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Early Maternal Care Predicts Reliance on Social Learning About Food in Adult Rats

ABSTRACT: *Many vertebrates rely extensively on social information, but the value of information produced by other individuals will vary across contexts and habitats. Social learning may thus be optimized by the use of developmental or current cues to determine its likely value. Here, we show that a developmental cue, early maternal care, correlates with social learning propensities in adult rodents. The maternal behavior of rats* Rattus norvegicus *with their litters was scored over the first 6 days postpartum. Rat dams show consistent individual differences in the rate they lick and groom (LG) pups, allowing them to be categorized as high, low, or mid-LG mothers. The 100-day old male offspring of high and low-LG mothers were given the opportunity to learn food preferences for novel diets from conspecifics that had previously eaten these diets ("demonstrators"). Offspring of high-LG mothers socially learned food preferences, but offspring of low-LG mothers did not. We administered oxytocin to subjects to address the hypothesis that it would increase the propensity for social learning, but there were no detectable effects. Our data raise the possibility that social learning propensities may be both relatively stable throughout life and part of a suite of traits "adaptively programmed" by early developmental experiences.*
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Keywords: *adaptive programming hypothesis; behavior; development; food preference; epigenetic transmission; maternal care; oxytocin; rat* Rattus norvegicus*; social learning; stress*

INTRODUCTION

Individual differences in the propensity to use information provided by the activities of other individuals ("social information") and to learn from this information ("social learning") can have dramatic consequences for the spread of information through groups, for between-individual fitness differentials, and consequently for theoretical models of cultural transmission (Bouchard, Goodyer, & Lefebvre, 2007; Reader, 2004). Individual differences in social learning propensities could result from constraints, such as a lack of learning opportunities, cognitive shortcomings, or perceptual deficiencies. However, individual differences in social learning propensities may also represent adaptive optimization to both local conditions and to individual characteristics. In the latter case, individual differences could be relatively fixed across individuals of a particular class. For example, individuals of one class (e.g., one sex or age) might utilize social information because this propensity consistently provides a selective advantage for these individuals and not for others. Alternatively or in addition, development and learning could flexibly shape learning propensities within a lifetime, creating individual, class, or population differences that optimize the payoffs of social learning. Recent experience has been shown to shape reliance on social information (Kendal, Coolen, van Bergen, & Laland, 2005; Leadbeater & Chittka, 2009), but early experience may result in long-term individual differences that persist into adulthood. Such developmental influences would provide advantageous flexibility in slowly changing environments, while avoiding the costs of assessing the current value of social information.

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Developmental influences resulting in differing social learning propensities are thus potentially important but have not been extensively documented. Studies of birds and fish provide suggestive findings. Populations of Zenaida doves *Zenaida aurita* differ in their social learning propensities (Carlier & Lefebvre, 1997). However, it has not been established whether these differences arise from development, recent experience, or phenotypic differences between populations. Hand-reared house sparrows *Passer domesticus* raised with an artificial parent were biased towards social information use depending on the parent's previous reliability in indicating food (Katsnelson, Motro, Feldman, & Lotem, 2008). Guppies *Poecilia reticulata* reared at different stocking densities from early life differed in shoaling tendencies, affecting the propensity to follow conspecifics and thus to learn from them (Chapman, Ward, & Krause, 2008). In both the Katsnelson et al. and Chapman et al. studies, however, experimental manipulations were maintained until the time of testing, so the longevity of early-life influences are unknown. To our knowledge, the only evidence for a link between experiences restricted to early life and adult social learning propensities comes from rodents. Social learning of novel diets declines dramatically in Sprague–Dawley rats reared artificially and deprived of maternal care and littermates (Levy, Melo, Galef, Madden, & Fleming, 2003; Melo et al., 2006), raising the possibility, investigated here, that natural variation in maternal care will influence social learning tendencies when adult.

Here, we focus on maternal influences on the development of social learning propensities, by studying food preference learning in Norway rats *Rattus norvegicus*. Rats faced with a choice of novel diets prefer the food that a demonstrator conspecific has previously eaten (Galef, 2002; Galef & Wigmore, 1983). This social learning of food preferences combined with neophobia to novel foods should allow animals to exploit safe foods while avoiding potentially dangerous foods (Noble, Todd, & Tuci, 2001). Food preference learning thus provides an extremely well studied social learning task relevant to the ecology of rats and several other rodents (Choleris, Clipperton-Allen, Phan, & Kavaliers, 2009; Galef, 2002; Lesburgueres et al., 2011).

We took advantage of natural variation in levels of maternal care in rats, an extensively studied influence on brain and behavior. During the first week postpartum, rat dams show consistent individual variation in licking and grooming their pups (LG), although environmental stressors (e.g., food restriction, predator cues) influence LG rates, suggesting that maternal care provides a cue to the state of the external environment (Caldji et al., 1998; Champagne, Francis, Mar, & Meaney, 2003; McLeod, Sinal, & Perrot-Sinal, 2007). LG differences are associated with extensive variation in offspring gene expression, neuroendocrine development, and behavioral development (Caldji et al., 1998; Champagne et al., 2003). Compared to high-LG offspring, low-LG offspring show enhanced stress responses and increased anxiety. Such differences in risk sensitivity have been theoretically and empirically linked to social information use, with risk sensitive individuals predicted to utilize social information more (Coolen, van Bergen, Day, & Laland, 2003; Mathot & Giraldeau, 2008). However, anxiety and deficits in social interaction may also depress social information use (Choleris et al., 1998; Melo et al., 2006).

Styles of maternal care are transmitted across generations: cross-fostering studies show that genetic offspring of low-LG mothers raised by high-LG mothers show high-LG phenotypes when adult (Champagne & Meaney, 2007). Pups are likely to live in a similar habitat to their mother (Levine, 1994). Therefore, it has been suggested maternal care provides a route for ''adaptively programming'' offspring epigenetically to their (future) environment, without the pups having to experience this habitat directly themselves (Caldji et al., 1998; Diorio & Meaney, 2007).

The neuropeptide oxytocin and the closely related vasopressin are not only involved in a range of social behaviors, such as maternal care, aggression, pair bonding, sexual behavior, and social memory, but also in learning, anxiety related behavior, and stress coping (Neumann, 2008). Oxytocin increases recall of socially acquired food preferences (Popik & Van Ree, 1993), but the effects of oxytocin on acquisition of socially induced food preferences have not been explored (Choleris et al., 2009). Oxytocin could influence social acquisition through various routes, such as changes in social interactions or in approach, attention, or tolerance to conspecifics (Goodson, Schrock, Klatt, Kabelik, & Kingsbury, 2009; Madden & Clutton-Brock, 2011).

To investigate the joint effects of maternal care differences during development and oxytocin on social learning, we utilized the well-established social food preference learning paradigm (Galef, 2002), testing adult males. On the basis of maternal deprivation experiments (Melo et al., 2006), we expected high-LG offspring to show enhanced social food preference learning compared to low-LG offspring. That is, we predicted that early experience would have a lasting effect into adulthood on social learning propensities. Administration of oxytocin was predicted to enhance social learning, because oxytocin has been shown to facilitate recall for socially learned cues and to increase social approach (Madden & Clutton-Brock, 2011; Popik & Van Ree, 1993).

METHODS

Overview

We used adult male rats born to and reared by either high-LG or low-LG mothers. These ''observer'' rats received oxytocin or saline (control) administrations prior to interaction with a single ''demonstrator'' rat that had eaten one of two flavored diets. After the interaction, the observer was separated and allowed to choose between the two novel diets. We thus determined whether interaction with a demonstrator rat influenced observers' food preferences.

Subjects and Housing

Sixty-nine Long-Evans hooded male rats from a single cohort bred at the Allan Memorial Institute, Montréal, Canada participated in the experiment, 29 as demonstrators and 40 as subjects. Breeding procedures followed Champagne et al. (2003). Rats were selected as high-, mid-, or low-LG phenotypes based on their mothers' maternal behavior, defined according to Champagne et al. (2003). Maternal behavior of individually housed dams with their litters of >5 pups was scored daily for the first 6 days postpartum at regular times (0600, 1000, 1300, 1700, and 2100 hr). Within each observation period maternal behavior was scored every 3 min [for methodology see Champagne et al. (2003)]. Mean LG (±SD) for the cohort was 8.16 ± 2.13. Litters with LG over 10.30 (i.e., 1 SD above the mean) were categorized as ''high-LG'', litters with LG below 6.03 (1 SD below the mean) were categorized as ''low-LG'', with other litters categorized as ''mid-LG''. Twenty-nine mid-LG rats (mean LG ± SE = 8.93% ± .32) acted as demonstrators, with a mean mass ± SE of 436 ± 6.12 g at 90–107 days old, the beginning of demonstrator habituation. Twenty high-LG (mean LG ± SE = 11.36% ± .11) and 20 low-LG (mean LG ± SE = 4.94% ± .13) naïve rats were assigned as observers. Observers were drawn from five high-LG and five low-LG litters and were 90–107 days old at the beginning of the study with a mean mass ± SE of 471 ± 6.64 g. High-LG and low-LG rats did not significantly differ in mass (*t*-test; $t_{38} = 1.47$, $p = .15$). Observers were 107–124 days old when tested.

After weaning, rats were pair-housed with littermates in clear Plexiglas cages (20 × 23 × 44.5 cm) with sawdust bedding and rodent food pellets (Purina 5075-U.S., Charles River, Canada) and water provided ad libitum. Housing was maintained at 22 ± 4°C and 30 ± 5% humidity, with a 12 hr light–dark cycle with lights on at 0700 hr. One week prior to testing, ''experimental pairs'' were formed, housing together one high-LG and one low-LG offspring per pair. Thus, subjects had experienced an unfamiliar individual prior to the experimental test. In assigning experimental pairs, we matched ages within a pair as closely as possible. Demonstrators were unfamiliar to observers.

Procedures followed the guidelines of ASAB and the Canadian Council on Animal Care; protocols were approved by the McGill University Animal Care Committee (protocol #5642).

Diets

We used two diets novel in flavor to the rats: cinnamon and cocoa-flavored. We mixed regular ground rodent food (Purina 5075-U.S., Charles River, Canada) with either 1% by weight ground cinnamon (No Name Brand, Canada) or with 2% by weight cocoa (Cadbury Fry's Premium, Canada); proportions followed Galef and Wigmore (1983). A pilot study ($N = 12$ additional low-LG rats; feeding session of 24 hr) revealed diets were approximately equally matched, but with considerable individual variation and a slight (non-significant) preference for the cinnamon diet. We thus added granulated sugar to the cocoa diet (2% by mass) to increase its palatability relative to the cinnamon diet (Galef, 2002). We utilized a counterbalanced design to account for any prior preference for one diet in the observers, with half of the demonstrators fed the cocoa diet and the other half the cinnamon diet.

Procedure

Demonstrator Habituation. Demonstrator rats were habituated to a randomly assigned diet 1 day prior to observer testing and re-used when necessary after 1 week of rest. Demonstrators were housed individually and food deprived for 23 hr. They were allowed to individually feed on 15 g of their assigned diet for 1 hr in a housing cage with paper tissue bedding and water ad libitum. Flavored food was presented in a heavy (450 g) rectangular porcelain white container with two separate compartments (diameter 7 cm, 5 cm deep) and secured with tape to avoid overturning or excessive food spillage. Afterwards, the food was sieved to remove any foreign matter and re-weighed to measure demonstrator food intake. Observers received no habituation to diets, but food pellets were removed 1 hr before testing.

Testing. On the day of observer testing, demonstrator rats were food deprived for 22 hr, received 15 g of their assigned diet, and were allowed to feed for 2 hr with water available ad libitum. Only animals that consumed at least 3 g of their diet were used as demonstrators, following Galef and Whiskin (2001). One demonstrator did not meet the criterion and this session was not included in the diet preference analysis. Demonstrators mean consumption (±SE) was 9.53 ± .49 g. Demonstrators were placed with observers immediately after feeding.

We administered oxytocin or saline to observer rats 15 min prior to placing them with a demonstrator. Both animals within each low/high-LG experimental pair received the same administration. We injected 1 ml/kg subcutaneously of either oxytocin (OT; $C_{43}H_{66}N_{12}O_{12}S_2$; Sigma–Aldrich, Inc., Oakville, Canada) dissolved in 0.9% saline (0.9% sodium chloride injection USP) to a concentration of 3 ng/ml or saline as a control. We based the 3 ng/ml dosage on doses previously shown to facilitate social recognition and recall of a socially acquired taste preference when administered subcutaneously to male Wistar rats (Popik & Van Ree, 1993; Popik, Vetulani, & Van Ree, 1992). We allocated administrations so that equal numbers of high- and low-LG rats received oxytocin and saline. Similarly, age categories were matched

as far as possible between the oxytocin and saline administrations. Offspring from the same litter were evenly distributed across administration and demonstrator diet groups as far as possible. Rats were left undisturbed for 15 min before being placed with a randomly selected demonstrator.

A single demonstrator and a single observer were placed together for 30 min in a clean Plexiglas cage containing fresh bedding material only. After the interaction period, demonstrators were returned to their housing pairs. We moved single observers to a clean cage containing paper tissue bedding, water ad lib, and a weighed food cup containing 35 g of each diet (counterbalanced for location so that the cocoa diet was on the left for half the subjects and right for half the subjects). We determined individual intake of both diets after 2, 15, and 24 hr (thus at 20:00, 09:00, and 18:00 hr) by weighing the remaining food. Two sieves were used to avoid cross contamination of odors between the cocoa and cinnamon diets. If less than 10 g was left of one diet, we added 10 g extra. At the end of testing rats were returned to their housing pairs and the testing cage examined for excessive diet spillage. No data had to be disregarded because of spillage.

Analyses

Statistical analyses were performed in SPSS 16.02. We measured diet preference as the mass of cinnamon diet consumed subtracted from the mass of cocoa diet consumed. We analyzed administration (OT vs. saline), maternal style (high- or low-LG) and demonstrator diet (cocoa or cinnamon) as fixed effects. We investigated the effect of time period (0–2, 2–15 and 15–24 hr) as a repeated measure, and the amount eaten by demonstrators as a covariate, but neither had significant effects on diet preference, or interaction effects with independent variables ($p > .1$ in all cases), and thus these variables were eliminated from the model and not reported below. Hence we report diet preferences over the entire 24-hr testing period. Previous studies have measured food preference as the proportion of diet cocoa consumed out of the total eaten by a subject (Galef, 2002), and we use this intuitive measure for Figures 1 and 2. However, the proportional measure carries the disadvantage that preference data from rats eating very small and large amounts can be equivalent, leading us to prefer the difference measure. The proportional measure gave identical findings to the difference measure (see below). Data are archived online in the Dryad repository (http://datadryad.org).

RESULTS

Diet Preference

Observers exposed to demonstrators that had eaten a cocoa diet consumed more cocoa diet than did observers exposed to cinnamon diet demonstrators (ANOVA; $F_{1,31} = 9.73$, $p = .004$; Fig. 1). Thus, observers were biased towards their demonstrator's diet, concordant with observer social learning from demonstrators. However, not all observers were biased by demonstrator diet, which can be explained by investigating interaction effects with demonstrator diet. Maternal style (LG) had a significant statistical interaction with demonstrator diet on observer diet preference (ANOVA; $F_{1,31} = 4.81$, $p = .036$; Fig. 1). A similar interaction effect was observed using the alternative diet preference measure, the proportion of diet cocoa consumed (ANOVA; $F_{1,31} = 4.24$, $p = .048$). Thus, high-LG rats were significantly biased towards their demonstrator's diet (*t*-test comparing high-LG observers of cocoa vs. cinnamon-demonstrators; $t_{17} = 3.52$, $p = .003$), in

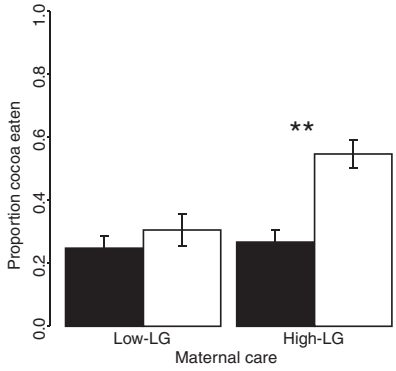

FIGURE 1 Mean proportion (±SE) of cocoa diet eaten by observers after exposure to demonstrators that had eaten either cinnamon (filled bars) or cocoa (open bars). Observers were raised by low-LG dams or high-LG dams. Asterisks indicate improved learning performance of the high-LG offspring ($p < .01$).

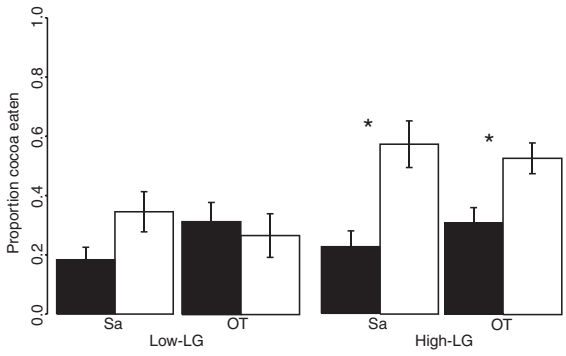

FIGURE 2 Mean proportion (±SE) of cocoa diet eaten by observers after exposure to demonstrators that had eaten either cinnamon (filled bars) or cocoa (open bars). Observers were administered with saline (Sa) or oxytocin (OT) 15 min prior to interaction with demonstrators. Observers were raised by low-LG dams or high-LG dams. Asterisks indicate improved learning performance of the high-LG offspring regardless of administration ($p < .05$).

both saline and oxytocin administered rats (*t*-tests; $t_7 = 2.70$, $p = .03$; $t_8 = 2.25$, $p = .05$; respectively; Fig. 2). However, demonstrator diet did not significantly influence low-LG rats' diet preferences (*t*-test; $t_{18} = .70$, $p = .50$), in either saline or oxytocin administered rats (*t*-tests; $t_8 = 1.65$, $p = .14$; $t_8 = .33$, $p = .75$; respectively). To partially account for the fact that observers were not all from independent litters, we took the mean diet preference for all observers from the same litter allocated to the same demonstrator diet and administration treatment combination and reanalyzed the data. Again, high-LG but not low-LG rats were significantly biased towards their demonstrator's diet (*t*-tests; $t_{12} = 3.63$, $p = .03$; $t_{13} = 1.05$, $p = .32$).

Administration of oxytocin versus saline had no significant interaction effect with demonstrator diet (ANOVA; $F_{1,31} = 2.57$, $p = .12$) or with demonstrator diet and maternal style ($F_{1,31} = .002$, $p = .97$; Fig. 2). Oxytocin administration also had no significant influence on the preference for cocoa over cinnamon diet ($F_{1,31} = .44$, $p = .51$). Thus maternal style but not oxytocin administration had significant effects on social learning.

Total Food Consumption

Observers' rate of feeding decreased over time, being most rapid in the first 2 hr of feeding (mean ± SE = 2.01 ± .25 g/hr) and dropping in the second (1.13 ± .10 g/hr over 13 hr) and third measurement periods (.41 ± .04 g/hr over 9 hr; repeated-measures ANOVA; $F_{2,76} = 30.34$, $p < .0001$). All observers sampled both diets within the 24-hr period, with a mean total consumption (±SE) of 22.41 ± 1.66 g. Oxytocin administration did not significantly affect total consumption (ANOVA; $F_{1,31} = .83$, $p = .37$), neither did maternal style ($F_{1,31} = .01$, $p = .91$) or demonstrator diet ($F_{1,31} = 1.84$, $p = .19$), nor were there significant interaction effects ($p > .1$).

Cocoa-demonstrators ate more than cinnamon-demonstrators (mean consumption ± SE = 11.32 ± .60 g, 7.84 ± .53 g, respectively, ANOVA; $F_{1,35} = 17.90$, $p < .0001$), but demonstrators assigned to high-LG observers did not eat significantly more than those assigned to low-LG observers ($F_{1,35} = .02$, $p = .89$), and there was not a significant interaction effect between observer maternal style and demonstrator diet on demonstrator food consumption ($F_{1,35} = .11$, $p = .74$). Moreover, demonstrator diet consumption was not a significant predictor of observers' total food consumption ($r = .12$, $F_{1,37} = .52$, $p = .48$). Thus our results cannot be accounted for by differences in feeding behavior between demonstrators.

DISCUSSION

Rats were biased towards the diet their demonstrator had previously eaten, showing social learning of food preferences for a novel diet, a well-established social learning effect (Galef, 2002). However, only adult rats that had experienced one style of maternal care (high rates of licking and grooming, ''high-LG'') utilized social information from demonstrators. High-LG offspring socially learned a food preference, whereas there was no evidence for such learning in low-LG offspring. This correlation between early developmental experience and social learning performance supports the idea that early maternal care could be a causal factor shaping adult social learning propensities. We found no significant effects of oxytocin on social learning.

Our finding that low-LG offspring show impaired social learning contrasts with the prevalent argument that risk-sensitive individuals are more likely to utilize social information (Coolen et al., 2003; Mathot & Giraldeau, 2008). However, and in line with our findings, predation risk decreased social learning of food preferences in rats (Galef & Whiskin, 2006). Our results emphasize that social learning is a multi-step process, and individual differences could arise during acquisition, retention, and/or performance. Moreover, the gathering of social information may be confounded or conjoined with other activities that show individual differences, such as vigilance. Since offspring of high and low-LG dams differ on numerous characteristics (Champagne et al., 2003; Champagne & Meaney, 2007), we cannot yet identify the causal factor explaining the differences we observe.

Variation in maternal care influences a number of brain regions and neurological systems, including several implicated in rodent food preference social learning such as the hippocampus (Champagne et al., 2003; Choleris et al., 2009; Curley, Jensen, Mashoodh, & Champagne, 2011). For example, hippocampal synaptic plasticity and cholinergic innervation is reduced in adult low-LG offspring compared to high-LG offspring, characteristics that have been linked to reduced learning and memory performance (Diorio & Meaney, 2007). Disrupted or low maternal care not only impairs HPA axis function, but also increases corticosterone sensitivity and thus stress sensitivity (Caldji et al., 1998). Such influences of maternal care on the brain could underlie the differences in social learning propensities we observed.

Differences in social interaction patterns between high and low-LG offspring could be an additional or alternative explanation for our results, since interaction patterns may determine exposure to social information. For example, Norway rats learn more effectively from

unfamiliar than familiar demonstrators, probably because they interact more with unfamiliar demonstrators (Galef & Whiskin, 2008). In contrast, in Mongolian gerbils *Meriones unguiculatus* unfamiliar individuals evoke high aggression and anxiety and observers will not acquire food preferences from unfamiliar demonstrators unless treated with an anxiolytic (Choleris et al., 1998). Adult high-LG offspring show diminished stress responses and reduced anxiety compared to adult low-LG offspring (Champagne et al., 2003), potentially promoting learning during social interaction with the unfamiliar demonstrator. Juvenile male offspring of low-LG mothers show increased rates of aggressive play fighting compared to high-LG male offspring (Parent & Meaney, 2008). Similar aggression maintained to adulthood might hinder social learning.

We speculate that high-LG offspring are developmentally adapted to more predictable environments, compared to low-LG offspring, with social learning thus providing greater payoffs (Boyd & Richerson, 1985). However, evidence for such an adaptive programming hypothesis would require understanding of both the developmental mechanisms influencing social learning, and the adaptive payoffs of strategies in different environments. It has been suggested that rodent food preference learning may be an adaptive specialization (Hoppitt & Laland, 2008), and theoretical simulations suggest such a system would evolve if toxic foods are generally lethal, and thus interactions with sick conspecifics are rare (Noble et al., 2001). Rats are peculiarly insensitive to the contingencies surrounding food preference learning, supporting this adaptive specialization hypothesis (Galef, Whiskin, & Horn, 1999). It is possible that where the costs of assessing the value of social information are high, developmental influences provide a low-cost mechanism to adopt behavior suited to the likely future environment.

Oxytocin administration had no significant effects on social learning. We observed no significant interaction effects between oxytocin administration and maternal style on any measure. However, no interaction effects were predicted, since in males, unlike females, oxytocin receptor expression in three brain areas was not found to differ between high-LG and low-LG offspring (Francis, Young, Meaney, & Insel, 2002). We used a dose established to improve retention in socially acquired flavored tea preferences in male rats (Popik & Van Ree, 1993). However, a vasopressin metabolite has been shown to increase or decrease retention of socially acquired food preferences dependent on the retention interval (Bunsey & Strupp, 1990; Strupp, Bunsey, Bertsche, Levitsky, & Kesler, 1990), while oxytocin has a U-shaped reaction curve (Klenerova, Krejci, Sida, Hlinak, & Hynie, 2009; Popik et al., 1992) and can attenuate or potentiate a range of processes depending on dosage. Given that we did not vary dosage but used a single dose and retention interval, no conclusions can be drawn on the efficacy of oxytocin as a modifier of social learning.

Maternal care influences development in many species. This raises the possibility that developmental influences on social learning will be widespread in vertebrates, representing both adaptive optimizing to local conditions and byproducts of general developmental effects. An open question is the extent to which developmental influences on social information use have fixed effects throughout life, or whether recent experience or other factors can override these effects. Negative effects on social information use caused by isolation rearing were reversed by housing the artificially reared rat pups with dams and pups for days 20–24 of life (Galef, 1981; social learning was not tested). Similarly, phenotypic differences in maternal and exploratory behavior between high and low-LG offspring can be abolished by manipulation of post-weaning environment (Champagne & Meaney, 2007). However, if animals choose habitats and foraging niches partially based on their social learning propensities, this may maintain or even strengthen differences between individuals.

Given the importance of developmental influences (West-Eberhard, 2003), early experience may have numerous direct and indirect effects on social information use and social learning, with interactions between genetic predispositions, development, and learning likely. Social learning plays a critical role in human development (Hermann, Call, Hernàndez-Lloreda, Hare, & Tomasello, 2007), so early influences on attention to social cues and learning from these cues could be vital in shaping human social and cognitive development. Moreover, deficits in appropriate social learning are relevant to a number of mental disorders (Olsson & Phelps, 2007). Thus, understanding of early influences on social learning has applied relevance to developmental and clinical psychology and psychiatry.

NOTES

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