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## Impulsive Rats are Less Maternal

**ABSTRACT:** Early life environment and maternal care can have long-lasting effects on behavior and physiology. Previously, we found that compared to mother-reared (MR) female rats, rats reared without mothers, siblings, and nest, through artificially rearing (AR), show reduced levels of maternal behavior when they grow up. These effects can be reversed if AR pups are provided with extra “licking-like” tactile stimulation during the preweaning period [Gonzalez et al. [2001] *Developmental Psychobiology*, 38(1), 11–42]. We also found that AR rats are more action impulsive and have reduced attentional capacities in comparison to their MR siblings [Lovic, Fletcher, & Fleming, in preparation; Lovic & Fleming [2004] *Behavioural Brain Research* 148: 209–219]. However, it is unknown whether increased impulsivity contributes to reduced levels of maternal behaviors. The purpose of this study was to assess the relationship between impulsivity and maternal behavior in AR and MR rats. Female rats were reared with (MR) or without mothers (AR) and half of the AR rats received additional stroking stimulation. As adults, AR and MR rats were mated and maternal behavior towards their own pups was assessed. In addition, rats were assessed on impulsive action (differential reinforcement of low-rate schedule; DRL-20s). Consistent with previous findings, AR rats were both less maternal and more action impulsive than MR rats. Partial correlations revealed that impulsivity was inversely related to pup licking-impulsive rats were less maternal. © 2010 Wiley Periodicals, Inc. *Dev Psychobiol* 53: 13–22, 2011.

**Keywords:** maternal; rat; impulsivity; deprivation; artificial; rearing

### INTRODUCTION

The quality and quantity of maternal behavior shown by mother rats have a substantial impact on the behavioral, endocrine, and neural development of their pups (see Kaffman & Meaney, 2007). Maternal deprivation for a few hours daily and variations in maternal care produce changes in offspring's emotional, cognitive, and social behavior and in the development of their underlying neuroendocrine and neurotransmitter systems (Kaffman & Meaney, 2007; Hall, 1998; Hall, Wilkinson, Humby, & Robbins, 1999; Matthews, Dalley, Matthews, Tsai, & Robbins, 2001; Vazquez, Lopez, Van Hoers, Watson, &

Levine, 2000). In general, in comparison to non-maternally deprived or highly licked pups, maternally deprived pups or pups of low-licking dams, are more active (Brake, Zhang, Diorio, Meaney, & Gratton, 2004), more emotionally reactive (Francis, Diorio, Liu, & Meaney, 1999; Francis & Meaney, 1999), exhibit altered spatial memory (Liu, Diorio, Day, Francis, & Meaney, 2000), social behavior (Parent & Meaney, 2008) and show reduced levels of both sexual (Cameron, Del Corpo, et al., 2008; Cameron, Fish, & Meaney, 2008; Cameron, Shahrokh, et al., 2008), and maternal behavior (Francis et al., 1999; Lovic, Gonzalez, & Fleming, 2001; Rees & Fleming, 2001). They also experience sustained elevations in their hypothalamic-pituitary-adrenal responses to stressors, through a reduction in glucocorticoid receptor sensitivity in the hippocampus (Francis & Meaney, 1999; Liu et al., 1997) and disruptions in dopamine function (Brake et al., 2004; Hall et al., 1999; Matthews et al., 2001; Meaney, Brake, & Gratton, 2002; Zhang, Chretien, Meaney, & Gratton, 2005). Although maternal deprivation studies, in conjunction with studies that compare the effects of being mothered by high- and low-licking

Received 21 May 2010; Accepted 25 June 2010  
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Contract grant sponsor: NSERC Grant

Published online 26 August 2010 in Wiley Online Library  
 (wileyonlinelibrary.com). DOI 10.1002/dev.20481

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mothers, strongly suggest that the predominant factor affecting the offspring is the actual amount of licking stimulation received, mothers that lick more also crouch more and may produce other differences to the entire litter situation and nest configuration that could also be affecting the individual offspring (i.e., there may be differences in total activity of the litter, thermal characteristics of the nest, and so on).

In order to isolate the role of the licking stimulation in pup development, we adopted a different strategy to determine the effects of early preweaning experiences on pup development. The paradigm we adopted, the pup-in-a-cup rearing regimen (Hall, 1998), involves rearing pups entirely without the mother and littermates in a controlled thermal and nutrient environment during the first 3 weeks of life, and providing pups with different amounts of stroking and/or social stimulation (Hall, 1998; Gonzalez, Lovic, Ward, Wainwright, & Fleming, 2001). Using this artificial-rearing (AR) paradigm, we have explored many developmental outcomes in pups, including emotional, cognitive, and social behaviors, endocrinology, and brain function and structure. In general, we have found that many of the same deficits reported for pups of low-licking mothers are also found for pups reared without mothers altogether (Burton, Lovic, & Fleming, 2006; Gonzalez et al., 2001; Lovic & Fleming, 2004; Lovic, Fletcher, & Fleming, 2006; Melo et al., 2006; Palombo, Nowoslawski, & Fleming, 2010) and some deficits that were not tested in the high- to low-licking paradigm (see also Akbari, Budin, & Kraemer, in preparation; Lomanowska, Rana, McCutcheon, Parker, & Wainwright, 2006); and for most outcomes the addition of 5–8 daily stroking episodes with a small paintbrush partially reversed the effects of isolation from mother, siblings, and nest. These findings reinforce the licking-based interpretation of results suggested by Meaney and colleagues (Kaffman & Meaney, 2007). Other early experience factors contributing to the AR effects on behavior and physiology continue to be investigated (Melo et al., 2006).

In our studies, we focused on the effects of AR and of somatosensory licking-like stimulation on the development of species-characteristic social behaviors, especially adult maternal behavior. We have found, for instance, that mothers who were raised apart from their mothers (AR) are less maternal towards their own offspring when they grow up. They show reduced levels of pup licking and time spent in crouch or lactating postures over pups (e.g., Gonzalez et al., 2001; Melo et al., 2006), effects that can be ameliorated or prevented by periodic stroking or by cohabitation with a same aged conspecific (Gonzalez et al., 2001; Melo et al., 2006).

How early AR experiences affect later maternal behavior is not altogether clear, although a number of potential mediating mechanisms have been ruled out. The

first hypothesis was that AR alters the hormonal profile that is known to facilitate the onset and/or expression of maternal behavior (Bridges, 1984). To assess the hormone hypothesis, Novakov and Fleming (2005) administered a sequence of progesterone and estrogen or control cholesterol to AR and MR adult virgin (ovariectomized) females and found, as expected, that all hormone-treated rats became rapidly maternal, showing all components of the behavior, whereas the control rats did not. However, among the hormone-treated animals only AR rats showed a reduction in licking and crouching, similar to parturient AR females (Novakov & Fleming, 2005). These results eliminated a role for hormonal effects of AR on maternal licking/crouching. A second and third hypothesis, undertaken simultaneously, was to determine whether the primary effect of AR might not be specific to the regulation of maternal “motivation” directly, but may be a more general effect on other behavioral systems and physiologies that contribute to the normal execution and patterning of maternal behavior. Hence, we explored the effect of AR on a number of the dopaminergically mediated mesolimbic and mesocortical function and systems, including those mediating attention and impulsivity (Burton et al., 2006; Lovic & Fleming, 2004; Lovic et al., 2006).

During our tests of maternal behavior, we observed that although AR mothers showed all elements of maternal behavior and were able to rear their pups through normal weaning, they tended to be somewhat erratic and frequently disengage from pup-directed activities, attending instead to extraneous stimuli in the larger environment (e.g., door opening). From this, we hypothesized that AR rats might have poor attentional and behavioral inhibition mechanisms and be more prone to distraction and that these effects of AR may account for the deficits in adult maternal behavior. In tests of this hypothesis, we found that AR rats exhibit greater levels of locomotor activity, selective attention, sensorimotor gating, action impulsivity, and flexibility while showing no deficits in simple associative learning (Lovic & Fleming, 2004; Lovic, Fletcher, & Fleming, in preparation). Again these effects could be reversed to various degrees by providing additional preweaning licking-like stroking stimulation (Lovic & Fleming, 2004; Lovic, Fleming, & Fletcher, 2004; Lovic et al., in preparation). Furthermore, the attentional performance of these rats, as measured by the attentional set shifting task and prepulse inhibition of the startle response, were both positively associated with levels of pup licking by females when they gave birth (Lovic & Fleming, 2004). Mothers who were inattentive on an attention task licked their pups less (Lovic & Fleming, 2004).

Following on our prior work on attention and mothering, the purpose of this study was to investigate the

relationship between impulsivity and mothering, using DRL (differential reinforcement of low-rate schedule) to assess impulsive action. The question then, was to determine whether the reduced licking and crouching previously found in AR rats was due to the fact that these rats are impulsive and, hence, engage in (exploratory) behaviors that preclude attending adequately to their pups. We also explored the effect of replacement stroking or “licking-like stimulation” on this relation.

## METHODS

### Subjects and Housing

Twenty female Sprague–Dawley rats (AR-MIN,  $n = 7$ ; AR-MAX,  $n = 6$ ; MR = 7) were used in this study. All rats were born at University of Toronto Mississauga animal vivarium. The rats at this facility were originally obtained from Charles River Farms in St. Constant, Quebec, Canada. At the time of weaning, rats were pair-housed in medium size Plexiglas cages (W 26 cm  $\times$  L 38 cm  $\times$  H 21 cm) with woodchips and ad lib access to rat Purina Chow food (unless otherwise specified) and water. The room temperature and humidity were maintained at 22°C and 40–50%, respectively. Lights were off at 20.00–08.00 hr.

### Apparatus

**Operant Conditioning Chambers.** Testing was carried out in 12 identical chambers (28 cm  $\times$  21 cm  $\times$  21 cm; Med Associates Inc., St. Albans, VT). Each chamber contained a lever (4.5 cm long), a food pellet dispenser, and a house light located on the wall opposite the dispenser. The apparatus was controlled by Med. Associates software and a Dell computer.

**Artificial Rearing. Groups and treatments.** Dams gave birth, and on the day of parturition (postnatal day—PND 0), their litters were culled to approximately 6 males and 7–8 females. On PND 2, three females were removed from the nest. Two females were implanted with a cheek cannula and raised AR, while the third female was sham-operated and returned to their mother (SHAM). One female sibling was not manipulated and was designated as a control (CON). Siblings that received cheek cannulae were randomly assigned to one of two conditions: (1) AR with minimal maternal-licking like stimulation (AR-MIN); and (2) AR with maximal maternal-licking like stimulation (AR-MAX). Therefore, there were four groups of rats: AR-MIN, AR-MAX, SHAM, and CON. SHAM and CON rats are usually not statistically different from one another and are combined into one group—mother-reared (MR; see Statistical Analyses Section).

**Cheek cannulae implants.** All PND 2–3 pups were weighed prior to surgery. Following local anesthesia (Lidocaine) cheek cannulae were implanted. The implantation of cheek cannulae lasted <1 min. SHAM rats were treated in an identical fashion to AR rats, except the cannula was not permanently implanted.

The SHAM rats were marked to distinguish them from the CON rats and returned to their nests.

**Artificial rearing of pups.** After the surgical implantation of the cannulae, pups were housed individually in plastic cups (11 cm in diameter  $\times$  15 cm deep), which were fitted into second weighted cups. Both cups floated in a temperature controlled water aquarium (water maintained at 36–40°C). The housing cups contained corn-cob bedding (Bed O’ Cobs) and the tops of the cups remained open to allow cheek cannulae tubing to emerge and connect to nearby syringes containing milk formula. The infusion of milk formula (Messer diet, taken from the University of Iowa; Hall, 1998) was executed and controlled by timer-controlled infusion pumps (Harvard Apparatus Syringe, PHD 2000). The pumps were programmed to infuse the diet for 10 min every hour, 24 hr daily. The amount of milk formula the pumps delivered was based on a specific fraction of the mean pup weight. We started by giving pups formula volume equal to 33% of their body weight. This amount was increased 1% each day, hence 34% of body weight on day 3 and 35% on day 4 and so on.. Every morning the pups were disconnected from the pumps, removed from the cups, weighed, and their tubing was flushed with 0.1 cc of distilled water. New syringes containing fresh formula were set up and the pump’s infusion rate was reprogrammed according to the new pup weight per pump. AR-MIN rats were stimulated twice a day, 30 s each (morning and night) with warm, wet, camel hair paintbrush, in order to stimulate urination and defecation. Only the pups’ anogenital region was stimulated. AR-MAX rats were stimulated eight times a day (2 min of body stimulation each stimulation period) in addition to two regular anogenital stimulations (30 s each). Stimulations were carried out from the day the pups were placed on the pumps (PND 2) to PND 16. On PND 18/19 all AR rats were taken off the pumps, placed in mouse cages (22 cm  $\times$  15 cm  $\times$  10 cm) and provided with milk formula, regular rat chow as well as the mixture of formula and chow. They were kept in these cages until the weaning day (see below).

**Weaning and groups.** On PND 21 AR rats were paired up with MR, non-experimental, social partners with whom they remained until adult testing. MR rats were weaned from their mother and paired together (MR-SHAM and MR-CON—from the same litter). All the rats were weighed and left undisturbed until adulthood.

**Behavioral Procedures. Maternal behavior.** At approximately 100 days of age, rats were mated. Twenty-one days after the introduction of males, the females were given two shredded paper towels as the nest building material, and placed in a room with other rats observed for their maternal behavior. On the day of pup birth (PND 0—rats giving birth before 17.00 hr) dam’s litters were culled to four males and four females. Maternal behavior was assessed on PND 2, 4, 6, 8, and 10. Testing was done in the following fashion: rat cages were gently placed on the table and the pups were removed from the nest and the dam’s cage was returned to her previous position on a cage rack. The pups were weighed and 5 min later they were returned to their mother’s cage. They were placed in the diagonally opposite

corner of the nest and the 10 min test was started. Observations were recorded using a computer-based event recorder (NEC PC 8300). During maternal observations, the following behaviors were of interest and reported here: (1) pup anogenital licking, (2) pup body licking, (3) lactating posture—female is over pups giving them access to her ventrum, (4) time spent in nest and a fifth (non-maternal) measure was included, namely (5) self-grooming.

**DRL-20s procedures.** Several weeks after maternal behavior assessment, rats were tested on the DRL-20s operant schedule. Procedures employed here were based on Fletcher (1995). Adult rats were gradually reduced to 85% of their free-feeding weights. They were trained to bar press for food (45 mg food pellets; Bio-Serv) on a continuous reinforcement (CRF) schedule during a 30-min session, on 7 consecutive days. All rats had three or four successful CRF schedule sessions (100 bar presses in 30 min) with the final session 1 day prior to being switched to the DRL-20s schedule. On the DRL-20s schedule, rats were reinforced only if they responded at least 20 s since their previous response. Responses made <20 s since the last response were not rewarded, and the 20 s period was reset. DRL-20s testing was done over 16 days (testing was done 6 days/week). Each session began with an illumination of the house light and insertion of the left lever into the chamber. The first response was always reinforced. For each session, the following measures were collected: number of responses, number of reinforcers earned, and percent efficiency [(number of reinforcers earned/number of responses made)  $\times$  100].

### Data Analyses

Maternal behavior data were averaged across 5 days of testing (PND 2–10) and analyzed using one-way analysis of variance (ANOVAs). DRL-20s data for each of the three measures was averaged across 4 days (for a total of four blocks) and analyzed using repeated measure ANOVAs (Group  $\times$  Block). Dunnett post hoc tests were used in order to assess which treatment group was different from the control group (MR). The relationships between maternal behavior and impulsivity were assessed using partial correlations (controlling for group effects; see below).

## RESULTS

### Maternal Behaviors

**Pup Anogenital Licking.** For all maternal behaviors see Figure 1. There were marginal overall group differences in durations of anogenital licking ( $F_{(2,19)} = 3.2, p = .067$ ), however, these differences were not statistically reliable. Post hoc analyses indicated that AR-MIN rats, but not AR-MAX rats, displayed significantly less anogenital licking than the MR rats ( $p < .05$ ).

**Pup Body Licking.** One-way ANOVAs indicated that groups displayed different durations of pup body

licking ( $F_{(2,19)} = 4.7, p < .05$ ). Post hoc analyses showed that AR-MIN rats differed significantly from the MR rats ( $p < .05$ ). AR-MAX rats were not different from either group.

**Hovering.** One-way ANOVA revealed marginal group differences in the duration of hovering over pups ( $F_{(2,19)} = 2.9, p = .082$ ), however, these differences were not statistically reliable. Post hoc tests pointed that neither AR group was significantly different from the MR group ( $ps > .083$ ).

**Time Spent in Nest.** Overall group differences were found ( $F_{(2,19)} = 4.9, p < .05$ ) and post hoc analyses revealed that AR-MIN rats, compared to MR rats, spent significantly less time in the nest ( $p < .05$ ). AR-MAX rats were intermediate between AR-MIN and MR and did not differ from the MR group.

**Self-Grooming.** There were no overall group differences in self-grooming behavior ( $p > .05$ ).

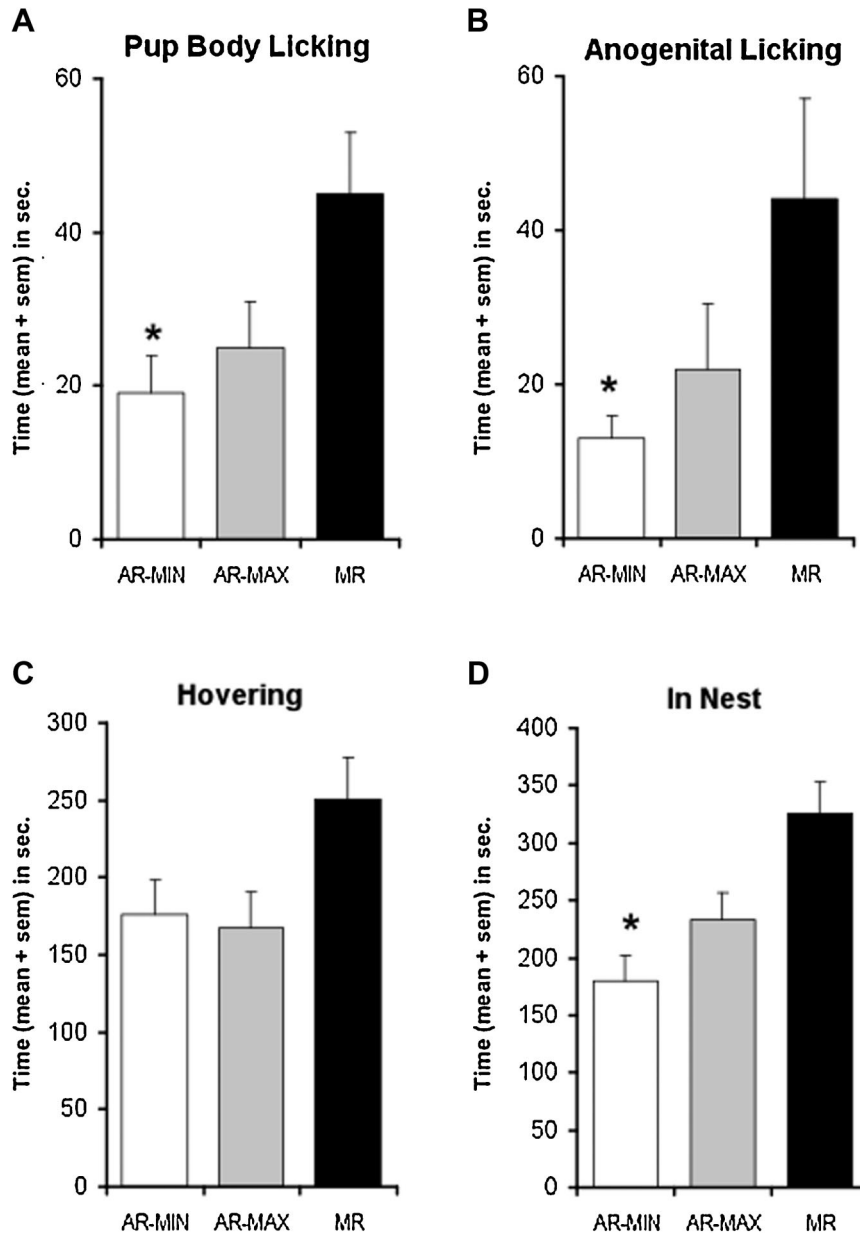
### DRL-20s

**Number of Lever Responses.** As can be seen in Figure 2, all groups showed a reduction in the number of responses across blocks (main effect of block;  $F_{(1,17)} = 40.6, p < .0001$ ). Groups were significantly different ( $F_{(2,17)} = 10.7, p < .05$ ) and Dunnett's post hoc analyses indicated that both AR-MIN rats and AR-MAX rats, made more lever response than the MR rats ( $ps < .05$ ; see Fig. 2).

**Number of Reinforcers Earned.** There was a significant increase in the number of reinforcers earned across test sessions (main effect of block;  $F_{(1,17)} = 21.9, p < .0001$ ). Groups were significantly different ( $F_{(2,17)} = 3.6, p < .05$ ) and Dunnett's post hoc analyses indicated that AR-MIN rats, but not AR-MAX rats, earned fewer reinforcers than MR rats ( $p < .05$ ; see Fig. 2).

**Efficiency.** Along with number of responses, efficiency was one of the measures of impulsivity. As shown in Figure 3, there was an overall increase in efficiency across test blocks ( $F_{(1,17)} = 25.8, p < .001$ ). There was also a main effect of group ( $F_{(2,17)} = 9.5, p < .05$ ). Post hoc analyses indicated that AR-MIN and AR-MAX rats were significantly less efficient than MR rats ( $ps < .05$ ). There were no significant interactions.

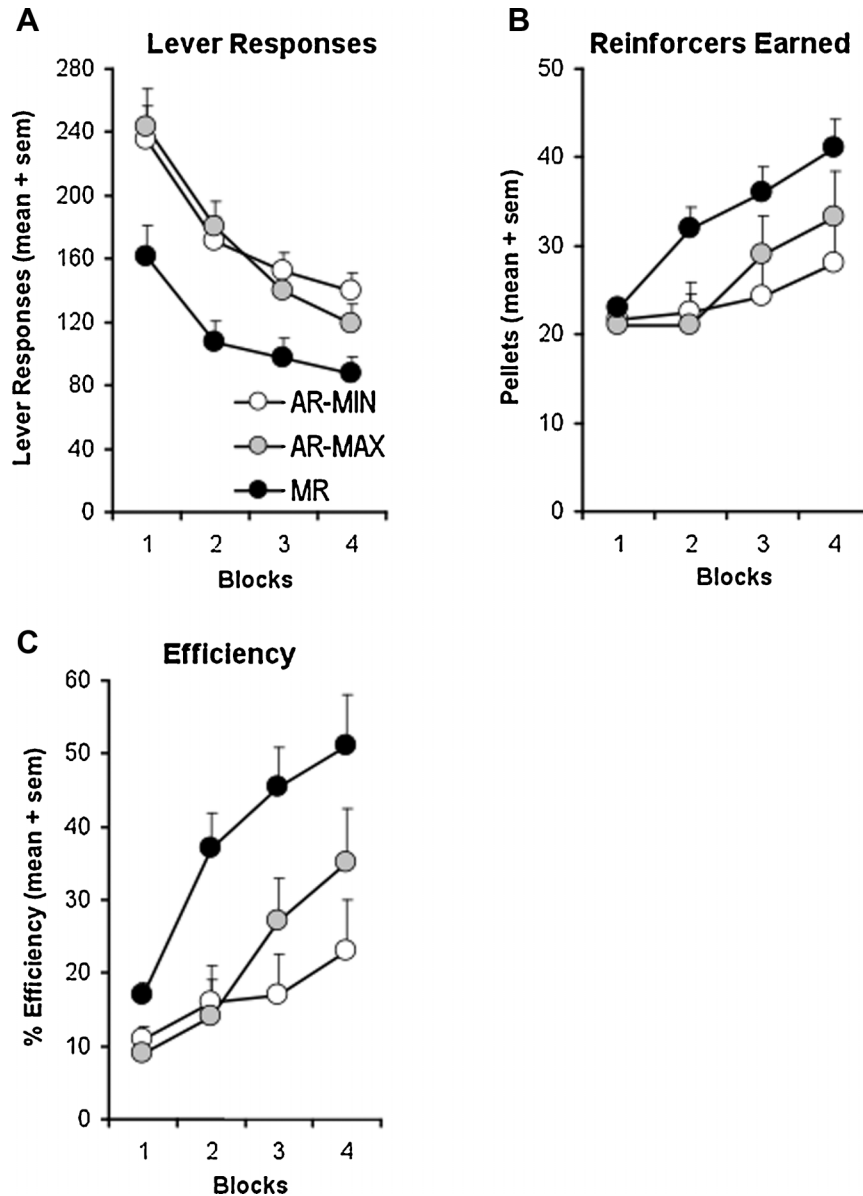
**Correlations Between Maternal Behavior and Impulsivity.** In order to investigate the relationship between impulsivity (DRL-20s task) and maternal behaviors, partial correlations were performed (controlling for group effects). Efficiency scores were averaged across four



**FIGURE 1** The figure depicts mean time (s) dams spent engaging in different maternal behaviors: (A) pup body licking, (B) anogenital licking, (C) hovering, and (D) in nest. \*Significant differences between MR and AR-MIN rats ( $ps < .05$ ).

blocks. We found a significant positive correlation between efficiency in the DRL-20s task and pup body licking ( $r = .431$ ,  $p < .05$ ), hovering over pups ( $r = .6$ ,  $p < .01$ ), and time spent in nest ( $r = .53$ ,  $p > .01$ ). There was also a non-significant correlation between efficiency and pup anogenital licking that was marginal ( $r = .37$ ,  $p = .06$ ; see Fig. 3). Efficiency was not correlated with self-grooming ( $p > .05$ ). There was also a correlation between number of reinforcements and body licking ( $r = .415$ ,  $p < .05$ ), hovering ( $r = .56$ ,  $p < .01$ ), and time

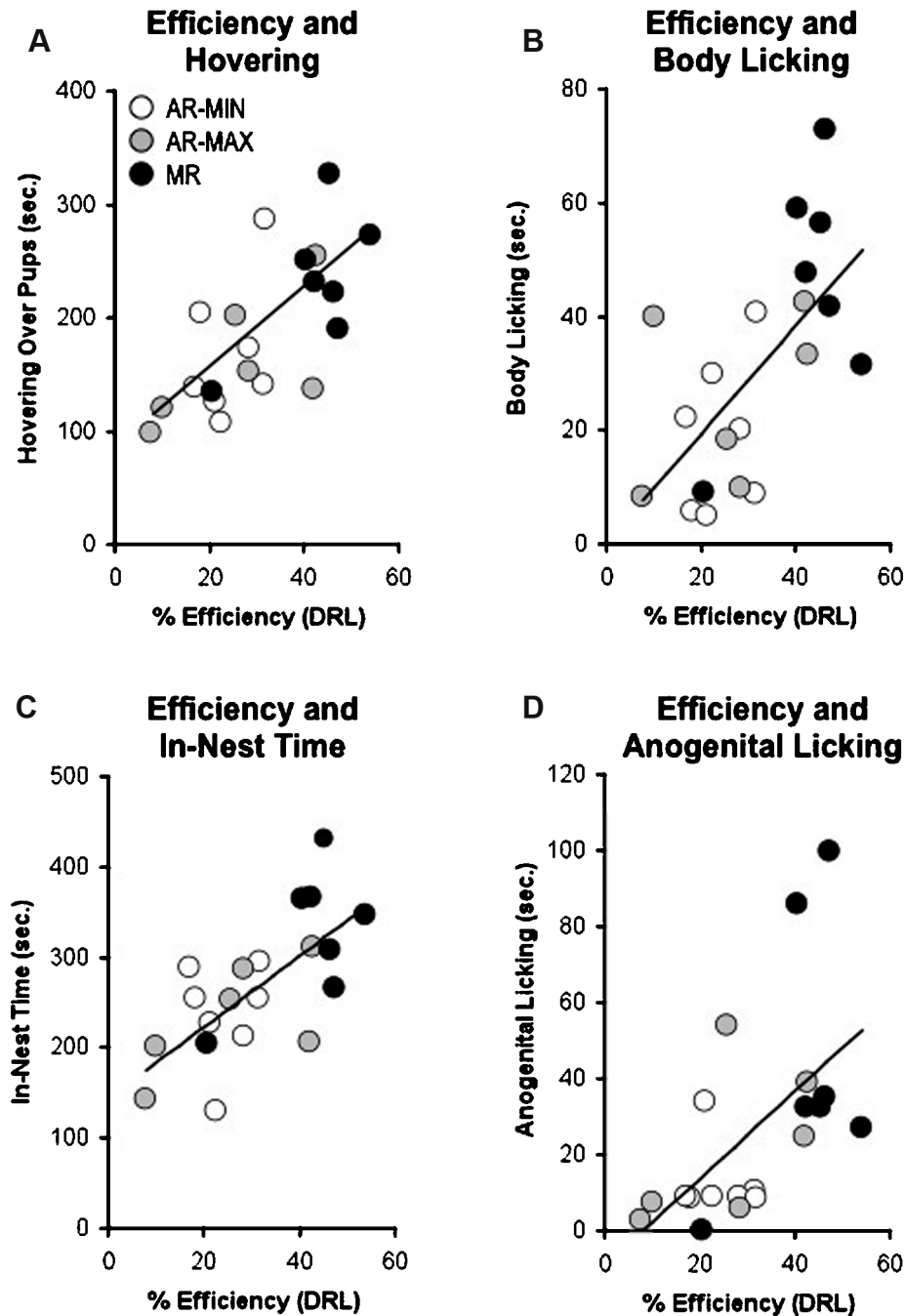
spent in the nest ( $r = .57$ ,  $p < .01$ ). Neither anogenital licking nor self-grooming were correlated with number of reinforcements ( $ps > .05$ ). Since efficiency was our main measure of impulsivity, we also performed linear regression on these variables with efficiency as a predictor variable of maternal behaviors in order to determine the percentage of variance accounted for this association. We found that a large percentage of the variance was explained by efficiency: pup body licking,  $R^2 = 0.412$ ; hovering,  $R^2 = 0.465$ ; in nest time,  $R^2 = 0.445$ .



**FIGURE 2** The figure depicts group differences in mean number of (A) lever responses. There was a significant decrease in lever responding across blocks ( $p < .001$ ). In addition, AR-MIN rats and AR-MAX rats made more lever response than MR rats ( $ps < .05$ ). (B) Number of reinforcers. There was a significant increase in the number of pellets that rats earned ( $p < .05$ ). In addition, compared to MR rats, AR-MIN rats earned fewer reinforcers across blocks ( $p < .05$ ). (C) Efficiency. There was a significant increase in efficiency across blocks ( $p < .001$ ). In addition, MR rats were more efficient than AR-MIN and AR-MAX rats ( $ps < .05$ ). Data averaged across four 4-day blocks of testing.

**Multivariate Analyses of Maternal Behaviors With Efficiency as a Covariate.** Given that there were significant group differences in time spent engaging in maternal behaviors and given that there was a significant correlation between some of the maternal behaviors and DRL-20s efficiency, we conducted multivariate analyses of maternal behaviors (separate analyses for each maternal behavior that was different between groups)

with efficiency as a covariate. Essentially, we asked a question whether group differences in maternal behaviors were driven by differences in DRL-20s efficiency. Consistent with our predictions, we found no group differences in maternal behaviors once efficiency was entered as a covariate (body licking, anogenital licking, in nest;  $ps > .05$ ). We also found no group differences with reinforcement entered as a covariate ( $ps > .05$ ).



**FIGURE 3** The scatter plot depicts a significant positive relationship between percent efficiency (DRL-20s) and duration of (A) pup body licking ( $r = .437, p < .05$ ), (B) hovering ( $r = .6, p < .01$ ), (C) in-nest time ( $r = .53, p < .01$ ), and a non-significant trend for (D) pup-anogenital licking ( $r = .37, p = .06$ ). Black regression line shown.

## DISCUSSION

The purpose of this study was to assess the relationship between maternal behavior and impulsive action in MR and AR rats. Consistent with previous findings (e.g., Gonzalez et al., 2001), we found that AR rats spent

significantly less time engaging in maternal behaviors than did MR rats. Also consistent with previous findings (Lovic et al., in preparation) was the observation that AR rats are more impulsive in the DRL-20s task; they made more lever responses, earned fewer reinforcements and were less efficient in earning rewards.

The data also suggest that time spent pup body licking and in lactating postures is positively correlated with efficiency in the DRL-20s task. Efficiency in the DRL-20s is an inverse measure of impulsivity. Rats that are more efficient are thought to be more behaviorally inhibited and less impulsive. This suggests that more impulsive rats are less maternal.

Previously, we have found that AR rats are less maternal than the MR rats (Gonzalez et al., 2001); however, the nature of this difference was not entirely clear. Rats can be less maternal for a variety of reasons such as reduced motivation and impaired learning. It is unlikely that AR rats are less maternal due to reduced motivation to be maternal. They readily approach pups, retrieve them and spend time with them indicating that pups are significant motivational magnets for AR rats (Gonzalez et al., 2001). AR rats do not have learning impairments in either maternal or non-maternal contexts (Lovic & Fleming, 2004). While parturitional hormones initiate maternal behavior in rats, maintenance of maternal behavior is regulated through experiential-learning mechanism (Orpen & Fleming, 1987). Since AR rats continue to be maternal well after the parturitional hormones have subsided, their continued responding must be maintained by intact experiential-learning mechanisms.

However, other factors, such as reduced behavioral inhibition and attention, might impact maternal behavior. Previously, we found a correlation between maternal behavior and measures of attention: prepulse inhibition of the startle response (PPI) and intra-dimensional shifting (ID shift; attentional set shifting task; Lovic & Fleming, 2004). PPI is thought to be a measure of sensorimotor gating, an ability to filter out and not respond to irrelevant environmental stimuli. Rats with lower PPI scores were less maternal as were those rats that took longer to make ID shifts (sustained attention); both suggesting reduced attentional abilities are associated with reduced levels of maternal behaviors. In this study, we report that reduced levels of maternal behavior in AR rats might be driven by their impulsive action (reduced behavioral inhibition). These two findings are complementary as it is likely that reduced sensory motor gating (PPI) represents a tendency to “attend” to multiple environmental stimuli and in the process the organism does not “focus” on relevant environmental stimuli (e.g., pups). The next major question is to determine the relation between mothering and each of the disrupted functions of attention and impulsivity. Do these functions make independent dissociable contributions, to maternal licking or are their effects overlapping? Unfortunately, until we test the same set of rats on all three measures, we cannot answer this question.

In regards to the impulsive nature of AR rats, it is possible that AR mothers have an altered subjective

perception of time (i.e., the experience of how much time has elapsed since the occurrence of an event). Time perception is one aspect of impulsivity measured by the DRL task; responses at particular time intervals are necessary to obtain reinforcement (e.g., Kelleher, Fry, & Cook, 1959; McClure & McMillan, 1997). Individuals who are impulsive overestimate time, thereby under-producing time intervals (e.g., Berlin & Rolls, 2004; Reynolds & Schiffbauer, 2004). Timing judgments are also an important component of associative learning (e.g., Gibbon, Malapani, Dale, & Gallistel, 1997). In AR mothers, deficits in timing measurement may lead to insufficient durations of bouts of maternal responsiveness or deficient contingent responding to pup cues. Previous findings from our laboratory provide some support for this interpretation; although AR mothers enter the next site as often as MR mothers, they show the most robust deficits in the duration of time spent engaging in maternal behaviors (e.g., Palombo et al., 2010). We also have found that lesions of the prefrontal cortex, which produce deficits similar to those found in AR mothers, disrupt the sequential structure (i.e., timing) of female maternal behavior (Afonso, Sison, Lovic, & Fleming, 2007). Further studies exploring the role of time production in AR rats may provide a better understanding of the specific cognitive deficits related to reduced maternal behavior in AR rats.

While these novel findings represent a second psychological mechanism of reduced maternal behavior in AR rats, we do not know which brain mechanisms mediate these effects and how the brain mechanisms of impulsivity, attention, and mothering impact one another. Early life adversity in the form of stress, periodic maternal deprivation, or isolation (artificial rearing) alters the DA system (Brake et al., 2004; Hall et al., 1999; Lovic et al., 2006). These manipulations increase the tone of DA systems. Increased DA levels have been associated both with increased impulsivity and reduced sensorimotor gating (Bayley, Bentley, & Dawson, 1998; Geyer, Krebs-Thomson, Braff, & Swerdlow, 2001; Peterson, Wolf, & White, 2003; van Gaalen, Brueggeman, Bronius, Schoffelmeier, & Vanderschuren, 2006). DA also plays a critical role in the neural networks involved in interval timing (e.g., Meck, 1986). Furthermore, given that DA systems are involved in motivation, learning, and stimulus salience (Berridge, 2007), it is not surprising that AR rats' motivation for natural rewards (food and pups) and learning are unaltered. In addition, based on their sensorimotor gating deficits and stimuli driven disinhibition, we suggest that AR rats are over-attributing salience to numerous environment stimuli and acting impulsively towards them at the expense of being maternal.

It should be noted that although providing tactile stimulation to AR rats partially reversed their maternal



behavior deficits, it did not modify all impulsivity responses in the DRL-20s test. Specifically, tactile stimulation only altered some of the effects of AR for number of reinforcements. However, our main measure of impulsivity (i.e., efficiency) did not show a reversal in deficits with additional tactile stimulation. This lack of reversal may be due to small sample sizes in the present study. Indeed, we have shown a MAX effect for efficiency in a recent study (Lovic et al., in preparation).

In summary, we found that impulsivity is inversely related to the level of maternal behavior that rat mothers will show towards their pups. Furthermore, we have found that impulsivity influences group differences in maternal behaviors. However, since we do not have evidence of causal relationship between impulsivity and maternal behaviors, it is possible that a third variable (e.g., attention) might be influencing both dependent variables. Poor attention can lead to disengagement from focus on the pup and in turn lead to attention being diverted towards some other stimuli. This diverted attention is accentuated if rats have poor inhibitory mechanisms.

## NOTES

This work was supported by an NSERC Grant to A.S. Fleming. The authors would like to thank the vivarium staff for all their help with animal care and maintenance of the facilities, Michael Nowoslawski & Shannon Mischler for help with behavioral testing.

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