

Housing Pregnant Mice (*Mus musculus*) in Small Groups Facilitates the Development of Odor-Based Homing in Offspring

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Infant mice (*Mus musculus*) born to dams housed in isolation throughout pregnancy (IsoPreg) begin differentially approaching homonest bedding over clean bedding on Postnatal Day 6. Offspring of dams housed with 2 other potentially pregnant conspecifics (SocPreg) display such homing behavior on Day 4. Earlier onset of homing reflects facilitated olfactory responsiveness in SocPreg pups, rather than qualitative or quantitative differences in IsoPreg versus SocPreg nest odors, body growth, or motoric capabilities. Exposing pregnant IsoPreg dams to SocPreg bedding also accelerated homing onset in the offspring, though not to the same extent as the full social context. Thus, it appears that the facilitation of homing is mediated through the pregnant dam by a combination of chemical cues and other social stimuli.

The influence of social contexts on mammalian brain and behavioral development is an emerging topic of interest (e.g., Cioppo et al., 2002), and there now exists an extensive literature with rodents demonstrating how adult behavior and physiology can be influenced by surrounding social factors (for a review, see Bronson, 1979; Tang-Martinez, 2003). The available, pertinent studies have focused on effects associated with mothers (e.g., Atchley, Logsdon, Cowley, & Eisen, 1991; Moore, 1995; Rosenblum, 1987), with fathers (Dewsbury, 1985; Elwood, 1983; Gubernick & Alberts, 1987), or with littermates (Porter, 1990; Ryan & Vandenberg, 2002; Thiels, Cramer, & Alberts, 1988). Much less attention has been applied to questions of how dimensions of social environments beyond immediate kin might influence the developmental trajectories of the offspring. Similarly, the prenatal environment deserves more attention, especially as a target of stimuli that are transduced through the mother to the offspring.

Surrounding the body of data relevant to social effects on development are substantial changes in developmental theory. In contrast to more conventional views, modern developmental theory holds that the course of development results from continuous, context-dependent interactions between factors distributed throughout an organism and its structured environment (Lerner, 2002; Lickliter & Honeycutt, 2003; Michel & Moore, 1995; Oyama, Griffiths, & Gray, 2001). This “probabilistic” view of development (cf. Gottlieb, 1970) leads researchers to include contextual features in their analyses of development in that these factors can play a formative (rather than supportive) role in the development of individuals. Given this development contingency, it is likely that any phenomena one is studying (be it gene transcription, neural organization, or social interaction) can be quan-

titatively or qualitatively different across various contextual conditions. Manipulating contextual factors, especially those relevant to a species’ typical ecology, provides a powerful procedure to help identify and understand the factors that structure developmental processes.

The current study was designed to assess whether and how a mother’s social context during pregnancy influences postnatal patterns of offspring development. Some research of this type already exists, but nearly all of it is based on manipulations known to promote maternal stress. For instance, a pregnant mother’s social context has been manipulated through social crowding (Allen & Haggett, 1977; Christian & LeMunyan, 1958; Crump & Chevins, 1989; Keeley, 1962), group instability (Kaiser & Sachser, 1998; Sachser & Kaiser, 1996), or repeated agonistic confrontations with other pregnant female mice (Marchlewska-Koj, Kruczek, Kapusta, & Pochron, 2003). In most cases, the long-term effects of these prenatal manipulations on offspring outcomes appear to be detrimental. Besides low birth weights and delayed sexual development, male offspring appear feminized and behave bisexually, whereas female offspring appear masculinized and are less attractive to adult male mice. Although these findings are important experimental demonstrations of how a mother’s social environment during pregnancy can influence offspring outcomes, the exclusive focus on stressful social contexts portrays a rather limited view on the potential contributions to offspring development that can be attributed to extrafamilial social contexts.

In other words, if the past work were considered as a complete representation of early social effects, then it would seem that group housing during pregnancy only influences offspring development through its influence on maternal stress levels and endocrine responses. However, social housing makes available a host of sensory stimuli that could influence offspring development directly or indirectly through the mother. Besides an obvious increase in odors and flavors that arise with group housing, a wealth of proximal sensory stimulation is potentially made available during bouts of social grooming, nuzzling, and huddling. In addition to whatever direct effects these activities have on the mother, it is possible that these actions result in increased amounts of fetal

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sensory stimulation. Thus, being in contact with conspecifics during pregnancy could contribute to the structure of fetal development by regulating the types, amounts, and timing of fetal stimulation, all of which could potentially influence the rate and/or course of offspring development.

In an interesting study, File and Goodall (1976) examined the effects of different gestational housing conditions on infant rats' responsiveness and habituation to air puffs. Some pregnant rats were maintained in groups of four until the day prior to birth, whereas others were housed singly during gestation. Relative to pups born to dams housed singly during pregnancy, they found that pups born to socially housed mothers displayed more overt responses to air puffs and required more stimulus presentations to habituate during testing on Postnatal Days 5–12 (P5–P12). Cross fostering yielded no discernable postnatal effects. Thus, their results suggest that prenatal housing can influence early perceptual and behavioral development. Clearly more research is needed to unpack the influence of prenatal housing conditions on perceptual and behavioral development.

In the current study, we addressed these issues by investigating whether pregnant mice housed socially (with two other female mice) or singly could generate different patterns of postnatal perceptual and behavioral development in the offspring. Specifically, we asked whether social housing during pregnancy would facilitate or delay the emergence of offsprings' responsiveness to nest-specific odors in the days and weeks following birth. Eight experiments were designed to address this issue. Experiments 1–3 demonstrated and replicated differences in homing responses by mouse pups gestated in socially housed (SocPreg) or isolated (IsoPreg) dams. Experiments 4–6 sought to eliminate alternative explanations of homing differences of IsoPreg and SocPreg pups. The final two experiments were designed to identify critical factors associated with social housing that may have generated the differences between IsoPreg and SocPreg pups.

Materials and Methods

Certain methodological and procedural features are common to each of the experiments. These shared aspects are discussed first.

Subjects

Subjects were derived from ICR/Alb mice (*Mus musculus*), originally obtained from Taconic Farms (Germantown, New York), born in the Animal Behavior Laboratory at Indiana University. Virgin female mice that had been reared with 2–3 other female siblings since weaning were paired with breeder male mice. After several days, or on the appearance of copulatory plugs, female mice were separated from the male mice and placed in standard mouse tubs (11.5 × 7.25 × 5 in) until scheduled parturition.

Procedure

Some female mice were placed in cages with two other potentially pregnant female mice (SocPreg dams), of which at least one was pregnant. Within the SocPreg conditions of each experiment, no differences were found in the distribution of homing patterns between pups born to dams housed with two pregnant female mice compared with those born to dams housed with one pregnant and one nonpregnant female mouse. Each litter in the SocPreg conditions was taken from a single female mouse in each

housing group. The remaining female mice were kept in cages individually (IsoPreg dams).

During the 24 hr prior to scheduled birth (G17 or G18), all female mice were transferred to clean cages containing fresh bedding (Sani-Chips; P. J. Murphy Forest Products Corporation, Montville, New Jersey). Only those litters that were born to mothers that gave birth during this 24-hr window were tested. Parturition was monitored at about 1700 each day. The day the litter was first observed was designated as Postnatal Day 0 (P0). Litters were culled to eight pups with equal numbers of male and female mice (when possible) on Postnatal Day 2 (P2). All litters were reared by their own mothers. Food (Labdiet #510; PMI Nutrition International, Brentwood, Missouri) and water were available to mothers ad lib through the stainless steel bars of the cage lid. All mice were kept on 14:10 light cycles in ventilated rooms with other colonies of mice at 23 °C.

Testing

Subjects were tested postnatally. Each litter was removed from its home cage and placed in a holding cage until the time of testing (approximately 10 min later). The timing and number of tests varied by experiment. A test involved placing an individual subject in the center of an unfamiliar, transparent mouse tub. A rubber mat (7.5 × 6.5 × 0.06 in) was on the central area of the floor of the test tub to improve traction for the pup's locomotion. On the floor adjacent to the 7.25-in. sidewalls, 25 mL of shavings were spread evenly, creating a strip of bedding material approximately 2-in. wide along the two ends of the testing chamber. The sets of shavings were not placed on the rubber mat.

The testing cage was divided into three equal parts, demarcated by lines drawn on the long sides of the cage. At the beginning of each trial, the subject was placed in the middle third of the testing chamber equidistant to the two sets of shavings with its body axis perpendicular to the long sides of the cage. The two remaining thirds of the testing chamber represented approach areas. We recorded the amount of time it took each subject to enter each approach area (latency scores) and the total, accumulated amount of time spent within each approach area (duration scores) using a system of hand-held stopwatches during a 3-min test. An approach was scored when a subject's snout crossed into one of the approach areas. An approach ended when the snout of a subject was no longer in the approach area (even when other body parts remained inside the approach area). If a subject did not enter either approach area, then it was given a latency score of 180 s and a duration score of zero. To eliminate the effects of turning biases, we counterbalanced the placement of the shaving stimuli between subjects. After the 3-min test, the subject was removed from the testing chamber and placed in a separate, unfamiliar holding cage. Subjects were not returned to the original holding cage, lest they expose their siblings to the testing odors. We wiped the rubber mat clean using paper towels saturated in an odor neutralizing detergent (Roccal-D Plus; Pharmacia & Upjohn, Peapack, New Jersey). After each subject in each litter was tested, the litter was returned to its home cage.

For thermal control during testing, both the holding cage and test tub were located in an Isolette infant incubator (Model C-35; Air Shields, Hatboro, Pennsylvania) that maintained an ambient air temperature of 25.5 °C (± 1 °C).

Data Analysis

Latency to enter approach areas, and the total duration of time spent in each approach area were the primary dependent measures. We analyzed differences among latency and duration scores using two-tailed Wilcoxon signed-rank matched pairs tests. Because Wilcoxon tests place more weight on larger differences, sign tests were used to determine whether the overall number of subjects showing a greater duration near one stimulus was greater than the number of subjects spending more time at the other stimulus (henceforth called response distribution). Two-tailed independent

samples *t* tests were used to assess differences in weight between groups. Alpha was set at .05 for all analyses. For descriptive purposes, means and standard error scores are displayed in tables and graphs.

Experiments 1–3: Onset of Homing by Mouse Pups Gestated in Socially Housed or Isolated Dams

Experiments 1–3 were designed to determine whether onset of homing responses by infant mice—that is, the age at which they first orient and move toward nest-specific odors—differs between pups born to mothers housed socially or housed alone during pregnancy. Offspring born to these females are referred to as SocPreg and IsoPreg respectively.

A standardized test of homing behavior can be viewed as a kind of olfactory discrimination task: a pup is placed in a test environment with a source of nest odors in a discrete location and with a different or null odor source similarly positioned in a comparable location. If the pup orients and moves toward the nest odor, then this can be considered positive evidence of an olfactory discrimination between the nest odors and other odors in the environment. Thus, in Experiments 1 and 3, we formalized this discrimination task and placed individual pups in a chamber that contained a small amount of bedding material from the homenest at one end and an identical quantity of clean bedding material at the other end (Own Home vs. Clean). Experiment 2 was a variant of this task in which the discrimination was between bedding from the pup's own nest and bedding from another, similarly aged mouse nest (Own Home vs. Other Home). We included Experiment 3 as a replicate of Experiment 1 using more precisely controlled experimental procedures.

We considered a priori, that the Own Home versus Clean testing situation to be an easier discrimination than Own Home versus Other Home (see also Gregory & Pfaff, 1971). Given the dramatic postnatal development of the olfactory system in mice and other altricial rodents (Alberts, 1976, 1984), pups 2–7 days of age were given the easier task and pups 8–11 days of age were given the more difficult discrimination. It is important to note also that this task required pups to demonstrate their perceptual and behavioral preferences by actively approaching a stimulus source. Experiment 1 was essential to the current program because such homing behavior has not previously been demonstrated in mouse pups, as it has in infants of other species (e.g., rat [Brown, 1982; Carr, Marasco, & Landauer, 1979; Cornwell-Jones & Sobrian, 1977; Gregory & Pfaff, 1971], hamster [Gregory & Bishop, 1975]).

Experiment 1: Homing by 2-to-7-Day-Old Mice Gestated by SocPreg or IsoPreg Dams

Female ICR mice were mated and then housed either in small social groups or alone until the last day of gestation when they were separated (see Methods and Materials section). Testing in Experiment 1 began on Postnatal Day 2 (P2) when pups were offered a choice between Own Home versus Clean bedding. Pups were tested daily under these conditions through P7.

Method

Subjects. A total of 80 mice pups born to 10 dams were used as subjects. Half of the subjects were born to female mice (five litters) housed socially during pregnancy (SocPreg). In the current experiment, the num-

ber of litters derived from dams housed with two other pregnant female mice versus one pregnant mouse, and one nonpregnant female mouse was not recorded. The remaining subjects were born to mothers (five litters) housed alone during pregnancy (IsoPreg).

Procedure. In Experiment 1, pups were tested each day from P2 to P7 with Own Home bedding on one side of the testing chamber and Clean bedding on the other side. One IsoPreg litter was tested for the first time on P3. For all litters, partial bedding changes (approximately half of the total bedding was replaced with clean bedding) occurred once per week on a designated day.

Results

The first row of results in Table 1 characterizes the overall performance of SocPreg pups in the homing tests in terms of the distribution of responses. For instance, the first cell (leftmost, top row) indicates that 21 of the 40 SocPreg pups tested on P2 moved sufficiently in the 3-min test to enter an approach area. Of the 21 responders, about half spent more time near Home (11) compared with those who spent more time near Clean bedding (10), evincing no overall preference. On P3, SocPreg pups began moving reliably more (31 of 40 entered an approach area), and of the 31 responders, significantly more pups spent more time near Home bedding than Clean bedding (24 vs. 7; $z = -2.79$, $p = .005$). With increasing age there was a steady increase in the number of subjects responding and, even more impressively, an increase in preference for Home odors compared with Clean bedding that was maintained quite consistently through P7.

The second row in Table 1 displays the response distribution scores for IsoPreg pups. On P2, 17 of the 32 IsoPreg pups entered approach areas during testing, and about half spent more time near Home bedding (9) compared with those who spent more time near Clean bedding (8). It was not until P6, that IsoPreg pups began to display biased homing responses to their own Home bedding. Specifically, on P6, all of the 40 IsoPreg pups responded during testing, and of these 40 responders, significantly more spent a greater amount of time near their Home bedding compared with Clean bedding (31 vs. 9; $z = -3.32$, $p = .001$).

The far-left panel of Figure 1 provides more detailed information. The paired data on the left show the average duration spent near each of the two bedding sources by IsoPreg pups for each day. As can be seen, not until P5 do the lines begin to diverge, indicating the beginnings of homing behavior by pups from IsoPreg mothers. The difference in average duration scores, however, did not attain statistical significance on P5 ($z = -1.94$, $p = .053$). By P6, the differences in the average amount of time IsoPreg pups spent near Home was significantly greater than that near Clean ($z = -3.32$, $p = .001$). Although this is an impressive ability of 6-day-old altricial infants, the onset of homing was evinced on P3 by SocPreg pups ($z = -2.79$, $p = .005$) as shown in the paired data on the right side of the far-left panel in Figure 1.

Latency data shown in Figure 2 corroborate these findings. The right side of the far-left panel of Figure 2 shows that SocPreg pups entered the approach area of their Home bedding sooner than that of the Clean bedding on P3 (109 s vs. 155 s, respectively; $z = -2.79$, $p = .005$). The left-hand side of the far-left panel shows that IsoPreg pups did not display differences in their latencies to approach Home and Clean bedding until P6 (57 s vs. 118 s, respectively; $z = -2.80$, $p = .005$).

Table 1
Response Distribution Data for All Experimental Conditions

Group	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11
Experiments 1 ^a and 2 ^b										
SocPreg	11/10	24/7*	24/8*	28/6*	31/7*	33/4*	24/15	20/19	28/12*	28/12*
IsoPreg	9/8	16/18	17/15	23/15	31/9*	32/8*	21/19	19/21	28/12*	29/11*
Experiment 3 ^a										
SocPreg			24/3*	26/1*	22/5*					
IsoPreg			14/14	16/16	24/8*					
Experiment 4 ^b										
SocPreg			18/8							
IsoPreg			11/16							
Experiment 5 ^c										
IsoPreg			15/1*							
Experiment 7 ^a										
Early SocPreg			11/14	15/15	21/1*					
Late SocPreg			20/8*	25/4*	26/3*					
Experiment 8 ^a										
Clean X			9/13	14/12	26/1*					
Bed X			17/7	20/5*	25/4*					

Note. Values in cells indicate the number of subjects spending more time near their own home shavings followed by the number of subjects spending more time near the other shavings. P = Postnatal Day; SocPreg = mouse infants gestated in socially housed dams; IsoPreg = mouse infants gestated in isolated dams; Clean X = pups born to isolated mothers that had clean bedding added to their cages; Bed X = pups born to isolated mothers that had soiled bedding added to their cages.

^a Test between Own Home versus Fresh. ^b Test between Own Home versus Other Home. ^c Test between Own Home versus None.

* $p < .05$.

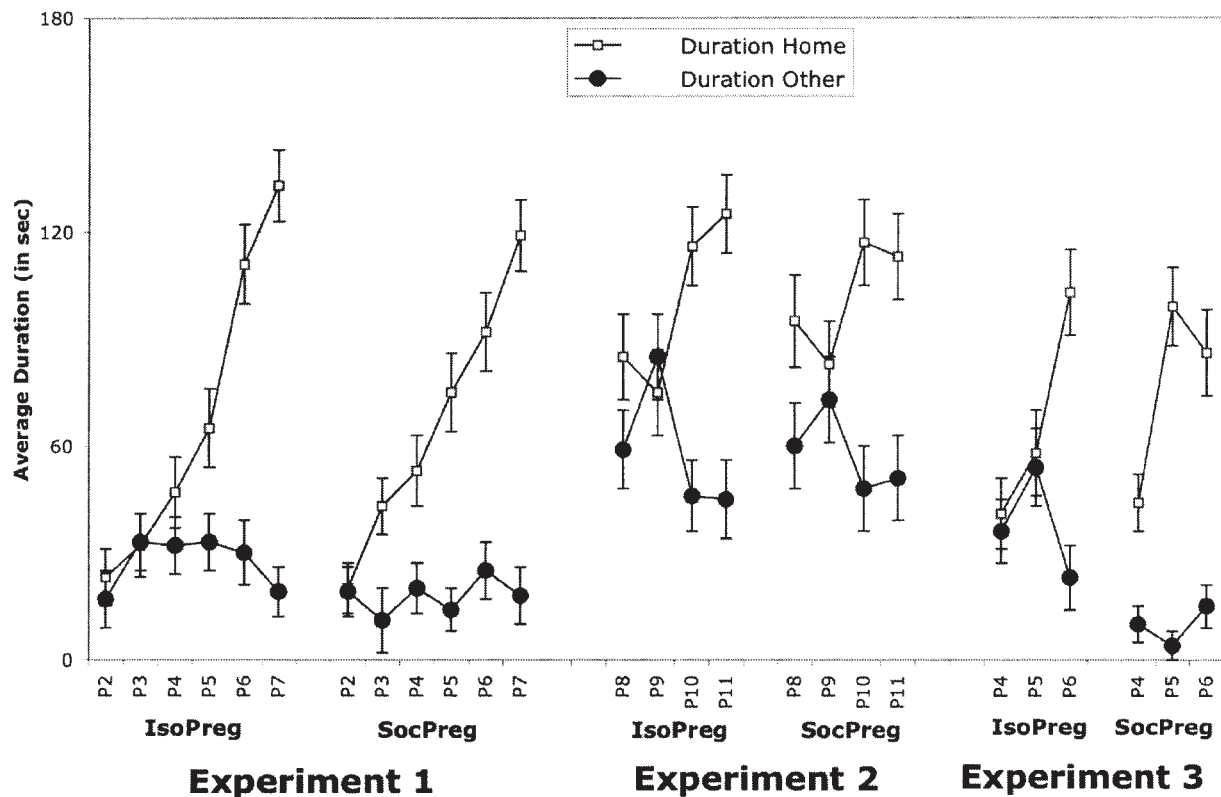


Figure 1. Duration scores for mouse infants gestated in isolated dams (IsoPreg) and mouse infants gestated in socially housed dams (SocPreg) in Experiments 1–3. P = Postnatal Day.

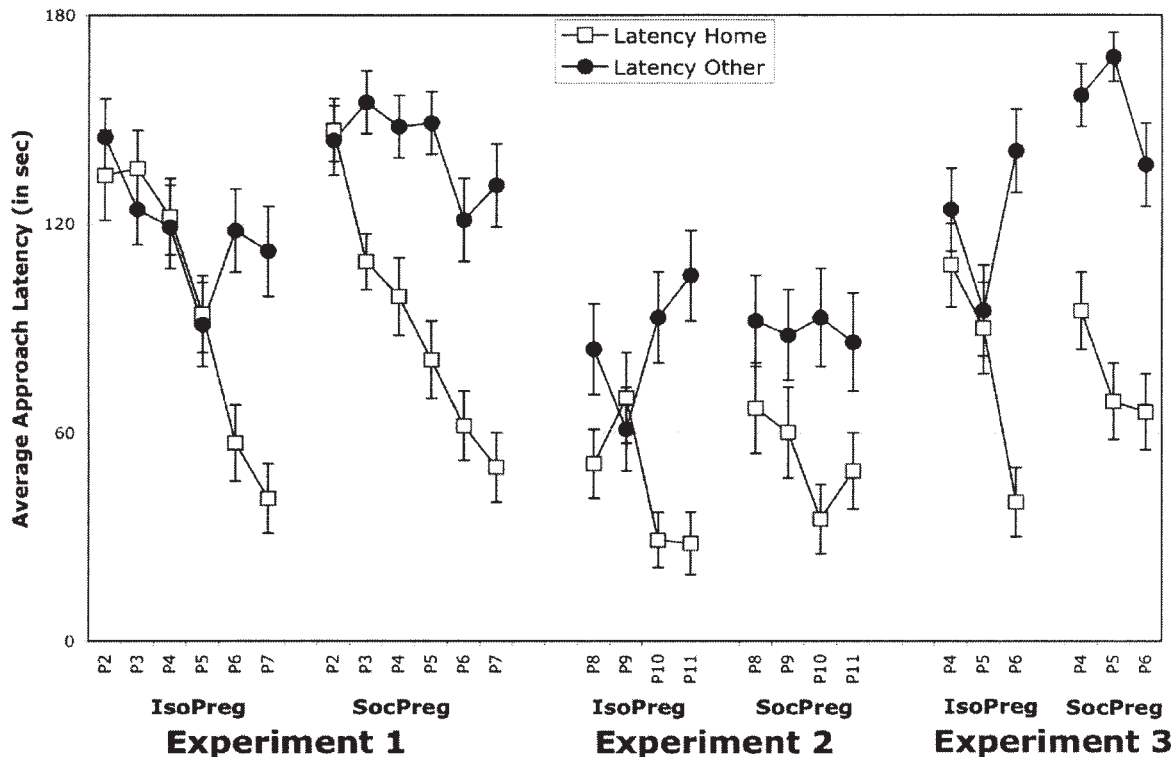


Figure 2. Latency scores for mouse infants gestated in isolated dams (IsoPreg) and mouse infants gestated in socially housed dams (SocPreg) in Experiments 1–3. P = Postnatal Day.

Experiment 2: Homing by 8-to-11-Day-Old Mice Gestated by IsoPreg or SocPreg Dams

In Experiment 2, we tested mouse pups 8–11 days of age using a discrimination task presumed to be more difficult than that in the previous experiment. Each pup was placed between soiled bedding samples taken from its Own Home versus Other Home. The samples of Other Home bedding were from nest tubs that contained a primiparous, ICR/Alb dam and her litter that were maintained on the same diet. Each litter from which bedding was drawn was comparable in terms of strain, age, and litter size as the subjects being tested.

Method

Subjects. The same 80 mice used in Experiment 1 served as subjects.

Procedure. Testing took place each day between P8 and P11. Testing involved a choice between bedding taken from a subject's Own Home and bedding taken from a different, similarly aged (± 24 hr) litter's home bedding (Other Home). For each litter tested, the Other Home bedding on each day of testing was taken from the same nest tub, and no two litters were tested with the same Other Home bedding.

Results

Response distributions in the Own Home versus Other Home discrimination task are shown in the upper two rows of Table 1. On P8 and P9, neither SocPreg nor IsoPreg pups displayed an overall preference for either bedding. By P10, significant and reliable

response biases toward Own Home bedding over Other Home bedding characterized both SocPreg (28 vs. 12, respectively; $z = -2.37$, $p = .018$) and IsoPreg (28 vs. 12; $z = -2.37$, $p = .018$) pups.

Similar patterns were found in latency and duration measures. More specifically, the middle panels of Figures 1 and 2 show that the duration and latency scores for both groups do not reliably diverge on P8 or P9. By P10, SocPreg pups approached their Own Home bedding sooner (latency: $z = -2.66$, $p = .008$) and spent more time near their Own Home bedding (duration: $z = -2.54$, $p = .011$). Likewise, IsoPreg pups on P10 showed similar biases toward their Own Home bedding in their latency ($z = -2.69$, $p = .007$) and duration ($z = -3.10$, $p = .002$) scores.

Experiment 3: Homing by 4-to-6-Day-Old SocPreg and IsoPreg Mice in Own Home Versus Clean Tests Under More Stringent Conditions

Experiment 3 was conducted to provide a replicate of the basic phenomenon described in Experiment 1. The experimental design was more focused and more precisely controlled as an attempt to eliminate and to identify key variables in the phenomenon of accelerated onset of homing behavior by mouse pups. In Experiment 3, testing was restricted to P4–P6. Moreover, to better control the potency of Home bedding stimuli during testing, the wood chips for each litter were left undisturbed from the time the mothers were placed in clean cages with fresh bedding shortly

prior to birth until the completion of testing on P6. Also, records were kept in regards to whether SocPreg female mice were housed with two other pregnant female mice versus one pregnant and one nonpregnant female mouse.

Method

Subjects. A total of 64 subjects taken from eight litters were tested each day from P4 to P6. Half the subjects were born to mothers housed socially during pregnancy, and the remaining subjects were born to mothers housed singly. Two SocPreg dams were housed with two pregnant female mice. The remaining two SocPreg female mice were housed with one pregnant female and one nonpregnant female mouse.

Procedure. All of the procedures were identical to those in Experiment 1, with the exceptions that testing took place between P4 and P6, and that the bedding materials were systematically left undisturbed from the time mothers were placed in clean cages on G17 or G18–P6. Thus, in Experiment 3, stimulus strength was better standardized and may have been stronger because there was no dilution by partial replacement of bedding as in Experiments 1 and 2. Also unlike the previous experiments, pups in the current experiment were weighed (to the nearest .10 g) each day after testing.

Results

Table 1 shows the distribution of the pups' homing behavior. Of the responders (about 75% in both groups) on the 1st day of testing (P4), nearly all of the SocPreg pups displayed an overall preference for Home (24) over Clean (3) shavings ($z = -3.85, p < .001$). Homing by SocPreg pups was maintained for the remainder of testing. No differences were found in response distribution scores between SocPreg pups born to dams housed with two pregnant female mice (12 of 13 on P4, 13 of 14 on P5, 12 of 14 on P6 showed homing) and SocPreg pups born to dams housed with one pregnant and one nonpregnant female mouse (12 of 14 on P4, 13 of 13 on P5, 10 of 13 on P6 showed homing). As can be seen in the fourth row of data in Table 1, IsoPreg pups were evenly divided in their approaches on P4 (14 vs. 14) and on P5 (16 vs. 16), showing no specificity of homing behavior. Onset of homing was apparent on P6 for IsoPreg pups (24 Home vs. 6 Clean; $z = -2.65, p = .008$).

Analyses of duration and latency scores support these findings. On P4, SocPreg pups displayed longer durations near their Home bedding ($z = -3.17, p < .001$) and shorter latencies to approach their Home bedding ($z = -3.36, p = .007$). SocPreg pups continued to show these biases through P6. Differences in duration and latency scores on each day are clearly depicted on the right sides of the far-right panels of Figures 1 and 2. Note that the lines are noticeably and significantly divergent on each day of testing in each figure. The left sides of the far-right panels in Figures 1 and 2 also show that the lines representing duration and latency scores for IsoPreg pups do not diverge on P4 or P5. By P6, IsoPreg pups more quickly approached their Own Home bedding (latency: $z = -3.81, p < .001$) and spent greater amounts of time near their Own Home bedding (duration: $z = -3.32, p = .001$).

Discussion

The most dramatic result from Experiments 1–3 was the discovery that pups born to dams housed in small social groups during pregnancy showed a significantly earlier onset of homing

behavior compared with pups raised identically but gestated by dams housed alone during pregnancy. Social housing during pregnancy facilitated the onset of a perceptually based, adaptive behavior in the offspring by about 40%. The results from Experiment 3 replicated these findings. Nevertheless, by the end of Experiment 1 (on P7), for example, IsoPreg and SocPreg pups were performing at similar levels in their Own Home versus Clean bedding tests.

This pregnancy-related, postnatal developmental effect appeared to affect the onset of homing, but earlier onset did not result in differential performance 1-week later. On P8, the start of Experiment 2 in which the homing test required discriminating between Own Home and Other Home bedding, both groups of pups were indiscriminate. Both IsoPreg and SocPreg pups developed the ability to make the more difficult discrimination by P10.

Apparently, the pregnancy effect is either confined to the onset of behavior or it does not last more than a week after the termination of the differential social stimulation. Henceforth we shall describe this acceleratory trend in homing as an instance of experiential *facilitation*. Gottlieb (1976) and Aslin (1981) used the term *facilitation* to refer to a role of experience in which exposure to certain stimuli or events influences the acquisition or rate of development but not necessarily the final level. In the current study, SocPreg pups displayed an enhanced ability to distinguish or prefer their own home bedding over clean bedding in the 1st postnatal week, but this difference apparently did not extend into the 2nd postnatal week under a more difficult odor discrimination task. The facilitative effect of social housing during pregnancy on offspring development during the 1st postnatal week, though clear and dramatic, requires further definition and understanding, which is the main goal of Experiments 4–8.

Experiments 4–6: Alternative Explanations of Homing Differences of IsoPreg and SocPreg Pups

Results from Experiments 1–3 revealed differences between mouse pups born to socially housed (SocPreg) and singly housed (IsoPreg) mothers and were presumed to reflect the pups' olfactory ability to discriminate between nesting material that contained home odors and material that did not contain such odors. Additional tests were needed to assess potential nonolfactory explanations of the differences in homing between IsoPreg and SocPreg mice. For instance, it is possible that the olfactory abilities of IsoPreg and SocPreg pups did not differ, but that the nesting material from the IsoPreg and SocPreg litters had different stimulus properties, such that when pups were tested with Own Home versus Clean bedding, the IsoPreg and SocPreg pups were confronting different discriminative stimuli. Experiments 4, 5, and 6 were conducted with 4-day-old mice because pups of this age display reliable differences in homing as a function of the dams' social environment during pregnancy (Experiments 1 and 3).

Experiment 4: Stimulus Potency of SocPreg and IsoPreg Bedding

IsoPreg pups in Experiments 1 and 3 failed to prefer their home-nest materials at a time when SocPreg age mates displayed reliable preferences. Experiment 4 was designed to determine whether this apparent difference in onset of homing could be attributed to differences in the potencies of the bedding used in the

tests, rather than in the pups' abilities or responsiveness. That is, differences in homing between IsoPreg and SocPreg groups may have reflected differences in the strength or composition of the bedding odors from IsoPreg and SocPreg nests, rather than differences between pups of the two groups.

In Experiment 4, IsoPreg pups were tested with the nest materials from SocPreg nests (vs. Clean bedding), and SocPreg pups were similarly tested with IsoPreg nest materials versus Clean bedding. The stimulus potency explanation would be supported if IsoPreg pups displayed a preference for the home (i.e., SocPreg) bedding or if SocPreg age mates failed to display homing.

Method

Subjects. A total of 64 pups taken from a total of eight litters (four social, four isolated) were tested once on P4. Three of the four SocPreg female mice were housed with two pregnant female mice.

Procedure. SocPreg pups were tested with clean bedding and bedding from the home cages of isolated pups of the same age (IsoPreg Home vs. Clean bedding). Likewise, we tested IsoPreg pups using clean bedding and bedding taken from cages of SocPreg litters of the same age (SocPreg Home vs. Clean bedding). Within the SocPreg conditions, each litter was tested with bedding from different SocPreg cages ($n = 4$). Likewise, each IsoPreg litter was tested with bedding from different SocPreg cages ($n = 4$). Thus, no two litters were tested with the same bedding. All other methods and procedures were identical to those in Experiment 3.

Results

IsoPreg pups failed to display evidence of homing to SocPreg bedding. No differences were found in their response distribution (row 6, Table 1). The latency and duration scores for IsoPreg pups shown in Table 2 indicate equivalent responsiveness by IsoPreg pups to SocPreg and Clean bedding.

In contrast, 4-day-old SocPreg pups showed evidence of homing to the bedding IsoPreg litters. Table 1 shows that the total number of subjects spending more time near the Home shavings (18),

though biased toward the IsoPreg bedding, did not achieve a statistically significant difference from the number spending more time near the Clean bedding (8). Nevertheless, as shown in the top four rows of Table 2, SocPreg pups displayed shorter latencies to approach ($z = -2.20, p = .028$) and longer durations in remaining near ($z = -2.80, p = .005$) the IsoPreg bedding compared with Clean bedding.

Experiment 5: Single-Choice Homing by IsoPreg Pups

At 4 days of age, IsoPreg pups approached, with equal frequencies and latencies, sources of odor from soiled bedding material and clean bedding material (Experiments 1, 3, and 4). Their equivalent attraction in a two-choice test is consistent with the hypothesis that they cannot discriminate between these two sources of complex odors. An alternative explanation is that the IsoPreg pups are simply insensitive to odors of the bedding material in general, and that their "approach behavior" in the earlier tests was nonoriented activity. To eliminate this alternative explanation, we tested 4-day-old IsoPreg pups in a single-choice condition, with only soiled nest materials on one side of the chamber. If these pups are insensitive to odor of nesting materials, then we would not expect to see homing (approach to the bedding), but we would observe them to either move indiscriminately between the bedding side and the empty side of the chamber or remain relatively inactive because they were understimulated.

Method

Subjects. A total of 16 IsoPreg pups derived from two litters were tested once on P4.

Procedure. Except for the stimuli used during testing, all methods and procedures were identical to Experiments 3 and 4. Subjects were tested with their Own Home bedding on one side of the testing chamber. No other bedding was placed on the opposite side of the chamber.

Table 2
Latency and Duration Scores for Groups in Experiments 4–8

Group	Latency						Duration					
	Day 4		Day 5		Day 6		Day 4		Day 5		Day 6	
	Home	Other	Home	Other	Home	Other	Home	Other	Home	Other	Home	Other
Experiment 4 ^a												
SocPreg	97* (13)	147 (10)					62* (12)	14 (6)				
IsoPreg	118 (12)	105 (12)					29 (9)	32 (8)				
Experiment 5 ^b												
IsoPreg	57* (14)	161 (13)					105* (16)	8 (8)				
Experiment 7 ^c												
Late SocPreg	97 (11)	136 (10)	59* (11)	160 (9)	65* (11)	144 (12)	59* (10)	22 (8)	98* (12)	11 (6)	99* (11)	16 (8)
Early IsoPreg	131 (12)	120 (13)	23 (8)	35 (11)	50* (12)	139 (14)	23 (8)	35 (11)	51 (12)	43 (10)	100* (13)	4 (2)
Experiment 8 ^c												
Clean X	144 (10)	121 (12)	117 (12)	123 (12)	64* (10)	166 (8)	30 (8)	17 (6)	33 (9)	27 (9)	80* (12)	5 (4)
Bed X	117 (12)	137 (11)	90* (12)	145 (11)	66* (12)	137 (13)	46* (11)	17 (6)	54* (10)	16 (8)	90* (12)	9 (5)

Note. Values depict means (in seconds) with standard errors in parentheses. SocPreg = mouse infants gestated in socially housed dams; IsoPreg = mouse infants gestated in isolated dams; Clean X = pups born to isolated mothers that had clean bedding; Bed X = pups born to isolated mothers that had their bedding changed.

^a Test between Own Home versus Other Home. ^b Test between Own Home versus None. ^c Test between Own Home versus Fresh.

* $p < .05$.

Results

When IsoPreg pups were placed in an environment with only their Own Home bedding, they were capable of homing. All 16 subjects responded during testing (see Table 1), and of these, 15 pups spent more time near their home shavings ($p = .001$). Table 2 shows that pups displayed shorter latencies to approach ($z = -2.90$, $p = .004$) and longer durations in remaining near ($z = -3.21$, $p = .001$) their Own Home bedding.

Experiment 6: Equivalent Developmental Status of IsoPreg and SocPreg Pups

Another general explanation of the performance differences of IsoPreg and SocPreg pups is that they differ in overall developmental status. Experiment 6 was a retrospective analysis of possible differences in growth and motor capability, two general parameters that could affect the infant's behavior in homing tests and possibly confound the interpretation of sensory discrimination that was offered as the basis of the differences in homing. To determine whether growth differed between IsoPreg and SocPreg pups, we compared the weights of IsoPreg and SocPreg litters in Experiments 3 and 4. As a general proxy for levels of motor performance, we compared the average latencies to make initial approach responses (regardless of direction) of IsoPreg and SocPreg pups on P4 in Experiments 1, 3, and 4. Differences in motor development would be supported if it were found that SocPreg and IsoPreg pups differed in how quickly they made their initial responses.

Method

Subjects. In the analysis of weight, data were taken from the eight SocPreg litters in Experiments 3 and 4, and from the 10 IsoPreg litters used in Experiments 3, 4, and 6 (note that Experiment 1 was not included because weights were not measured). The subjects in the comparisons of first latencies were the 208 pups (104 IsoPreg and 104 SocPreg) derived from the 26 litters in Experiments 1, 3, and 4.

Procedure. An independent-samples t test was used to compare the P4 body weights of pups from the eight SocPreg litters with those from the 10 IsoPreg litters. In the comparison of first latency scores, separate analyses were conducted on data from each of the three experiments (Experiments 1, 3, and 4) because there were procedural differences between the three experiments. Specifically, there were differences in either the bedding used during testing or in the subjects' prior experience with testing. In each of the three analyses, we compared for IsoPreg and SocPreg pups the average time to leave the start section and to enter an approach area, regardless of the bedding stimulus contained there.

Results

An independent samples t test revealed no significant differences between SocPreg ($M = 3.8$ g) and IsoPreg ($M = 4.0$ g) litters. Likewise, Mann-Whitney U tests revealed no differences in the average amount of time it took SocPreg and IsoPreg pups to make an initial response in Experiments 1 (31 vs. 37 s, respectively), 3 (60 vs. 51 s), or 4 (44 vs. 51 s).

Discussion

Although it seemed reasonable to interpret the variation in homing between IsoPreg and SocPreg in Experiments 1 and 3 as

evidence for differences in the pups' abilities to discriminate the odors of their homenest, we nonetheless sought to increase confidence in this conclusion by eliminating other explanations, such as possible nonolfactory differences in the test stimuli, and the pups' capabilities. Experiments 4–6 were conducted to rule out other explanations, such as possible differences in the test stimuli, as well as possible nonolfactory differences in the pups or the pups' capabilities.

In Experiment 4, we asked whether the differences in homenest stimulus characteristics could explain differential performance of IsoPreg and SocPreg. Might SocPreg nest material be quantitatively or qualitatively more potent than nest material from IsoPreg nests? When SocPreg pups were tested with IsoPreg bedding versus Clean bedding, the SocPreg pups displayed a preference for the soiled bedding, whereas IsoPreg pups failed to discriminate between SocPreg and Clean bedding (see Table 2). Thus, the results indicate that the differences in performance between the two groups could not be attributed to the attractiveness of the testing stimuli.

Experiment 5 was included to better understand why 4-day-old IsoPreg pups failed to demonstrate homing. To rule out the possibility that IsoPreg pups are insensitive to the bedding material used during testing, we tested IsoPreg pups with their Own Home bedding on one side of the test chamber. The other side was left empty. The results indicate that IsoPreg pups are sensitive to the odors of bedding material during testing, in that all 16 pups tested entered an approach area. Of the 16 pups, 15 behaviorally preferred their Own Home bedding during testing, indicating that IsoPreg pups can show oriented approach behavior. Unpublished work conducted in our laboratory has shown that when no sources of odors are present during testing, 4-day-old mouse pups were less likely to leave the start area and were overtly less active. Only about half of the subjects tested under this condition entered an approach area. The discrepancy in the number of subjects responding during testing when no odors were available compared with when one odor source was available does not support the idea that the failure of IsoPreg pups to show homing in earlier tests at this age (Experiments 1, 3, and 4) was due to being understimulated. On the contrary, pup activity appears to be stimulated in the presence of bedding odors. These findings lend additional support to the idea that IsoPreg pups at this age do not preferentially discriminate between soiled and Clean bedding material.

With the results of Experiment 6, differences in homing cannot be attributed to underlying differences in growth or in motor development. Similarly, each of the three analyses of the first latencies revealed that IsoPreg and SocPreg pups made their first responses at equivalent rates. Together, these findings suggest no developmental differences in motor performance between IsoPreg and SocPreg pups.

Collectively, the results from Experiment 4–6 implicate the developmental status of olfactory function in the pups is the likely source of the differential onsets of homing between SocPreg and IsoPreg pups.

Experiments 7–8: Critical Factors in Social Housing

Experiments 7 and 8 were designed to evaluate specific factors associated with social housing during pregnancy that might have generated the homing differences between SocPreg and IsoPreg

pups. Experiment 7 was a preliminary assessment of whether there are phases during pregnancy for the postnatal expression of altered development. Experiment 8 was designed to test whether chemical cues, such as those found in soiled bedding material, might control the effect on the offspring's homing behavior.

Experiment 7: Chemical Cues During Pregnancy Can Facilitate Early Onsets of Postnatal Homing

With Experiment 7, it was asked when during pregnancy does social housing influence the developmental trajectories of offspring? Two experimental groups were used. Some pregnant dams were housed in groups during the first 2 weeks of gestation (henceforth called Early SocPreg), whereas others were group housed during the final week of pregnancy (Late SocPreg).

Method

Subjects. A total of 64 pups from eight litters were subjects. Litters were equally divided into two conditions (Early SocPreg and Late SocPreg). Three of the four Early-SocPreg female mice were housed with two pregnant female mice, and three of the four Late-SocPreg female mice were housed with two pregnant female mice.

Procedure. Early-SocPreg pups were born to dams that were socially housed during the first 13 or 14 (G0 to G13/G14) days of gestation. After about 2 weeks of social housing, the dams were separated and placed singly into a clean cage with fresh bedding. Pups in the Late-SocPreg condition were born to mothers that were housed singly until G13 or G14, after which they were housed with two other potentially pregnant (at least one was pregnant) dams. As before, all female mice were placed in clean cages with clean bedding during the 24 hr prior to parturition, and their bedding was left undisturbed until completion of testing on P6. We tested pups each day between P4 and P6 using their Own Home versus Clean bedding.

Results

Homing was displayed by 4-day-old pups in the Late-SocPreg condition. Their preference for Own Home over Clean bedding was maintained throughout testing. The response distribution scores presented in Table 1 indicate that on P4, 20 of the 28 responders significantly preferred their Own Home bedding ($z = -2.08, p < .038$). This trend appeared to strengthen over time, such that by P6, 90% of those responding preferred their Own Home bedding. Table 2 shows that although Late-SocPreg pups did not take relatively less time to enter the approach area of the Own Home bedding on P4 ($p = .059$), they did display significant biases toward their Own Home bedding in duration measures ($z = -2.23, p < .026$).

Pups in the Early-SocPreg condition failed to provide any evidence of biased responsiveness to the test beddings in their latency and duration scores on P4 and P5 (see Table 2). Not until P6 did Early-SocPreg pups approach their Own Home bedding sooner (latency: $z = -3.31, p < .01$) and remained near this bedding longer (duration: $z = -3.95, p < .01$) than in their responses to Clean bedding. The response distributions (see Table 1) for each day, shown in Table 1, indicate that about half of the responders on P4 and exactly half on P5 spent more time near their Own Home bedding, but on P6, 21 of the 22 responders spent more time near their Own Home bedding ($p < .01$).

Experiment 8: Homing by Pups Gestated in Isolated Pregnant Mothers Exposed to SocPreg Bedding

The results of the previous experiment suggest that the effects of group housing on offspring homing are induced during the days just prior to parturition. Experiment 8 was designed to ask whether chemicals present in the bedding material of socially housed pregnant mice are sufficient to produce the postnatal effects on offspring homing associated with the SocPreg conditions. To assess this possibility, socially isolated pregnant mothers were exposed to the soiled bedding of socially housed female mice.

It is well established that mouse urine contains a variety of potent chemicals that can induce physiological and behavioral changes in conspecifics. Many of the known urinary chemicals in *Mus* reflect the sex and endocrine status of the donor (Schwende, Weisler, Jorgenson, Carmack, & Novotny, 1986), and exposure to these chemicals can influence reproductive physiology (Koyama, 2004) or aggression (Palenza, Parmigiani, & van Saal, 1994) in conspecifics. One intensely studied urinary pheromone resides in soiled bedding material. It markedly accelerates the attainment of puberty in young female mice (Vandenbergh, 1983) and is derived from sexually active, adult male mice. An interesting finding is that soiled bedding or urine from pregnant and/or lactating female mice also accelerates puberty in female mice (Drickamer, 1984), though the urine from nonpregnant female mice markedly delays puberty (Drickamer, 1982).

It is also important to note that late gestation mouse fetuses are known to be responsive to odors (Coppola & Millar, 1997). Thus, it seemed possible that fetal sensory experience might be influenced by odors in the maternal environment. To our knowledge, there is no identified pathway in *Mus* by which chemical cues in the maternal environment affects fetal olfaction. However, in other mammalian species, such as rats (Hepper, 1988) and humans (Schaal, Marlier, & Soussignan, 2000), there is evidence to suggest that newborns display olfactory preferences for chemicals that their mothers ingested during pregnancy.

Method

Subjects. Subjects were 32 pups taken from four separate litters born to dams housed alone during pregnancy.

Procedure. Each day beginning on G13 or G14, soiled bedding (50 mL) from separate groups of three pregnant dams housed together was added to the cages of the isolated dams. Each of the four pregnant female mice in this experiment was exposed to bedding of one (and only one) of four different groups. As in the previous experiments, during the 24 hr prior to birth, the isolated dams were placed in a clean cage with clean bedding that was left unaltered until completion of the experiment on P6. We tested pups each day from P4 to P6 using their Own Home versus Clean bedding. All other methods and procedures were identical to Experiments 3, 4, 5, and 7.

Results

On P4, pups born to isolated mothers who had their bedding changed (henceforth called Bed-X pups) showed a trend to prefer their Own Home bedding more than Clean bedding. Though not statistically significant ($p = .064$), 17 of the 24 responders spent more time near their Own Home bedding (see Table 1). By P5, 20 of the 25 Bed-X responders spent more time near their Own Home bedding ($p = .004$), which was even greater on P6.

Analyses of latency and duration measures yielded more detailed information. As shown in Table 2, although Bed-X pups on P4 approached their Own Home bedding sooner than the Clean bedding (117 s vs. 137 s, respectively), this difference was not statistically significant. Statistically shorter latencies in approaching their Own Home bedding emerged on P5 ($z = -2.68$, $p = .007$) and continued to be found on P6. However, in terms of duration measures, Bed-X pups spent relatively more time near their Own Home bedding on P4 ($z = -2.04$, $p = .041$) and the remaining 2 days.

Discussion

Experiments 7 and 8 were conducted to better understand some of the parameters of social housing critical to the postnatal facilitation of offspring homing. In Experiment 7, we focused on temporal parameters of social housing. The findings from this experiment indicated that the effects on offspring olfaction due to housing pregnant female mice in groups is limited to the days that lead up to parturition. Late-SocPreg pups displayed a preference for their Own Home bedding on P4, which was the same day of homing onset displayed by SocPreg pups in Experiment 3. In contrast, housing pregnant dams socially during the first 2 weeks of pregnancy did not lead to olfactory enhancements in the offspring (Early-SocPreg group). Onset of attraction to Own Home bedding of Early-SocPreg pups was on P6, matching the onset for IsoPreg pups in Experiment 3.

The results from Experiment 8 indicated that exposing isolated, pregnant mothers to samples of soiled bedding from socially housed pregnant female mice can also facilitate the onset of homing in offspring. Pups born to these mothers (Bed-X pups) displayed earlier onsets of homing relative to IsoPreg pups in previous experiments. Evidence of such homing facilitation began to emerge in the Bed-X pups on P4 (in duration scores only), though it was not until P5 that facilitation was reflected in all three measures. Given that IsoPreg (Experiment 3 and 4) and Early-SocPreg (Experiment 7) pups did not begin showing reliable evidence of homing until P6, it seems that Bed-X pups in Experiment 8 showed a slight 24-hr facilitation in homing ability. The strength of facilitation, however, was not as robust as that observed in SocPreg and Late-SocPreg pups.

The possibility exists that the homing enhancements observed in Bed-X pups was not due to exposure to the bedding of group-housed female mice per se, but instead reflected experiencing daily manipulations of their environment. These repeated manipulations may have altered endocrine levels, behavioral activity, or arousal levels that could have influenced offspring development. This alternative, unfortunately, was not controlled for in the current study. Future investigations will test this possibility.

General Discussion

In the current study, we described a new phenomenon in infant mice of accelerated onset of odor-based homing behavior, and we elucidated some of the parameters and stimuli that are necessary and sufficient for this developmental effect. Offspring born to a mother housed socially during late pregnancy develop olfactory-guided homing earlier than offspring born to a mother that lacked such social stimulation during pregnancy (Experiments 1, 3, and

7); the effective social stimulation was provided by two adult female mice, at least one of which was pregnant.

Experiments 1 and 3 converged to show that during the 1st postnatal week, pups born to mothers housed socially (SocPreg pups) displayed response biases toward their own home cage bedding over clean bedding at least 48 hr before pups born to mothers housed alone during pregnancy (IsoPreg pups). These differences did not extend into the 2nd postnatal week (Experiment 2). Earlier onset of homing could not be attributed to stimulus properties specific to bedding from SocPreg or IsoPreg nests; instead, the homing differences reflected pups' differential olfactory responsiveness (Experiment 4). Other potential explanations were eliminated, including insensitivity of IsoPreg pups to bedding odors (Experiment 5), differential body growth (Experiment 6), or altered motor performance (Experiment 6).

Collectively, this work stands as only the second study of which we are aware that assesses the impact on offspring development of housing pregnant dams in small social groups. It is also the first to chart the emergence of odor-based homing by altricial mice, and the first to identify an effect on offspring associated with the pregnant mother's exposure to chemical cues found in the soiled bedding of conspecifics.

By the end of the 1st postnatal week, infant rodents (mice, rats, and hamsters) demonstrate preferences for nest-specific odors. It is difficult to compare mice with rats or with other species with respect to the onset of behavioral preferences for nest-specific odors. Variations in experimental procedures (e.g., group vs. isolated housing conditions; group vs. individual testing; lateral paw placement vs. approach responses) interfere with precise comparisons. Furthermore, there may be important differences in the sensory and perceptual mechanisms that mediate these rodents' early olfactory preferences. For instance, there is evidence that the vomeronasal system of *Rattus norvegicus* may be functional prenatally (Pedersen, Stewart, Greer, & Shepherd, 1984). Several early olfactory feats, including those that involve olfactory discrimination (Teicher, Shaywitz, & Lumia, 1984), are thought to be mediated by this system. In contrast, Coppola and colleagues suggest that the *Mus* vomeronasal system is not functional prior to birth (Coppola & O'Connell, 1989) and shows instead a protracted pattern of functional onset during early postnatal development (Coppola, Budde, & Millar, 1993). Thus, although rats and mice may show similarities in the emergence of when they display odor-based homing preferences, the mechanisms by which homing is achieved may be markedly different.

The prenatal precursors of divergence in odor-guided behaviors between SocPreg and IsoPreg pups occur in the final days before parturition (Experiment 7). Housing pregnant dams in social groups during the first 2 weeks of pregnancy failed to generate the olfactory enhancement in their offspring, whereas group housing during the final week of gestation accelerated the postnatal olfactory enhancement. We have not fully identified all the necessary and sufficient sensory stimuli associated with social housing during pregnancy that accelerate olfactory development in the offspring. It seems that chemicals contained in the bedding of SocPreg dams are sufficient to accelerate the offspring's olfactory functioning (Experiment 8), but facilitated onset of homing in IsoPreg pups exposed to SocPreg bedding was not as robust as the facilitation from group housing (onset on P5 vs. P4, respectively). This suggests the possibility that other, nonolfactory stimuli asso-

ciated with maternal housing may play a role in the facilitative effects on the offspring.

Perhaps the social housing used in the current studies provided stimuli that directly impinged on the fetuses. For instance, mothers may have ingested bedding, excreta, or detritus from the social group, and some of the stimuli may have altered the fetuses' amniotic environment. In utero exposure to augmented levels and kinds of chemicals could accelerate fetal olfactory development. Such intrasensory facilitation effects on auditory and visual responsiveness have been identified in precocial birds following in ovo exposure to sounds or lights (Lickliter, 1995). Studies with precocial birds also highlight numerous intersensory interactions: Enhanced prenatal proximal (tactile, proprioceptive, vestibular) stimulation, for example, can affect subsequent auditory and visual functioning (Honeycutt & Lickliter, 2003). An interesting finding is that group-housed rodents tend to spend much time engaged in huddling, allogrooming, nuzzling, and other behaviors that involve contact interactions, all of which could increase proximal stimulation of the fetuses in utero. Thus, the olfactory enhancements observed in IsoPreg pups may be attributable to either intra- and/or intersensory effects.

Group housing could also influence offspring development by altering maternal endocrine levels. For example, exposing juvenile rodents to soiled bedding from other conspecifics alters endocrine (especially luteinizing hormone) levels and accelerates sexual maturation (Vandenbergh, 1983). Although we do not know whether endocrine levels of pregnant female mice are similarly influenced, it is well established that stress-induced hormonal changes in pregnant dams (e.g., via overcrowding) can influence offspring development (e.g., see Allen & Haggett, 1977). To our knowledge, it is not known whether endocrine levels differ between mothers housed singly or in small groups, though it seems probable that being housed singly can be considered more stressful than being housed in small groups in that the female mice used in this study had never experienced social isolation prior to pregnancy. Thus, the delay in homing displayed by IsoPreg pups may have been in response to maternal stress responses.

Apart from the issue of how group housing influences offspring development, an additional unresolved issue concerns the extent of this influence on development. In other words, does social stimulation during gestation have general developmental effects or is its influence limited to olfaction? Clearly, more research is needed to address this issue, but on the basis of available data, we believe group housing leads to developmental effects beyond odor-based responding. Although the current study tested for and found differences in olfactory responsiveness between pups born to group-housed mothers and those housed singly, File and Goodall (1976) found differences between these groups in their overt responsiveness to repeated puffs of air, suggesting that housing pregnant female mice in groups can alter their offsprings' postnatal tactile responsiveness. Thus, gestational group housing can lead to effects across multiple perceptual and behavioral domains.

Observations in seminatural and natural conditions indicate that pregnant rodents often sequester themselves from the local colony by constructing buffered nests in which they raise their litters (e.g., Calhoun, 1963; Crowcroft, 1966). Nevertheless, pregnant female mice are probably not socially isolated. They may share a burrow with sires or a previous litter. In fact, many, if not most, pregnant rats and mice observed in the wild became pregnant during post-

partum estrous, indicating that these mothers were nursing a previous litter while pregnant with an additional litter (Bruce & East, 1956; Conaway, 1971). Even among those female mice that do separate themselves from the surrounding group and are not nursing a previous litter, the female mice likely encounter stimuli associated with other conspecifics when they leave the nest (e.g., to defecate or forage). The results of the current study show that merely encountering the soiled bedding of other conspecifics can facilitate perceptual development.

In a general sense, the current study underscores the importance of taking into account and manipulating contextual factors in developmental analyses. We reiterate a point made by File and Goodall (1976) and alert researchers to control for housing conditions of pregnant mothers and urge that these conditions be reported. We view the current study as a noteworthy addition to an appreciation of how social context, even during prenatal ontogenetic periods, can regulate the course of development.

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