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Maternal Separation Alters Social Odor Preference Development in Infant Mice (*Mus musculus*)

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This study examined whether daily periods of maternal separation during the first two weeks of life would decrease attraction to familiar nest odors in CD-1 mice 10 and 14 days old. We also investigated whether placing a group of mice (*Mus musculus*) in nest shavings during the 180-min separation period would mitigate possible separation-induced deficits. The maternal separation procedure has been widely used as a rodent model for the effects of inconsistent or inadequate early caretaking on human development. From postnatal day (PND) 1 to 14, litters were separated from the dam, but not littermates for either 15 or 180 min, or were facility-reared controls. Control, facility-reared mice preferred home-cage nest to clean familiar shaving odors on PND 10, but not PND 14. In contrast, home-cage nest odors attracted maternally separated mice on both test days. Our results suggest that maternal separation maintains the olfactory tether to the nest in a period when the attraction normally begins to weaken.

Keywords: maternal separation, odor preference, nest odor, social behavior, infant development, mice

Odors associated with the mother and the perinatal environment attract mammalian infants from a wide spectrum of species including humans (for review, see Porter & Winberg, 1999), nonhuman primates (Kaplan & Russell, 1974), dogs (Hepper & Wells, 2006), cats (Rosenblatt, 1972), rabbits (Kindermann, Hudson, & Distel, 1994), and pigs (Morrow-Tesch & McGlone, 1990). The attraction to maternal nest odors is an adaptive mechanism, because it helps keep mobile newborn mammals near the warmth, safety, and food source provided in the nest (Alberts, 1978). In addition, odors encountered during infancy may aid in survival and influence behavior later in life (Fillion & Blass, 1986; Shah, Oxley, Lovic, & Fleming, 2002).

Among rodent species, the majority of evidence for neonatal olfactory learning has been produced by studies using rats (e.g., Cornwell-Jones & Sobrian, 1977; Gregory & Pfaff, 1971; Terry & Johanson, 1996). Several studies have shown that rat pups develop a rapid attraction to odor cues associated with maternal care during the first 9 days of life (for review, see Wilson & Sullivan, 1994). Pups will approach maternal odors early in development (Sullivan, Wilson, Wong, Correa, & Leon, 1990) and display preferences for odorants that are paired with artificial stimulation that mimics maternal licking (Sullivan & Leon, 1987).

With respect to other rodent species, infant attraction to maternal odors has also been established in hamsters (Cornwell, 1975; Devor & Schneider, 1974) and gerbils (Cornwell-Jones & Azar, 1982). However, relatively few investigations have used mice as subjects (except see Armstrong, DeVito, & Cleland, 2006), despite the extensive behavioral and genetic characterization of the mouse (for review, see Latham & Mason, 2004; Beck et al., 2000). Furthermore, there has been even less research examining the possible consequences of disrupted early olfactory experiences on the development of odor-guided behavior in any species of rodent.

The present study investigated whether disrupting the early olfactory environment of infant mouse pups by separating them from their mothers during the first two weeks of life would impair the attraction to familiar social odors. The maternal separation paradigm has been used as a rodent model for the effects of inadequate or inconsistent early caretaking in human psychosocial development (Plotsky & Meaney, 1993) and may involve disruption of several sensory processes, including olfactory development. The maternal separation procedure typically involves daily separation of the dam and pups for periods of 15 to 360 min during the first 2 weeks of life. Because the separation procedure reduces exposure to cues on which early olfactory learning depends (e.g., nest odors, tactile stimulation by the dam), we hypothesized that daily maternal separation of 15 or 180 min during the first 2 weeks of life would decrease preferences for familiar social odors in infant mice. In addition, this study investigated whether exposure to olfactory cues from the home-nest during the separation period would mitigate any negative effects of maternal separation on odor preference development.

Methods

Subjects

Three hundred forty-four CD-1 mice (*Mus musculus*) were used in this experiment. Both male (n = 172) and female (n = 172) mice were tested during infancy on postnatal day (PND) 10 and 14. Forty-three litters were bred at Syracuse University (stock originally acquired from Charles River Laboratories). Prospective mothers were housed in groups of four with one male for 14 days, following which females were placed individually in Plexiglas

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cages (43 × 23 × 15 cm) containing 2.2 L of hardwood bedding (Sani-chips, P.J. Murphy Forest Products) and one 5.08 cm^2 Nestlet (Ancare Corporation). On the day of birth, PND 0, litters were culled to 10 pups, with equal numbers of males and females. If the desired male/female ratio was not present on the day of delivery, litter cohorts were cross-fostered prior to assignment to a treatment condition. Cross-fostering was used because previous evidence (Armstrong et al., 2006) indicates that litter of origin does not significantly influence odor contingency learning in mice. Dams and litters were housed in Plexiglas cages (43 × 23 × 15 cm) in hardwood bedding (2.2 L) with ad lib access to food (LabDiet Rodent Chow, Nutrition International) and water. All litters were maintained with the dam in a temperature (20 ± 2 °C) and humidity (53%) controlled vivarium on a reverse 12:12 hr light: dark cycle with lights on at 19:00 h. All mice were maintained and tested in accordance with the ethical guidelines and regulations established by the Syracuse University Institutional Animal Care and Use Committee (IACUC).

Rearing Conditions

On the day after birth (PND 1). litters were randomly assigned to one of three experimental conditions that either involved maternal separation of 15 min, 180 min in clean hardwood shavings, or 180 min in home nest bedding. Additional litters were randomly assigned to a control condition, which consisted of facility-rearing. All experimental treatments occurred during the dark cycle between approximately 11:00 to 14:00 h. A schematic representation of the experimental design is shown in Figure 1.

Maternal Separation

Beginning on PND 1 and continuing until PND 14, litters assigned to the 15-min maternal separation condition ($n = 12$) were subjected to daily separations of 15 min from the dam, but not siblings (Plotsky & Meaney, 1993). The dam was removed from the home cage prior to moving the litter from the vivarium to the laboratory in the home cage. Individual litters were placed in a small Plexiglas container (containing no shavings) and weighed as a group. At the end of the 15-min separation, pups were removed from the Plexiglas container and reunited with the dam in the home cage.

Two conditions of 180-min maternal separation were used and involved separation in either clean hardwood shavings ($n = 10$ litters) or nest bedding ($n = 11$ litters). The 180-min separation litters were weighed according to the same procedure as the 15-min separation litters. Following weight collection, individual litters were placed in Plexiglas cages (28 × 16.5 × 13 cm) and received daily separations of 180 min from PND 1 to PND 14. The separation cages either contained 750 ml of clean hardwood or 750 ml of nest bedding. Nest bedding was removed from the home cage on PND 1 and replaced with an equivalent volume of clean hardwood shavings. The shavings in the separation cages were not changed throughout the course of the experiment. During separa-

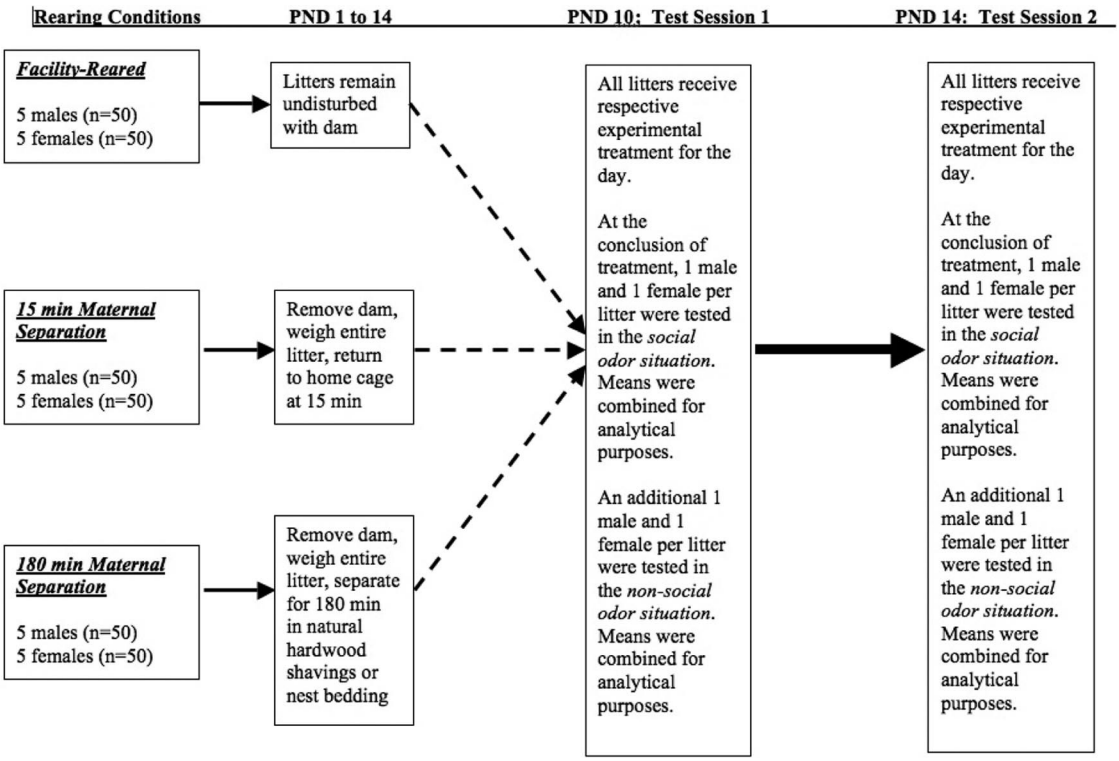

Figure 1. Experimental design and rearing procedures from postnatal day (PND) 1 to 14. $N = 43$ litters ($n = 10$ for facility reared, $n = 12$- for 15-min separation, $n = 11$ for 180-min separation in natural shavings, and $n = 10$ for 180-min separation in nest bedding). Males and females were tested only once in the odor preference test and randomly selected for testing on PND 10 and 14.

tion, litters were maintained at approximately nest temperature (28 °C ± 2 °C), in a dark, soundproof room within the laboratory. Upon completion of the separation period, the dam was returned to the home cage in the vivarium, followed by reunion with the litter.

Facility Reared

The control condition in this experiment was animal facility rearing. In this condition litters ($n = 10$) remained undisturbed during PND 1 to 14, except for normal animal husbandry and caretaking. Cage shavings were changed on an identical schedule to that of the other conditions and occurred at approximately PND 7 and 14. The facility-reared condition provided continuous exposure to all normal olfactory and tactile cues associated with the nest.

Testing Apparatus and Procedure

The odor preference test is a two-odor, free-choice situation that is conducted under red-light illumination (cf. Cornwell-Jones, Decker, Gianulli, Wright, & McGaugh, 1990). A diagram of the odor preference apparatus is shown in Figure 2. The testing apparatus consisted of a Plexiglas frame (29 × 22 × 10 cm) with a screen floor, which allowed mice olfactory, but not gustatory or tactile contact with shavings in two right triangle compartments below. A center triangle without shavings separated the two test odor compartments.

Each pup was tested in one of two odor preference situations. The social odor test stimuli were 250 ml by volume of nest bedding and clean hardwood shavings. Nest bedding was taken from the home cage on the day of testing and replaced with an equivalent volume of clean hardwood shavings. The nonsocial odor test examined responses of mice to familiar clean hardwood shavings and the novel odor of clean pine shavings. Pups were randomly selected from each litter for testing on PND 10 and 14. Testing was conducted during the dark phase of the light cycle at approximately 1500 h. On each test day one female and one male from each litter were tested once in the social odor test situation. An additional one male and one female were tested once in the familiar nonsocial odor test situation. Prior to testing, litters that were assigned to the separation conditions had completed their respective experimental treatment on the test day.

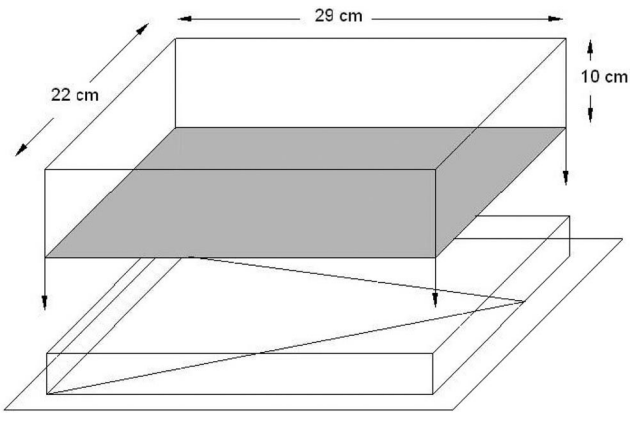

Figure 2. The odor preference apparatus used to examine social and nonsocial odor preferences. 90° triangles contained ~250 ml of shavings. Central triangle contained no shavings.

At the beginning of each test, one pup was removed from the litter and placed along the midline of the test apparatus, between the two test odors. Each mouse was videotaped for the course of a trial (180 s) and allowed to move freely about the test apparatus. A mouse was defined as investigating one of the three odor triangles when its snout and forepaws entered the area. Following each trial, the apparatus was cleaned with a diluted soap solution, rinsed, and thoroughly dried.

Behavioral analysis of the videotaped sessions was conducted with three raters (interrater reliability of $r = .92$). Each rater traced the mouse's path on a diagram of the floor of the testing apparatus. The dependent measures recorded for each mouse were the time spent over each type of shavings in the test odor pair, a difference score (calculated by subtracting the time spent over the less familiar odor from the time spent over the more familiar odor), the time spent in the central shavings-free area, and activity (measured by placing a transparent grid of 48 squares over the traced path of the mouse and counting total squares entered).

Statistical Analyses

Litter weight. Changes in litter weight were examined to assess whether the different durations of maternal separation influenced the health and maturation of the litters. Data were analyzed with a 3 × 14 (Condition × Age) repeated measures analyses of variance (ANOVA). The daily weight of each litter was the dependent variable and postnatal Days 1–14 were treated as the repeated measures factor. The between-subjects factor was rearing condition and included the groups of mice that were maternally separated for durations of 15 min, 180 min in natural hardwood shavings, or 180 min in nest bedding. The facility-reared group was not included in the analysis because they were only removed from the home cage once, during cage changing, during the first 2 weeks of life.

Olfactory preference data. To control for within-litter confounds, the mean of each litter (1 male and 1 female per test day) was used during all remaining statistical analysis, rather than individual pup values. Odor preferences were evaluated with repeated-measures ANOVAs. The five dependent measures that were evaluated in the social odor test situation were the time over nest bedding, time over clean hardwood shavings, time over the central zone, the difference score (calculated by the subtracting the time over clean hardwood shavings from the time over nest bedding), and activity scores. Familiar nonsocial odor preferences were evaluated with five additional dependent measures and included the time over clean hardwood shavings, time over clean pine shavings, time over the central zone, the difference score (calculated by subtracting the time over clean pine shavings from the time over clean hardwood shavings), and activity scores.

An initial analysis of the data from the social and familiar nonsocial odor test was conducted to determine if differences existed between mice that had been maternally separated for 180 min in clean hardwood shavings and mice that were separated for 180 min in nest bedding. The data were analyzed with 5 separate 2 × 2 (Age × Rearing condition) repeated-measures ANOVAs for each of the two test situations (social odor test and familiar nonsocial test). PND 10 and 14 were treated as the within-subjects

repeated variables and rearing condition was the between-subjects factor for each series of analyses. The results indicated that there were not significant differences between pups that were maternally separated for 180 min in clean hardwood shavings and those separated for 180 min in nest bedding for any of the dependent measures, $p > .05$. Because the groups did not statistically differ from one another, the data were combined to form a composite 180-min maternal separation group for the remainder of the analyses.

Following the initial analyses comparing the data between the two 180-min maternal separation groups, combined data was used to compare the olfactory preferences of pups that were facility-reared, pups that were maternally separated for 15 min, and pups that were maternally separated for 180 min from PND 10 to 14. The social odor test situation and familiar versus novel nonsocial odor test situation were each analyzed with five separate 2 × 3 (Age × Rearing condition) repeated measures ANOVAs, with PND 10 and 14 as the repeated variables and rearing condition as a between-subjects factor. Significant main effects of rearing condition included the calculation of an effect size (partial eta-squared, η_p^2) and were followed by post hoc comparisons using Tukey's Honestly Significant Difference (HSD). Significant main effects of the repeated measures factor (Age) were followed by paired-samples *t* tests for each rearing condition. Statistical significance for all analyses was set at $p < .05$. Statistics are reported with mean ± 95% confidence intervals.

We further examined the olfactory preferences of each group in each test situation using single sample *t* tests followed by the calculation of effect size (Cohen's *d*). The mean group difference scores were compared to zero, the score expected if there was no preference between odors. This procedure has been previously used to evaluate the odor preference development of rats (Cornwell-Jones et al., 1990). Means significantly greater than zero indicated a preference for the more familiar odor, while means significantly less than, or equal to zero indicated a lack of preference for the more familiar odor. Statistical significance for these analyses was also set at $p < .05$.

Results

Activity and Litter Weight

Activity during testing was analyzed to assess whether the maternal separation procedure produced any alteration in mobility, which could influence behavioral performance during testing. Irrespective of rearing condition, pups became more active with age in the social odor test situation, $F(1, 40) = 108.50$, $p < .001$. $\eta_p^2 = 0.73$ (PND 10, $M = 22.94 \pm 2.95$ s; PND 14, $M = 41.28 \pm 2.02$ s) and in the nonsocial odor test situation, $F(1, 40) = 97.06$, $p < .001$, $\eta_p^2 = 0.71$ (PND 10, $M = 20.89 \pm 3.14$ s; PND 14, $M = 40.10 \pm 2.63$ s).

The overall trajectory of weight gain did not differ between the three experimental groups over the course of the first two postnatal weeks ($p > .05$).

Social Odor Test (Nest Hardwood vs. Clean Hardwood)

Age and rearing condition interacted to influence time spent over clean hardwood shavings, $F(2, 40) = 5.13$, $p = .01$, $\eta_p^2 = 0.20$. Tukey's HSD tests showed that rearing condition did not affect this measure on PND 10 (all ps $> .05$), but on PND 14 the facility-reared group ($M = 67.23 \pm 12.25$ s) spent more time over the clean hardwood shavings compared to the 15-min maternal separation group ($M = 34.21 \pm 11.19$ s) and 180-min maternal separation group ($M = 32.40 \pm 8.45$ s), all ps $< .001$. In addition, the facility-reared group showed an increase in time spent over the clean hardwood shavings from PND 10 to 14, $t(9) = 2.44$, $p < .05$, $d = 1.63$. In contrast, the amount of time spent over the clean hardwood shavings by the 180-min maternal separation group was found to decrease from PND 10 to 14, $t(20) = 1.97$, $p < .05$. $d = 0.88$. The 15-min maternal separation group did not significantly change in their mean time spent investigating the clean hardwood shavings ($p > .05$). The main effects of age and rearing condition did not influence the time pups spent over clean hardwood shavings ($p > .05$).

Age, rearing condition, and their interaction did not significantly influence the time that pups spent over nest bedding or the central shavings-free area ($p > .05$). Average time (means ±95% CI) mice spent over each area during the social odor test can be found in Table 1.

Age and rearing condition interacted to influence mean difference scores (Figure 3), $F(2, 40) = 3.30$, $p < .05$, $\eta_p^2 = 0.14$. Tukey's HSD tests revealed that on PND 10 all groups similarly preferred nest bedding odor to clean hardwood odors (all ps $> .05$). However, on PND 14, the 15-min separation group ($M = 90.01 \pm 24.81$ s) and the 180-min separation group ($M = 89.86 \pm 18.77$ s) displayed a greater preference for nest bedding compared to the facility-reared group ($M = 27.88 \pm 27.18$ s), all ps $< .01$. For the 180-min separation group, mean difference scores increased from PND 10 to 14, $t(20) = -2.04$, $p < .05$, $d = 0.91$, but facility-reared pups and pups that were separated for 15 min did not display age-related changes in mean difference scores ($p > .05$). The difference scores were not influenced by age or rearing condition ($p > .05$).

Social odor preference development was tested for each condition with single-sample *t* tests against a hypothetical mean of 0. The analyses indicated that on PND 10 the facility-reared, $t(9) = 2.85$, $p < .05$, $d = 1.90$, 15-min maternal separation group, $t(11) = 3.53$, $p < .01$, $d = 2.13$, and 180-min maternal separation group, $t(20) = 2.55$, $p < .01$, $d = 1.40$ significantly preferred hardwood nest bedding over natural hardwood shavings. In contrast, on PND 14 the 15 maternal separation group, $t(11) = 7.33$, $p < .001$, $d = 4.42$ and 180 maternal separation group, $t(20) = 9.68$, $p < .001$, $d = 4.33$, but not facility-reared pups ($p > .05$) displayed a preference for nest bedding. Group preferences by age are shown in Figure 3.

Familiar Nonsocial Odor Test (Clean Hardwood vs. Clean Pine)

Irrespective of rearing condition, the time spent over the clean hardwood shavings increased from PND 10 to 14, $F(1, 40) = 5.70$, $p < .05$, $\eta_p^2 = 0.13$ (PND 10, $M = 85.31 \pm 11.25$ s; PND 14, $M = 101.47 \pm 10.93$ s). The between-subjects main effect and the interaction of age and condition did not reach significance ($p > .05$). Times spent over clean pine shavings and over the central area were not significantly affected by age, condition, or the interaction of the two variables ($p > .05$). Mean (±95% CI) time

Table 1
Average Time (S) Spent Investigating Odors in the Social and Nonsocial Odor Test

Variable	Age (days)	Facility reared	15-min maternal separation	180-min maternal separation
Social odors				
Time over nest bedding	10	109.77 ± 31.29	126.16 ± 28.57	97.53 ± 21.59
	14	95.12 ± 16.14	124.22 ± 14.73	122.26 ± 11.13
Time over natural hardwood	10	30.99 ± 26.49	37.18 ± 24.19	48.91 ± 18.28
	14	67.23 ± 12.25	34.21 ± 11.19	32.40 ± 8.45
Time over central area	10	39.23 ± 15.78	16.66 ± 14.41	33.55 ± 10.89
	14	17.65 ± 9.04	21.57 ± 8.25	25.34 ± 6.24
Nonsocial odors				
Time over natural hardwood	10	98.80 ± 22.20	81.50 ± 20.26	75.62 ± 15.32
	14	121.08 ± 21.58	83.52 ± 19.70	99.81 ± 14.89
Time over natural pine	10	58.27 ± 23.72	57.63 ± 21.65	55.31 ± 16.37
	14	33.87 ± 19.74	60.75 ± 18.01	54.60 ± 13.62
Time over central area	10	22.94 ± 24.59	40.87 ± 22.44	49.08 ± 16.96
	14	25.06 ± 9.68	35.73 ± 8.83	25.59 ± 6.67

Note. The values represent average investigation time (s) as mean ± 95% confidence intervals.

spent over clean hardwood shavings, clean pine shavings, and the central areas are presented in Table 1.

There was a significant increase in the mean difference scores from PND 10 to 14, $F(1, 40) = 4.17$, $p < .50$, $\eta_p^2 = 0.09$ (PND 10, $M = 28.24 \pm 19.66$ s; PND 14, $M = 51.73 \pm 20.37$ s), which was not significantly affected by rearing condition or the interaction of age and condition ($p > .05$). On PND 10, the facility-reared, $t(9) = 2.11$, $p < .05$, $d = 1.41$, but not 15-min or 180-min maternal separation groups showed a preference for clean hardwood shavings. On PND 14, the facility-reared group, $t(9) = 4.38$, $p < .001$, $d = 2.92$, 15-min maternal separation group, $t(11) = 2.55$, $p < .05$, $d = 1.54$, and the 180-min maternal separation group, $t(20) = 3.29 = p < .01$, $d = 1.47$, all showed a preference for natural hardwood shavings. Group preferences by age are shown in Figure 4.

Discussion

Infant mice (Honeycutt & Alberts, 2005) and rats (Sullivan et al., 1990) rapidly develop preferences for familiar nest odors. Our study investigated the hypothesis that mother–infant separations of 15 or 180 min from PND 1 to 14 would alter early olfactory learning for nest odors, leading to decreased preferences for social odors in infant mice. This study also examined the behavioral responses of infant mice to familiar versus novel nonsocial odors.

Maternal separation of either 15 or 180 min during PND 1 to 14 influenced the development of responses to social odors inside the nest, but not to familiar odors outside the nest in mice aged 10 and

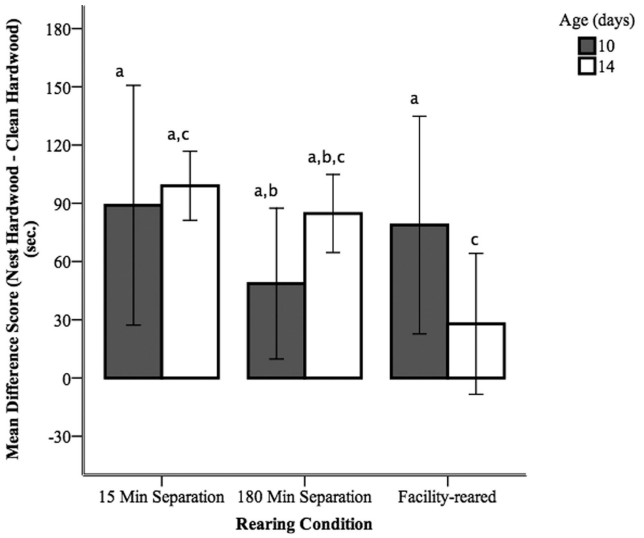

Figure 3. Mean (±95% confidence interval) difference scores (calculated by the subtraction of time over natural hardwood from time over nest bedding) from the social odor test situation. [a] Group preference for nest bedding, $p < .05$. [b] Age-related increase for 180-min separation group, $p < .05$. [c] Rearing condition differences, $p < .05$.

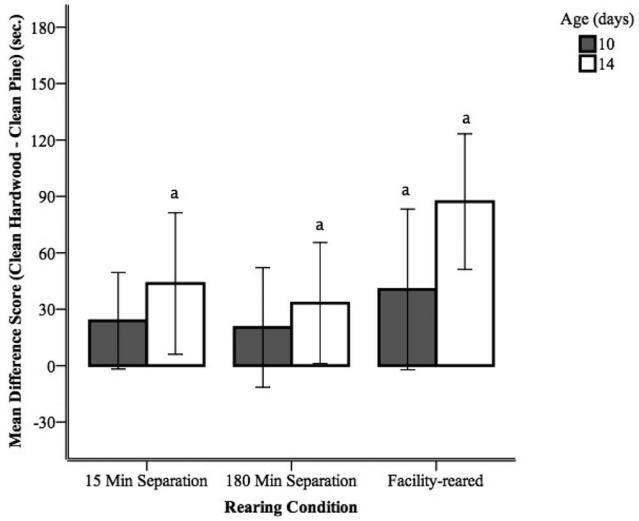

Figure 4. Mean (±95% confidence interval) difference scores (calculated by the subtraction of time over natural pine from time over natural hardwood) from the nonsocial odor test situation. [a] Group preference for natural hardwood shavings, $p < .05$.

14 days old. The observed pattern of behavioral development was adaptively compatible with other maturational variables for control, facility-reared mice, but not for maternally separated mice.

Familiar social odors attracted facility-reared mice on postnatal Day 10, but not Day 14. Ten-day-old mice cannot control their body temperature, have unopened eyes (Smith, 1981) and, as demonstrated in the current and others' data (Nagy, Murphy, & Ray, 1975; Williams & Scott, 1953), have limited motor ability. Mice of this age spend most of their time in the nest (Weber & Olsson, 2008), near the warmth and food provided by their mother, and attraction to maternal nest odors provides an olfactory tether for survival. By postnatal Day 14, the pups are homeothermic, their eyes have opened, and motor ability has greatly increased (for review see Latham & Mason, 2004; Smith, 1981). Pups of this age are now capable of exploring the environment outside of the nest, in preparation for weaning and the transition to solid food, which is complete by approximately Day 17 (Latham & Mason, 2004). In our study, the attraction to maternal nest odors decreased, and indeed disappeared in facility-reared mice by postnatal Day 14, while attraction to familiar odors outside the nest increased. In facility-reared mice, this series of behavioral changes would facilitate emancipation from the maternal nest.

In contrast to our hypothesis and the behavioral development of facility-reared mice, maternally separated mice were attracted to social nest odors on both postnatal Days 10 and 14, which suggest a prolonged tether to the nest environment. However, they also demonstrated an age-dependent increase in attraction to familiar odors outside of the nest. Similar to the ontogeny of odor preference behavior of facility-reared mice, this age-dependent increase in attraction to familiar nonsocial odors would drive them out of the nest. Simultaneous attraction to familiar odors within and outside of the nest might set up a conflict that alters interactions between the pups and the dam in the nest.

An extensive body of literature documents the important role of natural and artificial maternal stimulation in early odor learning that may involve imprinting processes (for review, see Wilson & Sullivan, 1994). Furthermore, maternally deprived rat pups display olfactory-guided social behavior and preference deficits (Lévy, Melo, Galef Jr., Madden, & Fleming, 2003) that are ameliorated by reconstituting aspects of maternal stimulation (Melo et al., 2006). In our study, differences in the social olfaction profiles of facility-reared and maternally separated mouse pups may have resulted from rearing condition induced differences in maternal caretaking. Francis and Kuhar (2008) recently observed increased licking and grooming directed at maternally separated rat pups compared to a group that was only handled for bedding changes. Further research in this area would benefit from testing the hypothesis that rearing induced differences in maternal stimulation during infancy influence early olfactory learning in the mouse.

In conclusion, our findings may provide a useful model that can be further developed to elucidate the etiology of psychosocial abnormalities that are the most prominent consequence of early inconsistent caretaking in humans (Perry, Sigal, Boucher, & Paré, 2006). Children are sensitive to social odors (Ferdenzi, Coureaud, Camos, & Schaal, 2008), including an awareness of smells associated with relatives and self-odor. Research on the effects of early social experience on olfactory learning in nonhuman infant animals may prove instructive and present an interesting methodological perspective to model human psychosocial development.

References

Alberts, J. R. (1978). Huddling by rat pups: Group behavioral mechanisms of temperature regulation and energy conservation. *Journal of Comparative and Physiological Psychology, 92,* 231–245.

Armstrong, C. M., DeVito, L. M., & Cleland, T. A. (2006). One-trial associative learning in neonatal mice. *Chemical Senses, 31,* 343–349.

Beck, J. A., Lloyd, S., Hafezparast, M., Lennon-Pierce, M., Eppig, J. T., Festing, M. F. W., et al. (2000). Genealogies of mouse inbred strains. *Nature Genetics, 24,* 23–25.

Cornwell, C. A. (1975). Golden hamster pups adapt to complex rearing odors. *Behavioral Biology, 14,* 175–188.

Cornwell-Jones, C. A., & Azar, L. M. (1982). Olfactory development in gerbil pups. *Developmental Psychobiology, 15,* 131–137.

Cornwell-Jones, C. A., Decker, M. W., Gianulli, T., Wright, E. L., & McGaugh, J. L. (1990). Norepinephrine depletion reduces the effects of social and olfactory experience. *Brain Research Bulletin, 25,* 643–649.

Cornwell-Jones, C. A., & Sobrian, S. K. (1977). Development of odor-guided behavior in Wistar and Sprague-Dawley rat pups. *Physiology & Behavior, 19,* 685–688.

Devor, M., & Schneider, G. E. (1974). Attraction to home-cage odor in hamster pups: Specificity and changes with age. *Behavioral Biology, 10,* 211–221.

Ferdenzi, C., Coureaud, G., Camos, V., & Schaal, B. (2008). Human awareness and uses of odor cues in everyday life: Results from a questionnaire study in children. *International Journal of Behavioral Development, 32,* 422–431.

Fillion, T. J., & Blass, E. M. (1986). Infantile experience with suckling odors determines adult sexual behavior in male rats. *Science, 231,* 729–731.

Francis, D. D., & Kuhar, M. J. (2008). Frequency of maternal licking and grooming correlates negatively with vulnerability to cocaine and alcohol use in rats. *Pharmacology, Biochemistry and Behavior, 90,* 497–500.

Gregory, E. H., & Pfaff, D. W. (1971). Development of olfactory-guided behavior in infant rats. *Physiology & Behavior, 6,* 573–576.

Hepper, P. G., & Wells, D. L. (2006). Perinatal olfactory learning in the domestic dog. *Chemical Senses, 31,* 207–212.

Honeycutt, H., & Alberts, J. R. (2005). Housing pregnant mice (*Mus musculus*) in small groups facilitates the development of odor-based homing in offspring. *Journal of Comparative Psychology, 119,* 418–429.

Kaplan, J., & Russell, M. (1974). Olfactory recognition in the infant squirrel monkey. *Developmental Psychobiology, 7,* 15–19.

Kindermann, U., Hudson, R., & Distel, H. (1994). Learning of suckling odors by newborn rabbits declines with age and suckling experience. *Developmental Psychobiology, 27,* 111–122.

Latham, N., & Mason, G. (2004). From house mouse to mouse house: The behavioural biology of free-living *Musmusculus* and its implications in the laboratory. *Applied Animal Behaviour Science, 86,* 261–289.

Lévy, F., Melo, A. I., Galef, B. G., Jr., Madden, M., & Fleming, A. S. (2003). Complete maternal deprivation affects social, but not spatial learning in adult rats. *Developmental Psychobiology, 43,* 177–191.

Melo, A. I., Lovic, V., Gonzalez, A., Madden, M., Sinopoli, K., & Fleming, A. S. (2006). Maternal and littermate deprivation disrupts maternal behavior and social-learning of food preference in adulthood: Tactile stimulation, nest odor, and social rearing prevent these effects. *Developmental Psychobiology, 48,* 209–219.

Morrow-Tesch, J., & McGlone, J. J. (1990). Sensory systems and nipple attachment behavior in neonatal pigs. *Physiology & Behavior, 47,* 1–4.

Nagy, Z. M., Murphy, J. M., & Ray, D. (1975). Development of behavioral arousal and inhibition in the Swiss-Webster mouse. *Bulletin of the Psychonomic Society, 6,* 146–148.

Perry, J. C., Sigal, J. J., Boucher, S., & Paré, N. (2006). Seven institutionalized children and their adaptation in late adulthood: The children of

Duplessis (Les Enfants de Duplessis). *Psychiatry: Interpersonal and Biological Processes, 69,* 283–301.

Plotsky, P. M., & Meaney, M. J. (1993). Early postnatal experience alters hypothalamic corticotropin-releasing factor (CRF) mRNA, median eminence CRF content and stress-induced release in adult rats. *Molecular Brain Research, 18,* 195–200.

Porter, R. H., & Winberg, J. (1999). Unique salience of maternal breast odors for newborn infants. *Neuroscience & Biobehavioral Reviews, 23,* 439–449.

Rosenblatt, J. S. (1972). Learning in newborn kittens. *Scientific American, 227,* 18–25.

Shah, A., Oxley, G., Lovic, V., & Fleming, A. S. (2002). Effects of preweaning exposure to novel maternal odors on maternal responsiveness and selectivity in adulthood. *Developmental Psychobiology, 41,* 187–196.

Smith, J. (1981). Senses and communication. In R. Berry (Ed.), *Biology of the house mouse.* London: Academic Press.

Sullivan, R. M., & Leon, M. (1987). One-trial olfactory learning enhances olfactory bulb responses to an appetitive conditioned odor in 7-day-old rats. *Developmental Brain Research, 35,* 307–311.

Sullivan, R. M., Wilson, D. A., Wong, R., Correa, A., & Leon, M. (1990). Modified behavioral and olfactory bulb responses to maternal odors in preweanling rats. *Developmental Brain Research, 53,* 243–247.

Terry, L. M., & Johanson, I. B. (1996). Effects of altered olfactory experiences on the development of infant rats' responses to odors. *Developmental Psychobiology, 29,* 353–377.

Weber, E. M., & Olsson, I. A. S. (2008). Maternal behaviour in *Mus musculus* sp.: An ethological review. *Applied Behaviour Sciences, 114,* 1–22.

Williams, E., & Scott, J. P. (1953). The development of social behavior patterns in the mouse, in relation to natural periods. *Behaviour, 6,* 35–65.

Wilson, D. A., & Sullivan, R. M. (1994). Neurobiology of associative learning in the neonate: Early olfactory learning. *Behavioral & Neural Biology, 61,* 1–18.

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