

Experience During Suckling Alters Later Spatial Learning

CATHERINE P. CRAMER*
JOHN P. PFISTER
KRISTINE A. HAIG
*Department of Psychology
The Johns Hopkins University
Baltimore, Maryland*

These experiments explore the role of preweaning experience in learning during the juvenile period. Pups that had been reared with many nipples available reached criterion on an 8-arm radial maze in a few trials; conversely, pups reared with only a few nipples required 3 times the number of trials to reach criterion (Experiment 1). Pups that had been reared with relatively few nipples available rarely nipple-shifted, while those that had been reared with a particularly high density of nipples shifted more frequently (Expt 2). A rearing procedure was devised that allowed precise experimental control of all phases of the suckling experience (Expt 3). Allowing or preventing a single behavior, nipple-shifting, while holding all other variables constant, was sufficient to affect acquisition of the maze task. In Experiment 4, the specificity of the early experience for later tasks was explored using a variety of nonspatial, lever-pressing operants. Rearing condition did not affect acquisition of a lever-pressing operant or of a visual discrimination task. However, pups reared with a high density of nipples responded at higher rates to a variable interval schedule and were more resistant to extinction. The possibility that strategy, rather than learning ability, was affected by rearing condition was assessed using a 2-arm maze task that was structured to present an optimal strategy of either win-shift or win-stay (Expt 5). The ease with which rats acquired the win-stay task was unaffected by rearing condition; all groups performed at about chance levels. However, pups reared with many nipples more readily acquired the win-shift task.

Introduction

In the course of ontogeny, young mammals can acquire a great deal of information from their environment. Interaction with the environment is clearly influential in, for example, the development of visuomotor coordination (Hein, 1972) and fine motor skills (Adams, 1968). Later, juveniles must acquire information such as the location of safe food sources (Galef, 1976) or appropriate responses to social cues (Harlow & Harlow, 1965).

Reprint requests should be sent to Dr. Catherine P. Cramer, Department of Psychology, Dartmouth College, Hanover, NH 03755, U.S.A.

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* Department of Psychology, Dartmouth College, Hanover, New Hampshire

Rather than study the adult manifestations of early experience, an alternative approach has been to focus on infantile capabilities during development, on the special circumstances that allow the expression of these capabilities, and on ways in which such capabilities might actually be utilized during the developmental period itself. The learning ability of very young rats has been demonstrated in a number of different paradigms, from acquiring a paddle-lifting operant task for oral infusions of milk (Johanson & Hall, 1979) to running simple mazes for the opportunity to suckle (Amsel, Burdette, & Letz, 1976; Kenny & Blass, 1977).

The learning capabilities of infant rats may also be functional in the nest situation. For example, the stimulation provided by the dam when she initiates a nursing bout may enable the pups to attach to the nipples, just as stimulating them in the presence of an unusual odor enables them to attach to that scent (Pedersen, Williams, & Blass, 1982). These data are consistent with the view expressed by Oppenheim (1981), who argues that development should not necessarily be seen as a progression towards the adult manifestation of a trait. Instead, characteristics during a particular developmental period may be adaptive to the organism at *that* point in time and not necessarily just as a precursor to some analogous feature at a later time. Thus, a behavior (such as suckling) may be specialized to meet an environmental demand that exists at a certain point in development.

An alternative approach, then, to the study of early influences could be to concentrate on how experience affects the manifestation of a behavior at a particular time in development. An understanding of how information can be utilized by the young animal for one purpose during a particular stage of development might be useful in determining what types of changes could be expected in the later behavior of that animal. Because the predominant activity of very young rats is suckling, it is possible that some aspect of this behavior provides the infant with experience that extends to performance in later tasks. Many demonstrations of early learning in the rat have been in the context of suckling. Moreover, the opportunity to suckle is itself sufficient to motivate performance in young rats, most notably in maze tasks (Blass, Hall, & Teicher, 1979). The experiments reported here seek a link between the early experiences of the infant rat while suckling and its ability to later acquire similar tasks.

Experiment 1

Preweanling rats are capable of various forms of learning, and these learning skills may be utilized during the normal course of mother–infant interactions, particularly those involving suckling. Experiment One asks whether the experiences gained by the infant during suckling would influence later behavior when searching for food after weaning.

Following a discrete, periodic milk letdown typical of rat lactation (Grosvenor & Mena, 1974), pups often leave the nipple and reattach to the same or another nipple. The incidence of this nipple-shifting behavior increases dramatically as the rats mature (Hall, Cramer, & Blass, 1975, 1977), peaking at about 21 days of age (Cramer, Blass, & Hall, 1980). In addition, the behavior is sensitive to deprivation; nondeprived rats shift far less than those that have been deprived (Cramer et al., 1980). One possible function of nipple-shifting behavior is increased milk intake. Relative intake during the limited number of letdowns that compose a normal suckling bout is perfectly correlated with the number of previously unsuckled nipples to which the pup attaches (Cramer & Blass, 1983).

The suckling rat, then, can maximize its intake by withdrawing the milk from the nipple to which it is attached during the letdown and then quickly moving to another, unsuckled nipple and withdrawing its contents. In many ways, the task demands placed on adult rats solving a radial maze (Olton & Samuelson, 1976) are somewhat similar. First, both the maternal ventrum and the maze present a spatial array of food sites. Second, in the pattern of discrete milk letdowns characteristic of rat lactation, each nipple is filled with a limited amount of milk once every few minutes. By comparison, each arm of the maze is baited at the beginning of the test session. Third, the milk in the nipple can be depleted by suckling, just as an arm of the maze is depleted once the rat has run down it and eaten the pellet. Returning immediately to the nipple or arm is not rewarded by additional milk or food, respectively. Both the infant rat suckling nipples and the adult rat solving the spatial maze can maximize intake by visiting each food site—nipple or maze arm—once and only once.

Because the nipple-shifting and radial arm maze situations share these similarities, experience gained during suckling may influence the later acquisition of the spatial memory task. If this is the case, young rats given ample opportunity to nipple-shift by having many nipples available to them should learn the task presented by the radial arm maze with greater ease than those whose nipple-shifting experience has been curtailed by having only a few nipples available. To test this hypothesis, rat pups were reared in litters of 5 either by a mother with all 12 nipples intact or by a mother with only 4 nipples.

Methods

Subjects

Primiparous and multiparous female Sprague-Dawley rats and their male offspring served as subjects in this series of experiments. Females were mated in our colony with Sprague-Dawley males from Camm Laboratories (Wayne, NJ) and were housed individually 3–7 days prepartum and during the entire nursing period in plastic tub cages (38 × 30 × 17 cm high) with stainless-steel wire lids. Hi-Protein Chow and water were continuously available in the lids. Nesting material (Sani-Chips) was changed twice weekly. Room temperature ranged from 23°C to 25°C, with humidity uncontrolled. Lights in the colony room were on from 0700 to 2300 hrs, EST. Nests were checked each evening for newborn pups. The day of birth was considered Day 0. All litters were culled to 10 pups on the day of birth. Pups remained with their natural mother for 5 days.

Rearing Procedures

On Day 5 postpartum, 2 males were taken from each of 5 litters. These 10 pups were then divided into 2 litter-matched groups of 5 pups each. These new “litters” were then given for the remainder of the nursing period (Days 5–24) to 2 dams, neither of whom was the natural mother of any of the experimental pups, but who had given birth on the same day as the natural mothers. One of these foster mothers was normal: all 12 nipples were intact. The other foster dam had only 4 nipples; the 8 additional nipples were surgically removed (under light ether anesthesia) prior to her mating. The pups remained with their 4-nipple or 12-nipple foster mother until Day 24. Two pups from each fostered “litter” were tested on

the maze. The rearing procedure was replicated 6 times to provide a total of 12 pups per cell.

To provide a baseline of normal juvenile maze performance, an additional 12 males, 2 from each of 6 litters, reared in standard litters of 10 by their natural, intact mother, were included.

A final replication of the two experimental groups was conducted with female rats ($n = 8/\text{cell}$) to assess any gender-related differences in performance or responsiveness to the early experience.

Apparatus

An elevated 8-arm radial maze similar to that of Olton and Samuelson (1976) was used. The center compartment was 34 cm in diameter with walls 15 cm high around the edge. Plexiglas guillotine doors were placed in the walls of the center compartment at the entrance to each arm. The arms were 9 cm wide and 56 cm long with a food cup 2 cm in diameter and 1 cm deep at the end of each arm. The first 10 cm of each arm had 8 cm high barrier walls on each side to discourage movement from arm to arm without returning to the central platform. The maze was constructed of wood and painted matte black. The testing room was well-illuminated, with a number of extramaze visual cues available.

Shaping Procedures

All pups began shaping at 21 days of age, when they were given pellets (45 mg, BioServ Precision Pellets) in the home cage. On Day 22, the second day of shaping, they were placed for 20 min in groups of 3–4 on the maze, with all the guillotine doors raised and pellets scattered liberally on all the arms. On the third day, they were placed on the maze in pairs, with pellets only on the outer half of each arm. On the fourth day, pups were placed individually on the maze for 10 min, with several pellets at the end of each arm. Following shaping on Day 24, pups were separated from their dams and deprived of food overnight.

Testing Procedure

Testing began on Day 25. Throughout the testing period, rats were maintained on a feeding schedule in which Purina Hi-Protein Chow was available for only 2–4 hr daily, beginning at irregular intervals after testing. Water was continuously available. Once a week, food was provided *ad libitum* for at least 24 hr. Testing was always preceded by at least 12 hr of food deprivation. This feeding regimen allowed the juveniles to grow, but at a somewhat slower rate. Their body weights averaged about 75–90% of normal juveniles allowed to feed freely during the same period.

At the start of each day's test session, 1 food pellet was placed at the end of each arm of the radial maze. The rat was placed in the center of the maze with all the guillotine doors down. A trial was begun by raising the doors at the entrance to each arm and allowing the rat to choose freely from among the 8 arms. A choice was defined as the point at which the rat's entire body and tail had passed through the plane of the door. In almost all instances, the rat continued on to the end of the arm and retrieved any available pellet. After a choice was made, the rat returned to the central platform and was confined for 10 sec before the next trial began. All

the doors were again raised, and the rat was again allowed to choose from among the arms. Testing continued in this manner until all 8 pellets had been retrieved, 10 min had elapsed, or 2 min had passed without the rat making a choice. In the case of this last option (which occurred on about 9% of trials on the first 3 days and rarely thereafter, independent of rearing group) the trial was excluded from the analysis if fewer than 4 choices had been made. On each trial, the doors approached and the arms chosen were recorded. Occasionally, young rats ran the full length of the arm and explored the food cup, but failed to eat the pellet. In these cases, which constituted a small percentage (2%) of the first day or two of testing, the pellet was removed following the trial and the failure to eat noted; the choice was still counted. Rats were tested once a day, 5 days a week, until they reached a criterion of 7 correct choices (i.e., to arms still containing food) in the first 8 trials for 5 consecutive test sessions. Analyses were conducted on the number of trials to the beginning of the criterion run and on accuracy of performance within each test day.

Results and Discussion

As is shown in Figure 1, rearing condition profoundly affected acquisition of the spatial maze task ($F(2,33) = 13.67, p < .001$). Control rats reared in litters of 10 by normal, intact dams learned the maze task quickly, performance comparable to that of adults (Olton & Samuelson, 1976). Rats reared in litters of 5 by normal, 12-nipple dams also performed well. The difference between these 2 groups was insignificant (Scheffe critical range = 6.11, $p = .05$; Scheffe c.r. = 8.73, $p = .01$). Thus, reduced litter size *per se* did not either improve or impede performance in the radial arm maze.

In contrast, rats reared in litters of 5 by dams with only 4 nipples available had considerable difficulty mastering the maze task, requiring a mean of 16 days to

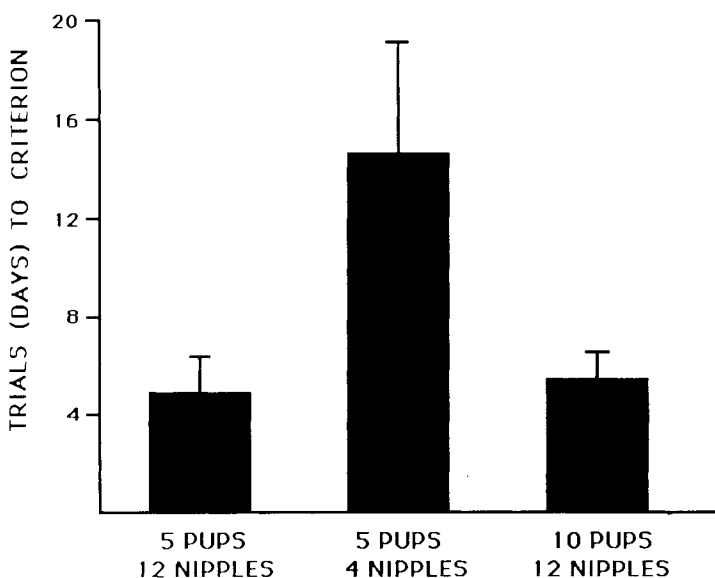


Fig. 1. Mean (\pm SEM) trials (days) to criterion on an 8-arm radial maze for rats from different rearing conditions.

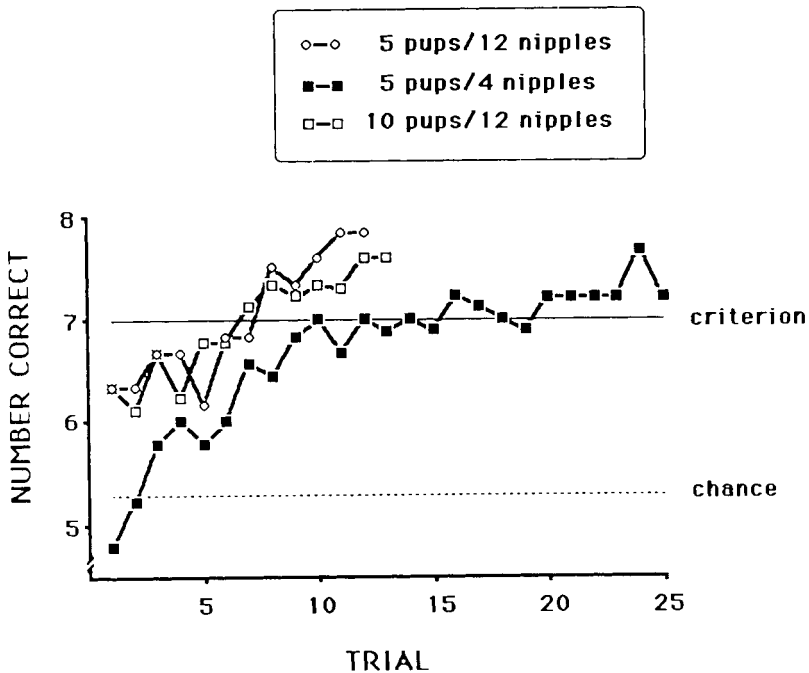


Fig. 2. Mean correct responses on each trial on an 8-arm radial maze of rats from different rearing conditions.

reach criterion. Their performance was significantly different from that of pups reared either in litters of 5 or in litters of 10 by intact dams.

A similar result was obtained with female rats reared in the same manner. Mean number of trials to criterion for pups reared in litters of 5 with 12 nipples was $5.8 (\pm .4)$ and for pups reared in litters of 5 with 4 nipples was $10.8 (\pm 1.3)$, a significant difference ($F(1,16) = 13.94, p < .01$). When these data were compared to those from male rats, neither a main effect of gender nor an interaction involving gender was significant.

The number of correct responses made by rats in each of the three rearing groups on the first eight choices is presented in Figure 2. Analysis of variance on the first 10 days of testing (when all groups are fully represented) revealed significant main effects of both rearing condition ($F(2,24) = 10.68, p < .001$) and trials ($F(9,18) = 21.52, p < .001$) and, more important, an interaction between rearing condition and trials ($F(18,216) = 2.65, p < .001$).

These results demonstrate that events during the preweaning period can influence performance on a complex spatial task later in life. Pups presented during suckling with many nipples later learned the maze task more quickly than their siblings who were presented with few nipples. Rats that had been offered (and presumably reinforced for seeking) a number of nipples during suckling began the maze task with a higher level of accuracy and improved more rapidly in their performance.

The results indicate that even the relatively limited experience presented by the normal litter situation of 10 pups with 12 nipples is sufficient for excellent performance on the spatial maze task. It is important to note, however, that the

maternal behavior of the rat may allow for even more shifting experience than would be predicted by simply the ratio of pups to nipples. Mothers in colony maternity cages were sometimes seen to divide large litters into two separate nests and nurse only one group at a time. Thus, in a given suckling bout, more than the statistically predicted 1.2 nipples might be available to each pup. Because a certain number of pups (4–5) must be attached to provide sufficient tactile stimulation to insure a milk letdown, such nest-splitting is unlikely among the two experimental groups.

Analyses were also conducted on the specific errors made by rats during the first 5 days of maze testing. These days represent the time during which both groups were still acquiring the task. The observed probability of a correct response was determined for each animal on Choices 2–8. The scores were then transformed to take into account the fact that an error will leave a greater number of baited arms still available for subsequent choices (see Olton & Samuelson, 1976, for details of the transformation). The transformed scores can range from 100, indicating perfect performance; through 0, indicating chance performance; to –100, indicating the maximum number of incorrect responses.

The results of this analysis for pups from the 2 experimental conditions are shown in Figure 3. Pups reared in litters of 5 by dams with 12 nipples showed a small, relatively stable decline in their choice accuracy over the successive choices. However, their scores were always substantially greater than 0, indicating greater than chance performance on even the 8th choice.

The performance of pups reared in litters of 5 by dams with only 4 nipples was quite different. They occasionally returned on the second choice to the arm that

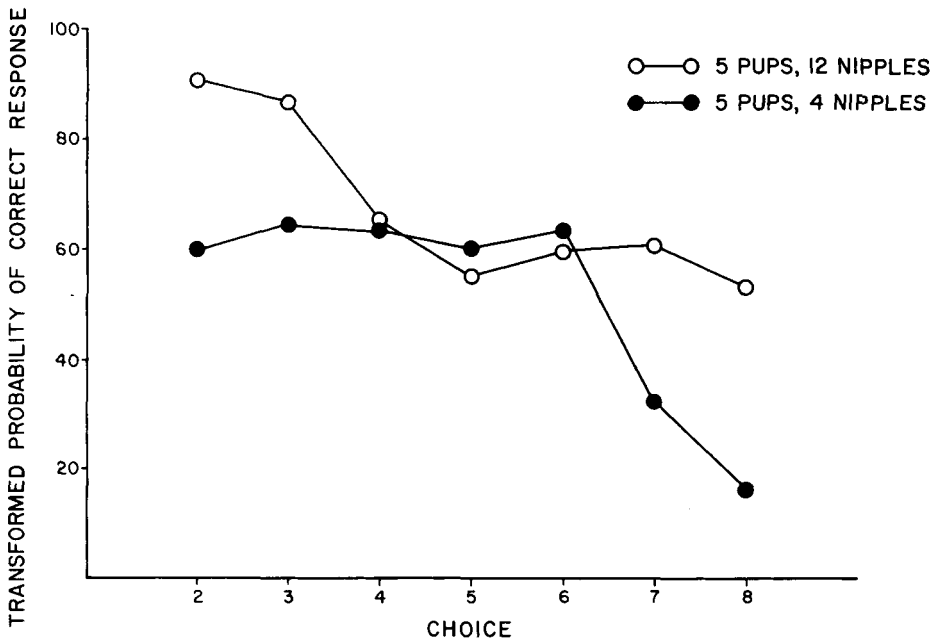


Fig. 3. Transformed error rates of rats from different rearing conditions. Error rates on the second through eighth choices during the first 5 days of maze testing were transformed as described in the text. A score of 100 indicates maximum number of correct responses; 0 indicates chance performance.

they had just visited on the first trial. While they did not have a tendency to return to the same arm (which would be indicated by a probability less than 0), or even drop to chance performance on this choice, their score was significantly less than that of pups from the 12-nipple group ($t(22) = 2.11, p < .05$). On choices 3–6, the performance of pups from the two groups was not significantly different. However, on the 7th and 8th choice, the probability of a correct response was significantly lower among pups reared with 4 nipples than pups reared with 12 nipples ($t(22) = 2.84, p < .01$ and $t(22) = 3.61, p < .01$, respectively). By the 8th choice, performance of the pups reared with 4 nipples had dropped to chance ($t(11) = 2.08, p > .05$). Thus, pups reared with only 4 nipples were not simply making more mistakes in a random fashion; they seemed to be less able to complete the maze task due to a higher rate of errors on the 7th and 8th choices.

Because nipple-shifting is related to greater milk intake (Cramer & Blass, 1983), differences in body weight would be expected following the experimental rearing conditions. This could present a problem in interpreting the results of this experiment, particularly in light of the finding of Jordan, Cane, and Howells (1981) that severe early (pre- and postnatal) undernutrition produces deficits in adult performance on radial arm mazes. However, despite the reduced number of milk sources available, the growth of pups reared with the 4-nipple dam was not adversely affected (Table 1). Weight differences between normal rats (10 pups with 12 nipples) and those with 4-nipple dams were not significant at any age. Thus, the poorer performance of the rats reared by mothers with only four nipples cannot be attributed to weight differences. Not surprisingly, rats reared in litters of 5 by normal mothers were significantly heavier by Day 20 ($t(22) = 3.82, p < .01$); however, this weight increase did not correlate with improved maze performance when compared to normal, 10-pup, 12-nipple litters.

As a further test that malnutrition was not a critical factor in this paradigm, another group of rats was tested on the maze following severe food deprivation. Nine pups were taken from 4 litters in which the dam was allowed only 70% of her normal food consumption during the last 2 trimesters of pregnancy and throughout the nursing period. This regimen was sufficient to allow most of the offspring to survive, but the pups were significantly reduced in size. Their average body weight at 30 days of age was 26.8 g ($\pm .95$ g), about half the average weight of normal 30-day-old rats. Following weaning on Day 24, these pups were allowed 3 days of *ad libitum* feeding during shaping; they were placed on the restricted feeding schedule and began testing on the 8-arm radial maze on Day 27. Despite their diminutive size, these malnourished rats were able to acquire the radial maze

TABLE 1. Mean (SEM) Body Weights of Rats from Different Rearing Conditions.

Age	5 pups		10 pups
	12 nipples	4 nipples	12 nipples
5 days	15.1 (.6)	14.8 (.4)	14.4 (.5)
10 days	29.2 (.7)	24.6 (.5)	25.1 (.6)
20 days	54.3 (1.2)	41.2 (.9)	42.6 (.9)
26 days	66.1 (1.4)	52.1 (1.2)	54.9 (1.5)

task relatively quickly. They reached criterion in a mean of 8.5 (± 1.8) days, no different from normal rats ($t(16) = 1.02$). Thus, the role of nutritional factors in the large deficits in maze performance of the pups reared with only 4 nipples available appears to be minimal.

Experiment 2

In Experiment 1, nipple-shifting experience was postulated to be the source of differences in maze performance of rats reared with either 4 or 12 nipples available. If this is the case, then nipple-shifting *per se* should also be affected, such that rats with ample nipples available should shift more than rats reared with few nipples. This experiment tested this hypothesis by studying the nipple-shifting patterns of rats from each of the three rearing conditions at 21 days of age by placing them with anesthetized dams.

Methods

Shifting behavior was assessed on an intact mother whose own pups were 18–22 days of age. The dam was anesthetized (Chloropent, 3 cc/kg, i.p.) and placed supine in a Plexiglas tub with perforated Plexiglas lid. Time-lapse video recordings were made to allow more careful review of nipple-shifting behavior (see Cramer, Blass, & Hall, 1980, for details).

Pups were reared as described in Experiment 1 until Day 20. They were deprived for either 4 or 24 hr and then placed, in groups of 3, with the anesthetized dam for 1 hr. The time of each nipple attachment, detachment, and subsequent reattachment was derived from the video recordings. For the analysis, a “shift” was defined as leaving the nipple, regardless of the particular nipple to which the pup reattached.

Fifty-four pups from 18 litters served as subjects ($n = 9/\text{cell}$).

Results and Discussion

As is shown in Figure 4, the incidence of nipple-shifting was profoundly affected by the number of nipples available to pups during the nursing period, independent of the level of deprivation to which the pups were subjected prior to testing. Analysis of variance revealed significant main effects of rearing condition ($F(2,48) = 9.76$, $p < .001$) and deprivation ($F(1,48) = 16.60$, $p < .001$) but no significant interaction ($F(2,48) = 2.68$). Thus, a suckling-related behavior typical of young rats can be modified in response to environmental conditions during development.

Interestingly, although the pups raised in litters of 5 with 12 nipples available shifted more often than those raised in litters of 10 with 12 nipples, the former performed only slightly but not significantly better on the maze task (Expt 1). This result suggests either that a certain amount of nipple-shifting experience is necessary and sufficient for rapid acquisition of the maze task or that the 8-arm radial maze task is not sufficiently sensitive to detect a difference (particularly in that rats from these groups were reaching criterion in only 5–6 trials). Use of a more challenging task, such as a 17-arm maze, could help resolve this issue.

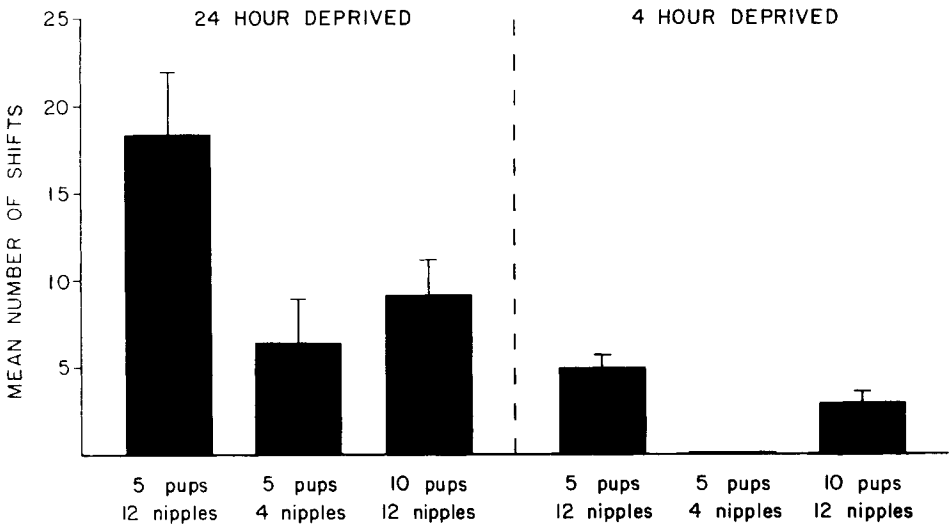


Fig. 4. Mean (\pm SEM) number of nipple-shifts of differentially reared pups deprived either 4 or 24 hr, during a 1-hr test with an anesthetized dam.

Experiment 3

The previous experiments assessed the importance of nipple availability during the preweaning period for the later expression of suckling behaviors and acquisition of a spatial maze task. The experimental rearing conditions were designed to merely encourage or discourage nipple-shifting while suckling. However, without continuously monitoring the nest cage, it is impossible to determine if, in fact, the relative availability of nipples actually led to the predicted differential experiences in the nest. Other potentially significant factors, such as patterns of maternal care and sibling behavior, could also differ between the various rearing conditions.

To increase experimental control over the experiences of infant rats during suckling, in this experiment pups were reared from Day 5 to Day 25 with all suckling limited to three daily periods with anesthetized, oxytocin-induced dams. To test the hypothesis that nipple-shifting was the critical behavioral experience for later maze learning, pups were either allowed to move freely among at least 3 nipples or restricted to a single nipple during each suckling session by blocking access to other nipples.

Methods

During the period of this experimental rearing, pups were housed with a dam without nipples; all of the foster dam's teats were removed (under anesthesia) prior to her mating. The dam, who was multiparous, was allowed to deliver her own pups and was given young pups to care for once daily for at least 5 consecutive days to ensure that her behavior was normal and that she was unable to deliver milk.

Experimental pups remained with their normal, natural mothers until Day 5 postpartum. At this time, 2 males from each of 8 litters were removed, numbered,

and given for rearing to the dam with no nipples. Except for the feedings, the pups remained with the foster mother until Day 24.

Feedings were given at 8 A.M., 4 P.M., and 10 P.M. daily. Dams to be used for the feedings were made milk-replete by 12–18 hr separation from their own young. For the feeding, the dams were anesthetized (Chloropent, 3 mg/kg, i.p.) and implanted with a PE-10 cannula in the ventral vein of the tail (for details, see Cramer & Blass, 1983). The cannula was attached to a 1-mL syringe containing oxytocin (Pitocin, Parke-Davis). Milk letdown (which had been blocked by anesthesia), were induced at 3–10-min intervals (on a random schedule) by infusing a threshold dose (0.0015 U in 0.1 mL isotonic saline) of oxytocin.

As many dams were used at each feeding as was necessary to provide the pups with at least 10% of their body weight in milk; usually 2 dams were sufficient. A battery of 36 dams, whose own pups were approximately the same age (± 5 days) as the test pups, was used to provide milk in each of the 2 replications. No dam was used more than 3 times during the 3 weeks of rearing, and a minimum of 5 days separated successive surgical procedures.

For each feeding, pre- and postfeeding body weight, time of each nipple-shift, and specific nipples suckled were recorded for each pup.

The experimental pups were divided into 2 sibling-matched groups. The first group was restricted (with the aid of Plexiglas barriers) to suckling from a single nipple during each feeding session. The second group was allowed unrestricted access to at least 3 nipples.

Shaping and testing on the 8-arm radial maze proceeded as described in Experiment 1.

Eight rats served as subjects in each of the 2 independent groups. Half were reared during each of the 2 replications of the rearing procedure.

Results and Discussion

As is shown in Figure 5, pups responded readily to the availability of nipples by increasing their incidence of shifting when allowed several nipples and rarely attempting to leave the nipple when restricted. (For this analysis, "shifting" was defined as leaving the nipple, irrespective of the nipple to which the pup subsequently attached.) Thus, the initial goal of this experiment, to modify nipple-shifting while keeping all other variables constant, was met.

Figure 6 demonstrates that the differential experience of nipple-shifting during the restricted suckling regimen was also associated with differential maze acquisition at weaning. Rats that had the opportunity to nipple-shift reached criterion far more quickly than rats that were not allowed to shift from nipple to nipple on the anesthetized dam ($F(1,14) = 10.27, p < .01$).

Once again, the differences in rate of maze acquisition cannot be attributed to variations in body weight. Table 2 compares the body weights of pups allowed to shift and those restricted from shifting. At no age did the pups that shifted differ in body weight from those that did not shift. Pups reared with anesthetized dams were, however, somewhat smaller than normal pups (see Table 1) at Days 15 and 20 postpartum ($F(2,21) = 20.50, p < .001$ and $F(2,21) = 7.41, p < .01$, respectively).

It must be emphasized that every aspect of the experimental treatments were identical except the shifting experience. Thus, the differences in maze perfor-

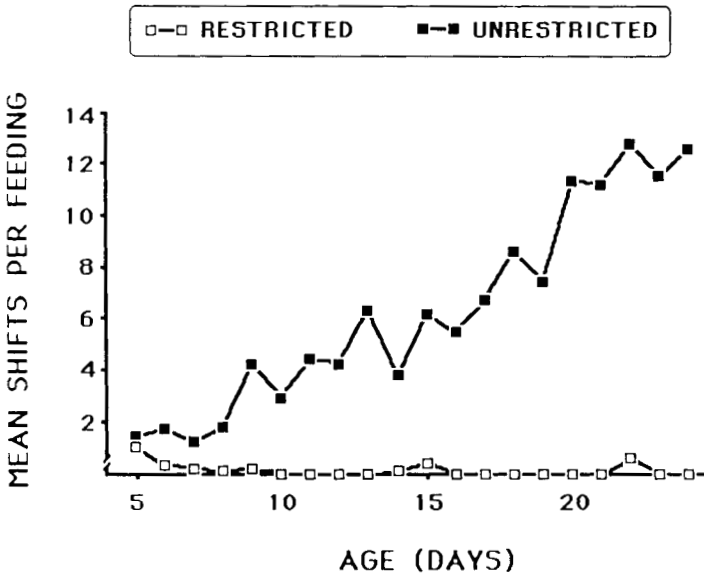


Fig. 5. Mean number of shifts per feeding session for pups either allowed to nipple-shift (Unrestricted) or prevented from nipple-shifting (Restricted). All suckling was with anesthetized, oxytocin-induced dams.

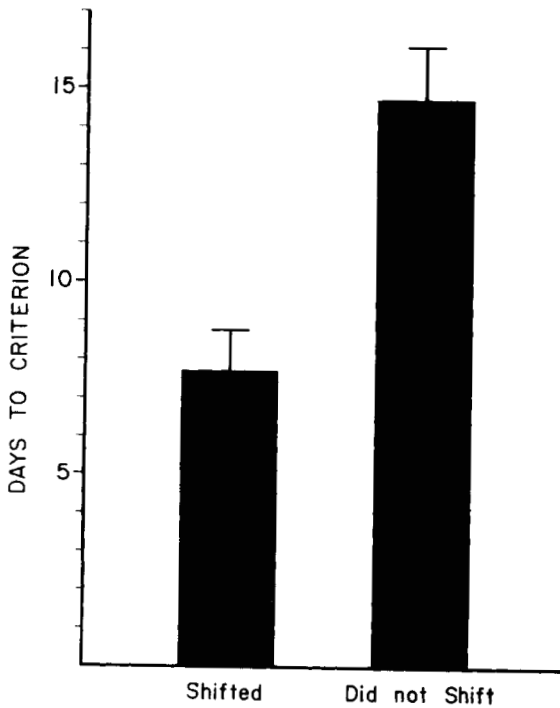


Fig. 6. Mean (\pm SEM) days to criterion on an 8-arm radial maze for rats either allowed to nipple-shift during suckling or prevented from nipple-shifting.

TABLE 2. Mean (SEM) Body Weights of Rats Whose Only Source of Suckling Intake from Days 5–24 Was with Anesthetized, Oxytocin-Induced Dams. One Group was Permitted to Nipple-Shift, the Other Group was Prevented from Nipple-Shifting.

Age	Shift	No Shift
5 days	15.8 (1.1)	15.6 (1.5)
10 days	21.6 (2.2)	21.7 (2.4)
15 days	24.2 (3.3)	22.9 (1.4)
20 days	36.0 (3.5)	33.9 (5.0)

mance between the two groups can be attributed to the presence or absence of nipple-shifting experience or its derivative consequences.

Experiment 4

In Experiment 1, experiences during suckling were shown to influence learning of a spatial maze task following weaning. The disparity in the performance of rats raised with different numbers of nipples available could reflect either a specific change in spatial learning capabilities or a more global alteration in learning ability or performance. Differences in spatial maze acquisition could be the result of more primary effects on behavioral processes.

To assess the influence of rearing condition on other learning tasks, rats were presented with a series of lever-pressing operant tasks. These procedures were designed to minimize spatial components. Rats reared in litters of 5 with either 4 or 12 nipples available were first trained to press a lever for continuous reinforcement. They were then presented with either a light-dark discrimination or variable interval (VI) reinforcement schedule followed by extinction.

One component of the 8-arm radial maze task is the animal's ability to discriminate, based on spatial cues, between arms that have been chosen previously and those not yet chosen. Olton and Samuelson (1976) have demonstrated that this is accomplished mainly by using extra maze visual cues. One potential source of the differences between the groups of differentially reared rats, then, could be their ability to make a visual discrimination. To test this hypothesis, one group of rats was trained on a simple visual discrimination operant.

Variable-interval reinforcement was used to determine any motivational differences between the groups (Clark, 1958). After several days of VI, they were tested for resistance to extinction.

Methods

All tests were conducted using standard operant equipment consisting of a rod-bottom Plexiglas testing chamber (16 × 22 × 12 cm high) placed within a wooden box (35 × 80 × 50 cm high) which could be sealed. Located on one wall of the testing chamber were a stainless steel response bar 4 cm from the floor, a food hopper 3 cm from the bar and 1 cm from the floor, and a small light 8 cm from the

floor. A buzzer outside the chamber was sounded when reinforcement was delivered. All shaping and testing sessions lasted 30 min.

Handling and shaping began after weaning on Day 24. Shaping proceeded by the method of successive approximation (Ferster & Skinner, 1954). All shaping procedures were conducted blind to the animal's rearing condition. This continuous reinforcement (CRF) schedule was maintained until a criterion of 80 responses was reached for 3 consecutive test sessions.

Following acquisition of lever-pressing for CRF, one group of rats was placed on a schedule in which reinforcement was given only when a small light in the test chamber was illuminated. Periods of "light-on" ranging from 2 to 5 min were randomly interspersed with periods of "light-off" from the same range. Two different schedules of 30 min each and containing approximately 15 min of "light-on" were presented in an ABBA pattern. Rats were presented with 1 of the 2 discrimination schedules daily (in an ABBA sequence), 5 days per week, until they completed 25 sessions. A criterion of 70% of responding in "light-on" for 3 consecutive days was used for the analysis. Fourteen rats from 4 litters served as subjects. All were reared in litters of 5, half by dams with 4 nipples and the other half by dams with 12 nipples.

Another group of rats was placed on a variable interval schedule in which an average of 1 reinforcement was given per minute. The intervals between reinforcements, randomly presented, ranged from 5 to 120 sec. Rats were given one half-hour session daily for 10 days. Following the 10 days of VI, all rats were placed on an extinction schedule, during which their bar-pressing was no longer reinforced by the delivery of pellets. Each rat spent one 30-min session in the chamber daily until reaching a criterion of 20 or fewer bar-presses per session for 3 consecutive sessions. Twelve rats from 4 litters served as subjects. All were reared in litters of 5, half by dams with 4 nipples and half by dams with 12 nipples; thus, there were 6 subjects per cell.

Results and Discussion

Figure 7 presents lever-pressing responding for each phase of the experiment. The sessions to criterion for each response are summarized in Table 3. There was no consistent difference in rate of acquisition of CRF between rats raised with 4 nipples and those raised with 12 nipples ($F(1,33) = 0.28, p > .5$). These data indicate that rearing condition has no effect on learning of this simple, largely nonspatial task, suggesting that the preweaning experience does not significantly

TABLE 3. Summary of Performance of Rats from Different Rearing Conditions on a Series of Nonspatial Lever-Pressing Operants.

	5 pups 4 nipples	5 pups 12 nipples
Days (trials) to criterion		
Lever-pressing operant	4.2 ± 0.4	3.9 ± 0.3
Visual discrimination	5.7 ± 1.5	4.7 ± 0.7
Extinction	4.8 ± 1.2	9.2 ± 3.5
Responses per 30-min session		
VI-1 min	578 ± 62	987 ± 246

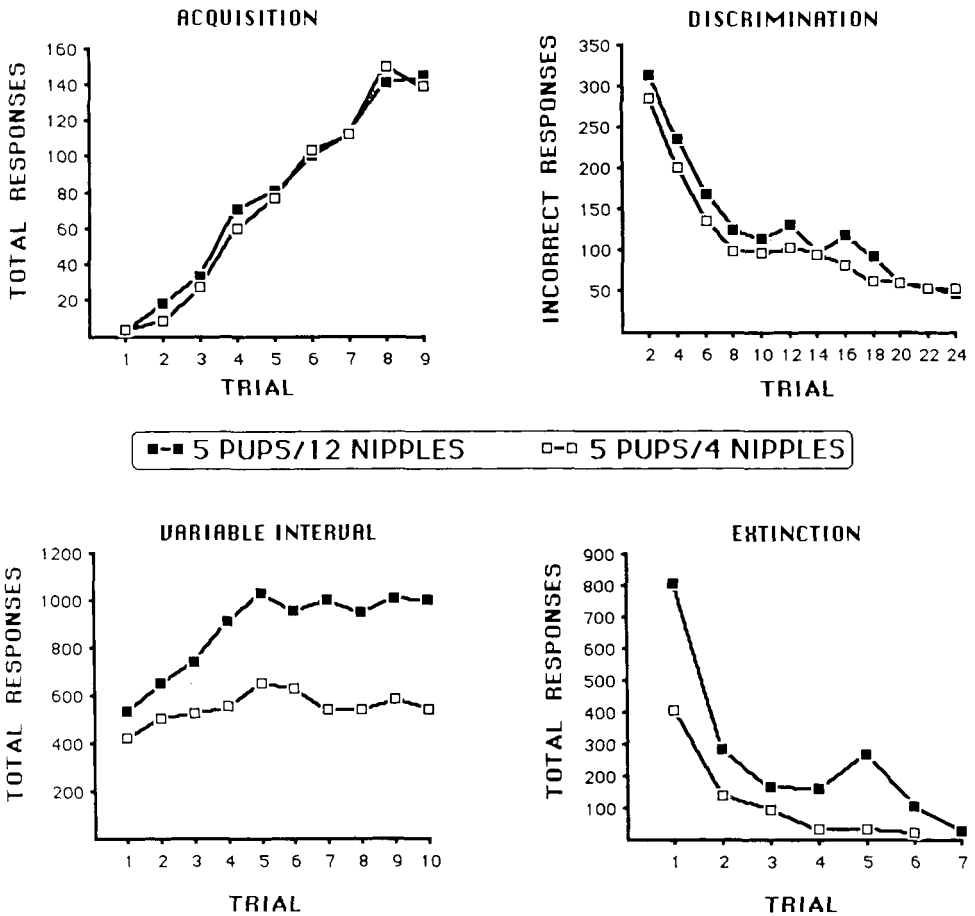


Fig. 7. Performance of rats on a series of nonspatial lever-pressing operants following differential rearing. Sequence of testing is described in the text.

affect such factors as neophobic reaction, level of motivation, or exploratory behavior, at least in ways which could bear on acquisition of a lever-pressing task.

Pups reared by dams with 4 nipples acquired the discrimination task as quickly as their siblings reared by dams with 12 nipples ($F(1,13) = 0.39, p > .5$). Thus the deficit in maze performance of the pups reared with 4 nipples cannot be attributed to an inability to make a visual discrimination.

The choice of criterion level for this task was determined by the asymptotic performance reached by young animals in a pilot study. It was, nonetheless, somewhat arbitrary. As a further confirmation of the results, a second analysis was performed, this time using a criterion of 90% responding during "light on" for 3 consecutive days. The mean number of days to criterion of the pups reared with 4 nipples was 16.2; for pups reared with 12 nipples the mean was 22.6 days. The difference between the 2 was again insignificant ($F(1,13) = 2.55, p > .05$). While the number of reinforced responses during each daily session was nearly equivalent, the rate of unreinforced responding was consistently higher among rats reared with 12 nipples.

Rats reared in litters of 5 with 12 nipples consistently responded to the vari-

able interval schedule at higher rates than rats reared in litters of 5 with 4 nipples ($F(1,90) = 16.86, p < .01$). Neither the trend toward increasing responses over test sessions nor the interaction between test session and rearing condition was significant.

Further, the rats reared by dams with 12 nipples were more resistant to extinction. Their responding began at higher levels and remained higher than that of the rats reared with 4 nipples for several days. Analysis of variance revealed a significant interaction between rearing condition and test session ($F(7,70) = 2.19, p < .05$), as well as a main effect of test session ($F(7,70) = 2.94, p < .05$). The two groups were significantly different from one another on the first 5 days of extinction (Scheffe *c.r.* = 62.4, $p < .05$). This difference is more clearly illustrated by examining the number of days to criterion required by each group. Pups reared in litters of 5 by dams with 12 nipples required 9.3 (± 2.2) days to reach the 20 presses per session criterion, while pups reared with 4 nipples required 5.1 (± 0.9) days ($F(1,13) = 5.62, p < .05$).

These data are consistent with the trends that first surfaced in the discrimination task. In all these situations, rats that had been reared with a greater density of nipples responded at higher rates. Thus, although there were no differences on the nonspatial tasks in learning capabilities between the groups, there was disparity in performance.

These variables could have affected performance on the 8-arm radial maze, but the relationship between responses in one setting and those in the other are not completely linear. The rats reared with 12 nipples displayed a tendency to persist in lever-pressing in the absence of reinforcement, however, they were rarely in the same situation on the maze: their choice accuracy was such that nearly all responses were reinforced. Conversely, although the rats reared with 4 nipples responded by bar-pressing at lower rates, they *did* respond, and on the maze they persisted in choosing arms despite repeated errors that were not reinforced.

Experiment 5

The 8-arm radial maze has been characterized as a series of decisions following a strategy of win-shift (Olton & Schlosberg, 1978). That is, the optimum strategy is to leave an arm once it has been depleted and to go to one on which food remains. The converse strategy, win-stay, is to locate a single food source and remain in or return to that same location. Reward is maximized by returning to the same place where food was previously found.

Normal adult rats have a strong tendency to follow a win-shift strategy. In a seminaturalistic environment, they will visit all known food sites before retrieving the day's food supply (Olton, Walker, Gage, & Johnson, 1977), a behavior pattern also seen on multi-arm mazes (Barnett & Cowan, 1976). Even when all the food is placed at a single location, rats will visit all the sites. Given a choice of only 2 arms, both with reinforcement, rats tend to spontaneously alternate on the basis of spatial cues (Dennis, 1939; Douglas, 1966). When reward contingencies on the 8-arm radial maze are altered to favor a win-stay strategy, rats have great difficulty learning the task (Olton & Schlosberg, 1978). Even in a 3-arm maze task, rats acquire a win-shift pattern more quickly than a win-stay pattern (Olton, Handelsmann, & Walker, 1981).

The rearing conditions of different nipple availability described in Experiment 1 could also be characterized as having opposite optimal strategies. The win-shift strategy is optimal in the situation of high nipple availability; intake can be increased by shifting from a depleted nipple to a milk-replete one. The rearing condition in which 5 pups must share 4 nipples may be an example of a situation where a win-stay strategy is optimal. A pup that leaves the nipple is not likely to find another nipple that still contains milk. In fact, a pup that leaves may lose its position to the extra pup that was not attached at the time of the milk letdown. A pup that remains attached will receive periodic milk letdowns as long as the dam remains in the nest.

If the performance deficits on the 8-arm radial maze reported earlier (Expt 1) result from differences in strategy acquired in the nest, then the ability to learn win-shift and win-stay tasks should reflect those differences. Rats from the high nipple availability condition should acquire the win-shift strategy with relative ease and the win-stay strategy with relative difficulty, while their siblings reared by dams with only 4 nipples should have more difficulty with the win-shift and less difficulty with win-stay tasks. This experiment tests this hypothesis using a Y-maze paradigm. The task presented to each rat was to maximize intake by adopting either a win-shift or a win-stay strategy.

Methods

Pups were reared in one of the three conditions described in Experiment 1: 5 pups with 12 nipples, 5 pups with 4 nipples, or 10 pups with 12 nipples. At weaning on Day 25, they were assigned to either the win-shift or the win-stay task.

Shaping began on Day 21 and proceeded as described in Experiment 1, except that the procedure took place on the Y-maze. Testing began on Day 25.

A trial was begun with a forced choice to one or the other arm. The particular arm for each forced run was determined by a randomized schedule. Following the forced run, the rat returned to the start box and was then allowed to choose freely between the arms. Following this choice, the rat was placed in a holding cage for a brief time (2–4 min) until the next trial. A trial was terminated any time that the rat failed to make a choice within 30 sec. Each rat received 8 trials in each daily test session and 5 sessions per week until completing a total of 15 sessions.

The shift and stay groups differed with respect to the goal arm that contained food during the choice run. Rats in the win-shift group were rewarded for choosing the arm not entered during the forced run of that trial. For example, if the right goal arm was entered during the forced run, food was available in only the left goal arm for the subsequent choice run. Thus, on each trial the rat was required to shift its response from the arm entered during the forced run to the other arm in order to get food.

Rats in the win-stay group were rewarded for returning to the goal arm entered during the forced run of that trial. For example, if the right goal arm was entered during the forced run, food was available only in the right goal arm for the subsequent choice run. Thus, on each trial the rat was required to return to the arm entered during the previous forced run in order to get food.

Forty-eight rats from 12 litters provided 8 subjects for each of the 6 independent cells.

Apparatus

An elevated, modified Y-maze was used in this experiment. The choice arms were 9×56 cm, with food cups at the end. The start area was a pentagonal platform. The 2 adjacent sides to which the arms were attached were each 20 cm long; the angle between the arms was 135° . Forming right angles to each of these sides were sides 23 cm long. The side farthest from the choice arms was 20 cm long. The maze was constructed of unpainted wood.

The choice arms were separated from the platform by wooden, 10-cm-high guillotine doors. For the forced choice, only the door to the baited arm was raised. For the free choice, both doors were raised. During the period of confinement between choices, both doors were lowered.

Results and Discussion

The results of performance on the Y-maze are shown in Figure 8. Analysis of variance revealed a three-way interaction between rearing condition, task, and test day ($F(28,420) = 2.80, p < .01$). In addition, the interaction between rearing condition and test day ($F(28,420) = 2.32, p < .01$) and the main effects of task ($F(1,30) = 23.32, p < .001$) and test day ($F(14,420) = 2.05, p < .05$) were significant.

The average Scheffe critical range ($p < .05$) between groups within a test day was 1.68. Using this value, the 3-way interaction can be summarized as follows: During the first 3 days of testing, the groups did not differ from one another; performance on either task hovered around chance. Chance performance on ei-

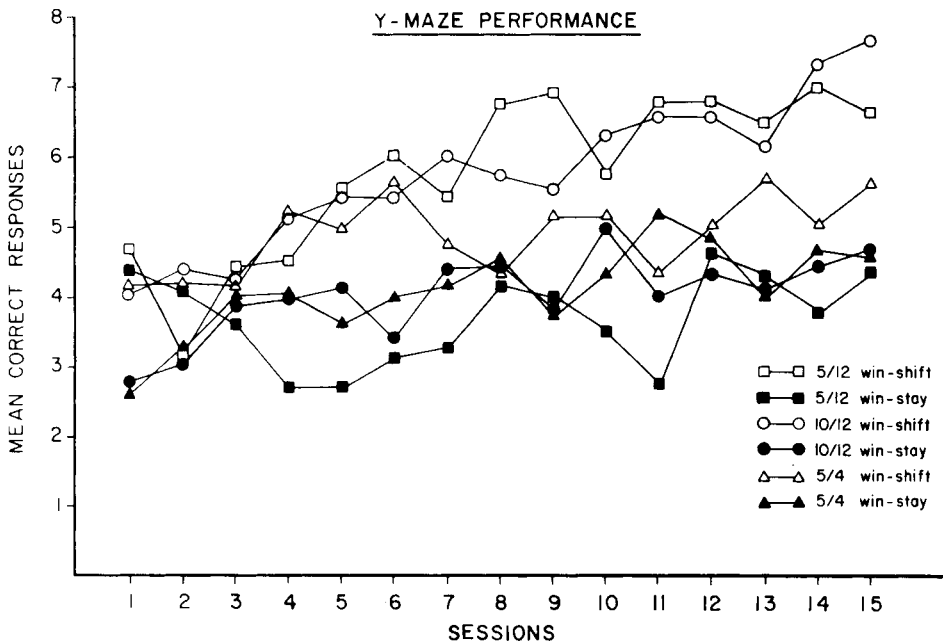


Fig. 8. Mean number of correct responses of rats from each of the three rearing conditions, given either a win-shift or a win-stay task in a Y-maze, for each of 15 daily sessions. There were 8 trials per session, thus chance performance is 4 correct.

ther task was 4 correct choices. On the 4th through 7th days of testing, rats in the win-shift task made fewer errors than those in the win-stay task, independent of rearing condition. Except for an occasional day's performance, rats in the win-stay group did not improve over the 15 sessions. This was true regardless of rearing condition. On the other hand, performance on the win-shift task, for most of sessions 8-15, was affected by rearing condition. Rats reared with only 4 nipples made more errors than rats reared with 12 nipples. In fact, on most days, the performance of the win-shift task by rats reared in litters of 5 with 4 nipples was insignificantly different from their performance of the win-stay task. The rats reared in litters of 5 by dams with 12 nipples did not differ from the rats reared in litters of 10 by dams with 12 nipples.

These data suggest that at least one reason why the pups reared with only 4 nipples did poorly on the radial arm maze was that they were less able to perform a win-shift task. Whether their deficit was in adopting the strategy or in remembering the specific arm to which they must go is not clear from these data. It is certainly not the case that they have adopted a win-stay strategy. Their performance of this task hovered around chance levels throughout the period of testing.

General Discussion

The results of the present experiments demonstrate that experiences gained by infant rats during the suckling period, and probably in the course of the suckling act itself, can influence later food-gathering behavior. The results of Experiment 1, in which the rate at which juveniles acquired the radial-arm maze task was altered by the availability of nipples during suckling, provide a striking example of an effect of early experience on at least one form of learning. A number of potential interpretations of these results are possible. Experiments 2-5 were aimed at further elucidating some of these considerations.

Maternal Behavior

Alterations in the pattern of maternal care can have effects on the later behavior of the young. For example, maternal effects have been demonstrated in such later reactions as avoidance behavior (Levine & Thoman, 1969), open field behavior (Reading, 1966), and aggressive behavior (Flandera & Novakova, 1974). One finding with potential significance for the present study is that rats whose mothers were stressed during the postnatal period were adversely affected on conditioned avoidance acquisition (Levine & Thoman, 1969). If the surgical procedures involved in reducing the number of available nipples to 4 in the present experiments were sufficiently stressful, then it is possible that the results may have reflected altered maternal care patterns rather than nipple availability.

A second potential source of difficulty with the nipple-removal procedure may be changes that reduced nipple number could produce in hormonal balance. The stimulation provided to the dam by the pups as they suckle has a very pronounced effect upon the functioning of the pituitary and particularly on the release of prolactin (Grosvenor & Mena, 1974). Prolactin levels decline rapidly if the pups are removed. Even the demands of the litter, expressed through the intensity of suckling, are reflected in the amount of hormone present. Raising the number of pups from 2 to 6 increases pituitary prolactin concentration 42% (Tucker, Paape,

& Sinha, 1967) and from 2 to 8 pups increases concentration 3-fold (Mena & Grosvenor, 1968).

Maternal behavior may be altered by changes in prolactin levels. Prolactin may stimulate the onset of maternal behavior (Riddle, Lahr, & Bates, 1942). However, the reproducibility of these results has been questioned (Lott & Fuchs, 1962; Beach & Wilson, 1963). Prolactin does not seem to be involved in the normal onset of maternal behavior at parturition (Stern, 1977; Baum, 1978). More important, the *maintenance* of postpartum maternal behavior does not depend upon prolactin, as blocking its release does not interfere with continued normal maternal caregiving (Zarrow, Gandelman, & Denenberg, 1971).

Although lactation and galactopoiesis are dependent upon prolactin, the performance of nursing behavior does not depend upon this hormone (or apparently any other, once the behavior has been initiated [Rosenblatt, Siegel & Mayer, 1979]). In fact, seemingly normal maternal behavior has been demonstrated in dams whose nipples or entire mammary glands have been removed (Moltz, Geller, & Levin, 1967; Zarrow, Johnson, & Denenberg, 1973). These dams performed all measured facets of maternal behavior (except, of course, milk delivery) in ways that were quantitatively and qualitatively indistinguishable from intact females. Thus, removing a few nipples, as was done in the present experiments to reduce nipple availability, is not likely to have had any apparent effect on maternal behavior.

Even if measurable patterns of maternal responsiveness were not undermined by the nipple removal procedure, it is still possible that more subtle changes in the mother-infant interaction could be occurring and that these alterations were the source of differential maze performance. A stronger case against such influences comes from the results of Experiment 3, in which pups suckled only anesthetized dams. Because they were housed with a single, thelectomized dam, all pups received virtually the same maternal care-giving. The only difference between the two experimental groups was nipple availability during the suckling sessions with anesthetized dams. This 1 factor was sufficient to modify maze performance. Thus, although maternal behaviors no doubt have profound influences on some later behaviors (perhaps including some of the lever-pressing tasks of Experiment 4), their impact on performance in the radial-arm maze was minimal when compared to the importance of nipple availability.

Stress, Timidity, and Neophobia

Coupled with the reduction in the number of nipples available is an increase in competition between the suckling pups. If this competition is similar in some ways to crowding, then the pups may be considered to have been subjected to a form of stress. Since it has been shown on numerous occasions that various forms of early stress and stimulation, including crowding, can influence "emotionality" and neophobic responses (e.g., Ader, 1959; Denenberg, 1967; Goldman, 1965), then it is possible that the poor maze performance of the pups reared with four nipples resulted from these influences rather than more cognitive factors.

Three pieces of evidence argue against such a position. First, pups reared in litters of 10 by a dam with 12 nipples may have been subjected to similar crowding and competition, particularly when the dam grouped them into a single nest. However, their maze performance was significantly better than that of the pups reared with 4 nipples. Second, when pups were reared with anesthetized dams,

there was little or no competition between pups in either condition. Neither initial attachment to the nipple nor subsequent reattachments were hindered by siblings. Restriction to a single nipple did not result from competition between siblings but rather from placement of an inanimate barrier. Moreover, pups restricted to a single nipple stopped even attempting to shift within a few sessions. Since pups reared by awake dams with 4 nipples also did not shift in the tests at Day 20, it is possible that, beyond the initial attachment, there was little competition between these pups, too. Finally, at least 1 neophobic behavior, freezing, was not apparent during maze testing of pups reared with 4 nipples. The incidence of trials which had to be terminated because the rat did not move into an arm for 2 min was slightly lower among the pups reared with 4 nipples (5 trials) than it was among the pups reared in litters of 5 with 12 nipples (8 trials). Neither group of rats appears to be any more neophobic or timid when tested. Thus, although early stress may have been occurring in the reduced nipple situation, its impact, like that of changes in maternal behavior, does not seem sufficient to explain the large differences in radial maze performance.

Learning Capability

The general ability to acquire new responses does not seem to be affected by the early rearing conditions that led to differences in performance of the 8-arm radial maze task. Rats reared with few nipples available acquired the lever-pressing response and visual discrimination task as readily as their siblings reared with many nipples available.

It is possible that the relative complexity of the task was a variable, that the lever-pressing tasks were simpler than the 8-arm radial maze task. The fact that the performance of the pups reared with few nipples declined in the later choices of the 8-arm task supports such a notion. On the other hand, the rats reared with few nipples were also impaired on acquisition of the Y-maze task, which involved only 2 arms and thus would seem to be a simpler task. Experiments are currently underway to address this problem.

The ability of young rats to learn while in the nest was demonstrated by the study of nipple-shifting behavior *per se* (Expt 2). Young rats varied the incidence of their nipple-shifting behavior in response to the situation in which they suckled. In the case of pups that were restricted to a single nipple while suckling anesthetized dams (Expt 3), this represented the suppression of an existing response rather than a failure to acquire that behavior. Most of these rats attempted to shift during the early sessions, but ceased to do so within a short time. It seems to be the case that young rats are sensitive to conditions in the nest, such as the relative availability of nipples, and are capable of altering their patterns of suckling behavior in response to those contingencies.

Response Strategies

A further possible explanation for differences in performance on the 8-arm radial maze was the differential employment of certain simple response strategies. An inhibition of consecutive identical responses would lead to accurate maze performance, while perseveration in a single response would lead to poor performance. The suckling situations presented by either an excess or a paucity of nipples would seem to favor the adoption of one or the other of these strategies,

respectively. The Y-maze procedure was thus devised to assess the readiness of rats from the different rearing conditions to adopt one or the other of these response strategies. The ease with which all rats acquired the win-stay strategy was unaffected by rearing condition; all performed at about chance levels for several weeks. However, pups reared with few nipples available did not acquire the win-shift strategy as readily as did their siblings reared with many nipples available. This does, to some extent, explain their poorer performance on the 8-arm task, which is a more complex win-shift task. However, because they did not more readily acquire the win-stay task, it does not seem plausible that they are learning a particular strategy in the nest situation.

Implicit in the hypothesis that stimulated Experiment 1 was the idea that infant rats could be learning tactics while suckling that could then be extended to a similar food-gathering situation at weaning. Although, as hypothesized, performance in the 8-arm maze was affected, the data from the subsequent experiments do not support the notion that the mechanism was acquisition of response strategies during suckling. If the infants were learning strategies about gathering food in the nest and extending them to the 8-arm maze, then they should have been able to similarly extend those strategies to the simple Y-maze tasks. Although the rats reared with 12 nipples were able to perform somewhat better on acquisition of the win-shift task in the Y-maze, the fact that the rats reared with 4 nipples did not perform any better than chance on the win-stay task indicates that they have not acquired such a strategy in the nest. In addition, no rat, from any condition, showed a tendency toward either strategy in the Y-maze during the first 8 or so days, suggesting that they did not begin maze testing with an already established pattern of behavior and that any pattern emerging over repeated trials might be the result of differential learning.

Behavior of rats in the 8-arm radial maze has been compared to foraging by animals in the natural environment (Olton, Handelmann, & Walker, 1981). Many of the skills used in solving the radial arm maze task may approximate those utilized by adult rats when foraging for food. These skills include both adoption of a search strategy that maximizes the probability of finding food (which for rats is usually a win-shift strategy) and the ability to remember the specific spatial locations that have recently been visited and depleted and are thus unlikely to still contain food. Variables that affect either of these skills could influence foraging behavior. Although the use of a specific strategy does not appear to be affected by the early manipulations utilized here, the ability to use working memory to discriminate sites may be altered. To the extent that the radial arm maze approximates some of the foraging problems faced by feral rats, the data from the present experiments raise the possibility that the expression of normal foraging behavior may also be influenced by specific experiences gained by the infant while suckling.

Notes

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