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Postnatal Maternal Care Predicts Divergent Weaning Strategies and the Development of Social Behavior

ABSTRACT: Maternal care experienced during postnatal development predicts long-term neurobiological and behavioral outcomes. However, the cascade of behavioral changes that emerge in response to maternal care has not been elucidated. In the current study, we examine naturally occurring variation in postnatal licking/grooming (LG) in C57BL/6J mice to determine its impact on preweaning maternal and pup behavior, the weaning process, the pace of developmental change, the emergence of social behavior, and indices of anxiety-like behavior in adulthood. Our analyses indicate that lower postnatal LG is associated with truncated and more infrequent maternal behavior during the preweaning period. Moreover, compared to High LG dams, Low LG dams are observed to actively wean their offspring sooner and have offspring that play more frequently. The heightened pace of developmental change observed in offspring of Low LG dams suggests a more rapid transition to behavioral and nutritional independence, which could have implications for future reproductive strategies. © 2015 Wiley Periodicals, Inc. *Dev Psychobiol* 57:809–817, 2015.

Keywords: maternal care; postnatal; weaning; play behavior; social; anxiety-like; development

INTRODUCTION

The process of development involves dynamic shifts in the behavior of infants and caregivers dependent on behavioral and physiological needs. In altricial mammals, the postnatal period is characterized by offspring dependence on mothers for warmth, nutrition, protection, and tactile stimulation (Rheingold, 1963). In rodents, maternal care immediately following parturition includes high levels of nursing, nest-building and licking/grooming of pups, as well as elevated levels of eating to maintain the energetic demands of lactation (Rheingold, 1963). The transition to reduced maternal dependence is punctuated by several changes in both mother and offspring. In laboratory mouse pups, these

changes include increased locomotor activity, ability to thermoregulate, eye-opening, and the transition to eating solid foods associated with changes in gut enzyme activity (Gomendio, Cassinello, Bateson, & Smith, 1995). The weaning period continues for up to 2 weeks, during which pups decrease the amount of time they suckle, begin to spend more time away from the mother, and become involved in play and social behavior with peers (Konig & Markl, 1987; Martin, 1984). Concomitant with these changes in offspring, the mother spends less time nursing and interaction with pups is typically in the form of side-by-side contact without suckling. An increased occurrence of pup-mounting behavior by mouse dams is also observable during the weaning period and may facilitate the shift to independence of offspring through actively inhibiting sucking attempts (Curley et al., 2009b). Within these observational studies, it is clear that weaning is a process rather than an event or particular day and that this process involves a bi-directional interplay between mothers and offspring.

Manuscript Received: 11 January 2015

Manuscript Accepted: 1 May 2015

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Article first published online in Wiley Online Library
 (wileyonlinelibrary.com): 11 June 2015

DOI 10.1002/dev.21326 • © 2015 Wiley Periodicals, Inc.

Variation in the interactions between mothers and offspring can have a significant impact on growth, physiology, neural development, and behavioral outcomes. Disruption to the quality of mother–infant interactions through maternal deprivation or prolonged separation can lead to heightened stress reactivity in adulthood, impaired cognition, and reduced maternal behavior in adult offspring (Curley, Jensen, Mashoodh, & Champagne, 2011). Similar effects are observed in response to natural variations in maternal care. In rats, pups that receive low levels of licking/grooming (LG) from their mothers during the postnatal period have elevated hypothalamic–pituitary–adrenal (HPA) responses to stress, heightened fear responses to novelty, and perform poorly on learning/memory tasks (Meaney, 2001). Female offspring of Low LG mothers have increased sexual receptivity (Cameron, Fish, & Meaney, 2008b) and reduced maternal behavior toward their own pups (Champagne, Francis, Mar, & Meaney, 2003) compared to offspring of High LG mothers, suggesting a trade-off in reproductive effort. Though most of the outcome measures associated with low versus high maternal LG have focused on long-term changes in adulthood, there is increasing evidence that LG-associated effects may be observed earlier in development. Puberty onset is earlier amongst female offspring of Low LG mothers (Cameron et al., 2008a) and juvenile male offspring of Low compared to High LG mothers engage in higher levels of play fighting (Parent & Meaney, 2008). Similar enhancements in social play behavior by juveniles have been observed following manipulations that artificially reduce LG (Birke & Sadler, 1987; Moore & Power, 1992). However, the developmental trajectories that precede the onset of this variation in juvenile behavior in response to variation in postnatal LG have not been explored.

In the current study, we examine whether variation in maternal care experienced during the early postnatal period predicts preweaning maternal behavior and the dynamics of the weaning process. Within these analyses, we examine whether the emergence of social and play behavior during the preweaning period and adult exploratory/anxietylike behavior is likewise predicted by these early mother–infant interactions. Based on previous findings suggesting variation in juvenile behavior amongst offspring of Low versus High LG dams, we predicted an accelerated rate of developmental change during the preweaning period among offspring that received low levels of maternal care during postnatal development. This differential developmental pace may function to transition offspring to independence at an early age and contribute to the developmental pathways through which peer-directed social behavior emerges.

METHODS

Animals and Animal Husbandry

C57BL/6J (B6) mice used for this study were wild-type laboratory mice (*Mus musculus*) bred in the Sub-Department of Animal Behaviour at the University of Cambridge and descendent from offspring of mice from Harlan UK. The mice were housed in transparent *Plexiglas* cages (42 × 12.5 × 12.5 cm³) with steel wire lids on a reverse 12D:12L light cycle under a constant temperature of 21°C and 55% humidity and provided *ad libitum* water and food (RM1 E rodent chow diet, Lillico). All behavioral observations and tests took place during the dark period of the light cycle under dim red illumination. All procedures were done accordance with UK Home Office regulations.

Assessment of Home-Cage Maternal Behavior

The procedure for assessing home-cage maternal behavior in mice has been previously described (Champagne, Curley, Keverne, & Bateson, 2007). Maternal behavior was scored from postnatal (PN) days 1–6 and 19–27. Observers were trained to a high level of inter-rater reliability (i.e., >0.90). Dams were observed in their home cage during the dark-phase of the light cycle under dim red light (<5 lux) and not disturbed for the duration of the observation period. Each day consisted of 4 observation periods, 2 within the first 5 hr following the onset of the dark cycle (800–1,300) and 2 within 7 hr of the end of the dark cycle (1,300–2,000). Each observation was 60 min in duration and no observation session took place within the 1-hr period before or after the transition from the light to dark cycle. Within each observation period, the behavior of each mother was scored every 3 min (20 observations/period × 4 periods/day = 80 observations/mother/day). The following behaviors were scored: mother licking and grooming (LG) any pup (both body and anogenital licking were included), mother in nursing posture over pups, non-nursing physical contact with pups, nest-building (while in contact with pups, nursing pups, or not in contact with pups), self-grooming, eating, and drinking. In addition, frequency of “pup mounting” behavior was recorded in the litters observed from PN19 to PN27. This behavior was only observed during the later stages of the preweaning period and is characterized by the dam chasing and pinning the pup while maintaining a rigid thrusting posture over the pup for between a few seconds and a minute (Curley et al., 2009b) (see Supplemental Video File). This behavior is typically preceded by repeated attempts by the pup to suckle. All dams in this study were primiparous females.

Preweaning Pup Behavior

Home-cage pup behavior was assessed from PN19 to PN27 coincident with the observations of maternal behavior. During each 1-hr observation period, the behavior of each litter was scored every 3 min. During observation of the litter, the occurrence of the following behaviors was recorded: suckling from the dam, eating, social investigation (sniffing or

grooming a littermate), and social play, which included darting (fast sprint from one end of the cage to the other), chasing, and fighting (attacking and biting another mouse in a playful or antagonistic manner). The litter was rated such that any combination of behaviors was possible in a given observation.

Open-Field Behavior

The open-field test is a standard measure of exploration within an anxiogenic novel environment (Prut & Belzung, 2003). The open-field used was a $90 \times 90 \times 60 \text{ cm}^3$ plastic box. Male and female mice were tested at approximately PN60 and females were confirmed to be in diestrus on the day of testing following analysis of the cytology of a vaginal smear. On the day of testing, the mouse was removed from its home cage and placed directly into one corner of the open field. After a 10-min video-recorded session, the mouse was returned to its home cage. Counts of fecal boli were assessed at this time. All testing was conducted under red (dark phase) lighting conditions. During analysis of the video recordings of testing sessions, the field was divided into a grid of 10×10 squares. For the purposes of analysis, inner-field exploration was defined as the time spent in the inner 9×9 squares and activity was defined as the number of grid crossings. Latency to enter the inner area was also recorded.

Procedure

Adult B6 females were housed 2–3 per cage and mated with a B6 male for 2 weeks. At gestational day 16, females were singly housed and monitored daily for the birth of the litter. This breeding protocol generated 20 litters. On the day of birth, designated as PN0, pups were weighed and counted and the dam and litter were placed in a clean cage. Litter sizes ranged from 3 to 10 pups ($M = 5.8 \pm 0.41$). Maternal observations commenced on PN1 and continued through to PN6. Average frequencies of maternal behaviors were calculated based on the number of times a behavior was observed divided by the total number of observations. From PN7 to PN18, cages underwent routine cage cleaning. From PN19 to PN27, mother and pup behaviors were observed in the home-cage, and frequencies of these behaviors were calculated based on the number of times a behavior was observed divided by the total number of observations. Offspring were weaned at PN28 and housed 3–4/cage with same-sex cage-mates that had experienced similar levels of postnatal LG. At PN60, male and female offspring ($n = 1\text{--}2/\text{sex}/\text{litter}$) were tested in the open-field.

Statistical Analysis

All analyses were conducted with Stata v12.1 (College Station, TX). We took a generalized linear modeling approach, controlling for random effects with multilevel modeling when the data contained grouping factors (e.g., multiple observations within litter over time (Gelman & Hill, 2006; Rabe-Hesketh & Skrondal, 2008). We coded low frequency behaviors, for example, mounting, as present (1) or

absent (0) and modeled them with a logit link and Binomial error distribution (i.e., logistic regression). In all other cases, we used the identity link function and a Gaussian error distribution, making the coefficients and standard errors equivalent to the ordinary least squares estimates (i.e., regular linear regression). To visualize the interaction of time and LG, we split LG into three groups based on frequency of occurrence: Low LG (mean LG = $4.99\% \pm 0.49\%$, $n = 6$), Mid LG (mean LG = $9.18\% \pm 0.68\%$, $n = 9$), or High LG (mean LG = $15.91\% \pm 2.11$, $n = 5$). Low LG dams were thus defined as exhibiting a frequency of LG less than 6.5% and High LG dams as exhibiting a frequency of LG greater than 13.0%. There were no significant within-LG group correlations between maternal care and offspring outcomes. Due to the very high level of LG displayed by one of the High LG litters (LG = 24.33%), all analyses were conducted with the entire sample and also with the removal of this litter. All significant findings reported are maintained when this litter is removed from the analyses. As we did not standardize litter sizes or sex ratio of the litter, all effects were checked for robustness after controlling for these variables. Multiple regression analyses indicated that controlling for litter size and sex ratio did not affect the nature of the results; even after including these variables in the model, the effect of early LG remained consistent with the simple pairwise correlations reported below.

Results

Individual Differences in Maternal Care PN1-6

Postnatal LG occurring early in the postnatal period (E-LG) ranged from 4% to 24% and was not significantly correlated with other PN maternal behaviors. Frequencies of PN1–PN6 maternal behavior as a function of Low, Mid, and High E-LG are presented in Table 1. E-LG was found to be statistically different between Low, Mid, and High E-LG litters ($p < .0001$). Sex ratio of the litter ($48.23\% \pm 5.37$) was not correlated with the frequency of any of the postnatal maternal behavior (p 's $> .2$).

Individual Differences in Maternal Care PN19-27

Consistent with previous analyses of change in maternal behavior across the preweaning period (Curley et al., 2009b), several maternal behaviors were significantly lower at PN19-27 compared to PN1-6: LG ($1.9\% \pm 0.39$, $p < .0001$), nursing ($36.30\% \pm 2.01$, $p < .0001$), and nest-building ($1.10\% \pm 0.20$, $p < .0001$). In contrast, other behaviors increased significantly: non-nursing contact ($17\% \pm 0.84$, $p < .0001$), self-grooming ($5.52\% \pm 0.30$, $p < .0001$), and mounting, which was not observed from PN1-6 ($0.35\% \pm 0.11$, $p < .01$). Levels of eating ($22.25\% \pm 0.98$) and drinking ($1.52\% \pm 0.09$) remained

Table 1. Frequency (% \pm SEM) of Postnatal Maternal Behavior (PN1-6) in Low, Mid, and High LG Litters

LG (PN1-6)	Nursing	Non-nursing contact	Nest-build	Self-groom	Eating	Drinking
Low	64.89 \pm 2.48	1.81 \pm 0.18	5.62 \pm .87	1.15 \pm 0.22	22.21 \pm 2.31	1.40 \pm 0.36
Mid	59.99 \pm 1.97	2.45 \pm 0.41	5.40 \pm 0.74	2.35 \pm 0.68	22.84 \pm 2.16	2.06 \pm 0.39
High	63.47 \pm 3.47	1.79 \pm 0.75	6.99 \pm 1.87	3.64 \pm 0.81	21.52 \pm 2.16	1.30 \pm 0.30

relatively constant. During the preweaning period, frequency of LG was found to be positively correlated with frequency of nursing ($r = .59$, $p < .01$) and frequency of nursing was found to be negatively correlated with mounting behavior ($r = -.63$, $p < .01$). E-LG was a significant predictor of preweaning maternal behavior, having significant positive correlations with LG ($r = .60$, $p < .01$; Fig. 1A) and nursing ($r = .73$, $p < .001$; Fig. 1B). E-LG also predicted a significantly later onset of mounting behavior (Cox regression, $p < .05$; Fig. 1C).

Variation in Preweaning Pup Behavior Predicted by Maternal Behavior

E-LG was a significant predictor of preweaning pup behavior. We found a significant positive correlation between E-LG and suckling ($r = .68$, $p < .01$; Fig. 2A) and a negative correlation between E-LG and eating ($r = -.66$, $p < .01$; Fig. 2B) and social play ($r = -.60$, $p < .01$; Fig. 2C). Maternal behavior occurring during the preweaning behavior was likewise correlated with pup behavior, with frequency of preweaning nursing having a negative correlation with social play ($r = -.50$, $p < .05$) and eating ($r = -.65$, $p < .01$) and preweaning LG having a positive correlation with frequency of social investigation ($r = .64$, $p < .01$) and suckling ($r = .54$, $p = .01$) and a negative correlation with eating ($r = -.58$, $p < .01$). To determine the relative importance of E-LG versus preweaning LG, we regressed each pup behavior on maternal behavior from both timepoints (early and preweaning) simultaneously. Importantly, we found that E-LG was the stronger predictor of variation in social play (early $p < .0001$; preweaning $p > .4$), eating (early $p < .001$; preweaning $p < .05$), and suckling (early $p < .001$; preweaning $p < .05$). In contrast, preweaning LG was the only significant predictor of the frequency of social investigation (early $p > .4$; prewean $p < .001$).

Preweaning Maternal and Pup Behavioral Change Over Time

To determine the rate of behavioral change over time, we examined maternal and pup behaviors within a multilevel model, allowing each litter to have its own mean level of behavior (random intercept) and rate of change over time (random slope). For each behavior, we

tested whether the rate of change over time varied by early maternal care and found marginally significant interactions between E-LG and rate of weaning (all p 's $< .1$). Inspecting this relationship further, we found that for all behaviors whose rate of change varied by E-

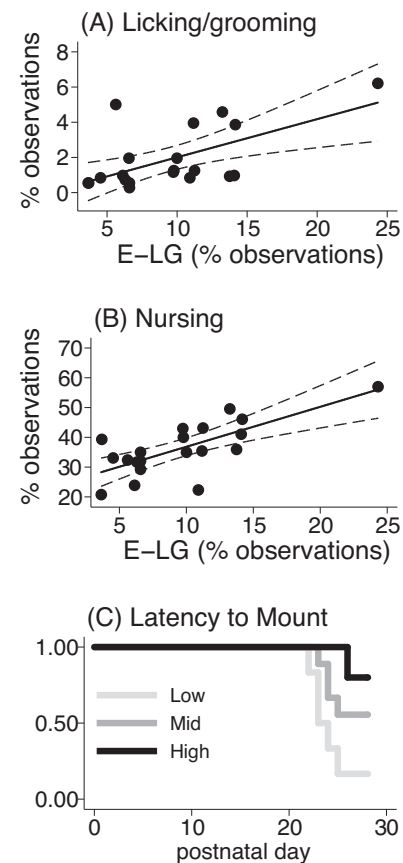


FIGURE 1 Correlations between the frequency of postnatal maternal licking/grooming (E-LG) and preweaning maternal behaviors. Significant positive correlations were observed between frequency of E-LG and (A) preweaning LG and (B) nursing. (C) Survival analysis of mounting behavior revealed that it occurred at a significantly later time in the preweaning period and at a lower frequency among High LG compared to Low and Mid LG dams. The time-to-event plot shows that at the beginning of the study, all the dams were in a state of not yet displaying mounting behavior, but that by the end of the study, 17% of the Low E-LG dams, 56% of the Mid E-LG dams, and 80% of the High E-LG dams had still not displayed mounting behavior.

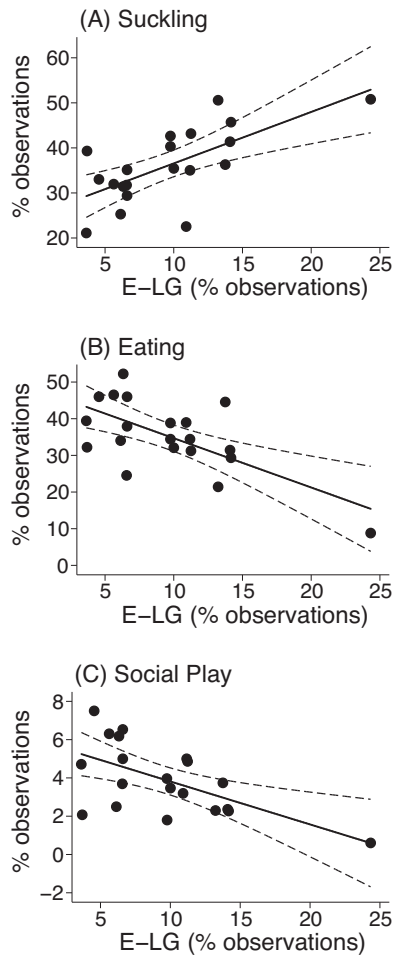


FIGURE 2 Correlations between the frequency of postnatal maternal licking/grooming (E-LG) and preweaning pup behaviors. (A) A significant positive correlation was observed between frequency of E-LG and preweaning pup suckling. Frequency of E-LG was negatively correlated with (B) preweaning eating and (C) social play by pups.

LG, the offspring of High-LG litters showed a significantly delayed developmental trajectory compared to the Mid- and Low-LG litters (see Fig. 3). High-LG litters were slower to reduce suckling (2.3 per day vs. 4.5 and 4.9 for the Mid- and Low-LG litters, respectively; interaction term $p < 0.01$), slower to increase eating (3.8 vs. 7.4 and 6.8 for the Mid- and Low-LG litters, respectively; interaction term $p < 0.001$) and marginally slower to begin playing (0.5 vs. .9 and 1.07 Mid- and Low-LG litters, respectively; interaction term $p = 0.12$).

Postnatal Maternal and Prewearing Prediction of Adult Behavior

Adult offspring were assessed in the open-field test on measures of total activity, latency to enter the inner

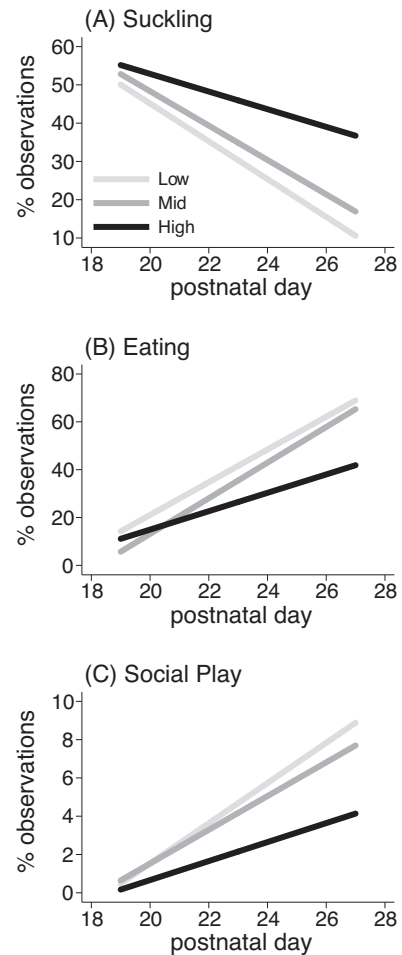


FIGURE 3 Change in pup behavior over developmental time during the preweaning period. Offspring of High LG dams (black line), were slower in their rate of reduction in (A) suckling and in their increase in (B) eating solid food compared to offspring of Low LG and Mid LG dams. (C) Offspring of High LG dams were also delayed in their increase in preweaning play behavior.

area, time spent in the inner area, and number of fecal boli produced during testing (male offspring: $n = 12$ Low LG, $n = 18$ Mid LG, $n = 8$ High LG; female offspring: $n = 9$ Low LG, $n = 18$ Mid LG, $n = 7$ High LG). We used multilevel models (random intercept by litter) controlling for sex. For the boli data, we used a log link and Poisson error structure, which is suitable for count data. All other outcome measures were approximately normally distributed. Means and standard errors of open-field measures as a function of Low, Mid, and High E-LG are presented in Table 2 (though it should be noted that for the analyses, E-LG was treated as continuous in the statistical models). Offspring that had experienced higher levels of LG during postnatal development engaged in reduced total activity

Table 2. Open-Field Behavior (Mean \pm SEM) of Offspring From Low, Mid, and High LG Litters

E-LG	Activity (squares crossed)	Latency to enter center area (s)	Time in center area (s)	Boli
Low	694.46 \pm 34.20	76.38 \pm 5.53	58.67 \pm 5.97	5.17 \pm 0.59
Mid	618.34 \pm 23.38	55.12 \pm 4.47	75.26 \pm 6.86	5.50 \pm 0.57
High	566.20 \pm 19.89	55.06 \pm 6.30	83.40 \pm 8.09	3.13 \pm 0.67

($p < .01$), reduced latencies to enter the inner area of the field ($p < .01$), increased duration of time spent in the inner area of the field ($p < .05$), and produced fewer fecal boli during testing ($p < .01$). Prewaning LG was also associated with reduced fecal boli production ($p < .04$), but this effect disappeared when controlling for E-LG ($p > .4$) suggesting the effect was driven entirely by the early environmental conditions. Home-cage social behavior did not moderate the effect of E-LG and no interactions between sex and rearing conditions were observed on these measures (p 's $> .2$).

Discussion

The quality of the early environment induces lifelong neurobiological and behavioral changes. Our analyses of the temporal features of development suggest that variation in maternal care during the early postnatal period is predictive of these long-term outcomes and of the pace of developmental transitions that occur during the preweaning period. Consistent with the hypothesis that low levels of maternal care lead to an earlier transition to independence and peer-directed behavior, we find that early postnatal LG is positively associated with frequency of preweaning sucking and negatively associated with frequency of eating and social play amongst preweaning pups. Postnatal LG also predicts a later onset of pup-directed mounting behavior, a maternal interaction with pups that increases in frequency in the preweaning period and which occurs in response to pup attempts to suckle (see Supplemental Video File). In addition, we find that the rate of behavioral change over time is slower amongst offspring who received High LG during the postnatal period and these offspring are delayed compared to Low LG offspring in transitioning to social play. Though early postnatal maternal care is predictive of the frequency of mother–infant interactions observed during the preweaning period, our analyses indicate that it is primarily early rather than later maternal care that is predictive of both preweaning and adult behaviors. Our data suggest that variation in maternal LG leads to divergent weaning strategies and the early emergence of individual differences in social behavior.

Maternal Care, Weaning Dynamics, and the Emergence of Play Behavior

Variation in juvenile play behavior has previously been demonstrated in response to the quality of mother–infant interactions experienced during the early postnatal period and at weaning. Maternal separation during infancy in rats leads to increased levels of play-fighting (Veenema & Neumann, 2009). Reduced postnatal levels of LG are associated with increased social play and decreased exploratory behavior in juvenile rats (Birke & Sadler, 1987; Moore & Power, 1992; Parent & Meaney, 2008). Inducing early weaning in cats results in increased object and social play in kittens (Bateson, Martin, & Young, 1981; Bateson & Young, 1981). Accelerating the weaning age of rat pups leads to elevated levels of play behavior both pre and postweaning in offspring (Smith, 1991). Smith (1991) determined that frequency of nursing behavior of rat dams at PN18 was inversely correlated with levels of play behavior exhibited by rat pups at PN29. Our findings build on this earlier report by indicating that naturally occurring low levels of maternal care during the early postnatal period is predictive of both decreased preweaning nursing behavior and increased play behavior.

The occurrence of increased play behavior in response to reduced maternal care experienced either early or later in postnatal development may be indicative of a compensatory developmental response. Play behavior has been speculated to allow opportunities for exploration (Byers, 1977), development of adult skills (Caro, 1995), opportunities to learn about social relationships (Eimon & Potegal, 1991), and provide experience with unexpected events (Spinka, Newberry, & Bekoff, 2001). Despite these potential benefits to play, there are also costs associated with play such as increased energy demands and possible risk of injury (Byers, 1977). However, the potential adaptive benefits are likely to outweigh any costs when the skills or learning opportunities are necessary for survival. When there are disruptions to the quality of mother–infant interactions, compensatory increases in play behavior may be a strategy for offsetting the potential deficits in functioning that would otherwise be predicted to occur

(Bateson, Mendl, & Feaver, 1990). Our data indicate that this increased play occurs within the context of early weaning by low care mothers.

Sensitive Periods for the Influence of Mother–Infant Interactions

Though the postnatal period has generally been conceived as a sensitive period, there has been limited exploration of how sensitivity to maternal care changes over time within this period. Neonatal handling, a manipulation that increases maternal care, is effective at modulating the HPA response to stress if conducted within the first week postnatal (Levine & Lewis, 1959; Meaney & Aitken, 1985). Cross-fostering pups between Low and High LG dams is effective at shifting offspring hypothalamic gene expression and behavior if conducted at birth or PN6 but not if conducted later in postnatal development (Champagne et al., 2006; Pena, Neugut, & Champagne, 2013). The temporal dynamics of maternal care and motivation toward pups may contribute to the occurrence of a sensitive period and the specific behavioral outcomes that emerge. Social play behavior is correlated with early LG and later nursing, with analyses indicating that early LG is the significant predictor of this outcome. In contrast, social affiliation/investigation is correlated with later but not early LG. Thus, there appear to be multiple sensitive periods that account for developmental shifts in specific features of social behavior.

Weaning Strategies: Accelerating the Pace of Development

The quality of mother–infant interactions is significantly influenced by broad ecological factors which impact HPA reactivity. In particular, frequency of postnatal LG has been demonstrated to decrease in response to prenatal stress (Moore & Power, 1986) and increase in response to social enrichment (Curley, Davidson, Bateson, & Champagne, 2009a). Our analyses of the patterns of weaning among lactating females that vary in postnatal LG suggests that these environmentally induced changes in maternal behavior set in motion a strategy that either accelerates or delays the transition by offspring to physiological and behavioral independence. This strategy is evident in both the maternal and offspring behavior. High LG dams engage in higher levels of preweaning nursing and delay engaging or fail to engage in mounting behavior to inhibit pup sucking. Consequently, offspring of High LG dams maintain high levels of suckling and are delayed in shifting to solid foods and play with littermates. The contrast is evident in Low LG dams and their offspring. We have previously observed mounting behavior toward pre-weaning

pups (Curley et al., 2009b) and this behavior has also been observed in rat dams to facilitate weaning (Gilbert, Burgoon, Sullivan, & Adler, 1983). This behavior typically consists of the dam pinning and immobilizing the pup following a nipple solicitation. We have not observed biting or any other overt acts of aggression toward pups during mounting, suggesting that this behavior consists of a display of dominance to reduce sucking attempts. The early occurrence of this behavior among Low LG dams suggests an active weaning process that shifts offspring to solid food, reduced maternal interactions, and increased peer interactions. Interestingly, this weaning strategy may influence the weaning strategy of female offspring, leading to developmental effects that persist across generations (Curley et al., 2009b).

The patterns of maternal behavior, weaning strategy, and developmental outcomes indicated in the current study are consistent with life history theory and its application to child development (Belsky, Steinberg, & Draper, 1991). Within this context, disruptions to the quality of the family environment are proposed to impact the quality of parent–offspring interactions, which consequently influences interpersonal relationships and predicts an early emergence of puberty and sexual behavior. In humans, there is increasing evidence for the link between disruptions to the early social environment and an early onset of puberty (Belsky, Houts, & Fearon, 2010; Ellis et al., 2003; Tither & Ellis, 2008). In rodents, low maternal care is associated with an early onset of puberty, increased sexual receptivity, and improved mating success (Cameron et al., 2008a,b). It has been proposed that an earlier onset of play behavior in rodents facilitates precocious sexual behavior (Birke & Sadler, 1987; Pellis, 1993) and deprivation of play during juvenile development has been reported to impair indices of sexual behavior (Gruendal & Arnold, 1974). Our analyses suggest that earlier weaning is an antecedent to the onset of play behavior and may serve as a significant cue to the acceleration of sexual development. The cost of this reproductive investment may be to the development of parenting motivation in offspring. Juvenile female offspring of Low LG dams exhibit reduced maternal responses to pups (Pena et al., 2013) and elevated motivation to engage in social interactions with peers compared to the juvenile offspring of High LG dams (Pena, Neugut, Calarco, & Champagne, 2014).

Conclusions and Future Directions

Understanding the pathways linking early life experience to long-term outcomes requires investigation of the

cascade of developmental changes that occur over time within the life history of an organism. The current study highlights the link between maternal care experienced during infancy and the characteristics of the transition to independence by offspring during the process of weaning. The weaning process is a sensitive period and our findings suggest that extending the duration of mother–infant interactions and delaying weaning may be effective as a strategy for reversing the effects of early life adversity. Similarly, manipulating the levels of play and social investigation of peers during the preweaning period may provide insights into the role of these behaviors in mediating long-term changes in social and reproductive behavior. Though we have focused on the emergence of play behavior as a potential precursor to adult sexual behavior, other systems may likewise undergo early maturation in response to reduced mother–infant interactions. An integrative analysis of changes to gonadal function, HPA, and neural systems associated with emotional reactivity, neuroplasticity, cognition, and social behavior are essential to understanding the biological and behavioral pathways underlying the impact of early life adversity. However, though laboratory studies can elucidate many of the basic processes occurring during postnatal development and weaning, it will be important to explore these questions in more ecologically diverse animal populations, where both weaning and reproductive strategies are likely to be responsive to selection pressures and environmental cues.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.