated with warmth (Jeddi, 1979; Rosenblatt, 1976, 1983). The odor cue that elicits huddling is not preprogrammed. Brunjes and Alberts (1979) were able to reassign rat pups' filial attachment by altering the social odors it experienced in the nest. Alberts and May (1984) further determined that an odor experienced in association with thermotactile stimulation (a heated tube) becomes a cue for filial attraction for a neonate. By Day 15, and thereafter, olfactory cues (specifically, cues from their own species) dominate huddling (Alberts & Brunjes, 1978) just as olfactory cues will mediate recognition, attachment, and other forms of social behavior in adults (Alberts, 1981).

The thermal ontogenetic niche of the pup changes as the pup's physiology changes and as it learns about its social world. Neonates meet their need for thermal homeostasis by behaviorally thermoregulating—that is, staying in contact with the dam and littermates. Older pups can meet their need for thermal homeostasis by physiologically generating and conserving heat. Pups must maintain contact with the huddle to obtain maternal care and social stimulation necessary for survival. Neonatal rats respond solely to warmth as a means of locating the huddle, while older pups respond to olfactory cues that they have associated with warmth in the 1st days after birth. Because of the profound dependence of the neonate upon warmth as a stimulus that satisfies a homeostatic need and as a cue to locating the huddle, it is easy to imagine that thermotaxic behavior has been naturally selected. The thermotaxic behavior then disappears in older, more thermally capable pups who respond to olfactory cues to locate the huddle.

The enhancement in learning for a warm reinforcer for 1-day-old pups reported in Experiment 1 now can be understood as an ontogenetic adaptation to the neo-

natal thermal niche. It is easy to imagine that it is evolutionarily adaptive that neonates be able to modify their behavior (learn) in order to obtain heat from sources of warmth in their environment. The ontogenetic adaptation of enhanced learning for warm reinforcers later disappears as older pups become capable of physiologically generating heat and use olfactory cues, instead of warmth, as a means of maintaining contact with the huddle. Thus, a change in the pup's thermal niche can be seen as an integral part of its ability to learn. We expect that future investigations into the ontogeny of learning and memory for thermal rewards will further support the ecological perspective of developmental process described herein and demonstrate the robustness of the current findings at a variety of ambient temperatures and reinforcer temperatures.

NOTES

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