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Propagation of maternal behavior across generations is associated with changes in non-maternal cognitive and behavioral processes

Vedran Lovic[a,*], Alison S. Fleming[b]

[a] Department of Brain and Cognitive Sciences, McGovern Institute for Brain Research, Massachusetts Institute of Technology, USA
[b] Department of Psychology, University of Toronto Mississauga, Canada

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ABSTRACT

Over a number of years we have studied the phenomenology of maternal behavior from endocrine, neural, experiential, and ontogenetic perspectives. Here, we focus on the effects of early life experiences with and without the mother on subsequent maternal and non-maternal behaviors of the offspring. We have used an artificial rearing procedure, which entails removing rat pups from their mother and raising them in isolation, while controlling and manipulating several aspects of their upbringing. As adults, mother-reared (MR) and artificially-reared (AR) rats are assessed on their own maternal behavior, as well several other behaviors. While both AR and MR rats nurse and successfully wean their young, the AR rats spend less time licking, grooming, and crouching over their young. Hence, being raised in social isolation does not seem to affect primary maternal motivational dynamics. Instead, isolation rearing produces alterations in the ongoing execution of the behavior and its effective organization. Here, we present evidence that changes in maternal behavior, as a result of social isolation from mother and siblings, are due to changes in top-down (e.g., sustained attention, flexibility) and bottom-up process (e.g., increased stimulus-driven behavior). These changes are likely due to alterations in brain dopamine systems, which are sensitive to early life manipulations and are modulators of bottom-up and top-down processes. Finally, we draw parallels between the rat and human maternal behavior.

This article is part of a Special Issue entitled: In Honor of Jerry Hogan.

1. Forward

When I (ASF) first arrived at University of Toronto in 1975, Jerry Hogan was among the first people I met and I recall feeling quite intimidated by him. He attended my job talk and asked all the hard questions I wanted to avoid. But doing so, he was also an influence on my decision to come to University of Toronto. I could see that he both questioned and sympathized with my need to unpack 'innate' behaviors and to dissect the complex behavioral mechanisms that underlie species-characteristic behavior. His work focused on learning, but not in the traditional laboratory animals, but rather in a variety of 'exotic' species, such as jungle-fowl, chickens, and paradise fish. He did not study them in strictly artificial settings, but in settings and stimulus contexts with ecologic validity. I admired his behavioral and more ethologic approach to science and his belief in the role of experience in the development of species-characteristic behavior. The years in the 'chicken house' reinforced my admiration for his science and for his keen mind.

There are numerous differences between mammals and other types of animals, but perhaps the most salient differences relate to the quality and quantity of parental care mammalian parents provide to their young. Mammalian offspring require significant parental care, such as food, warmth, and protection, in order for the young to survive and thrive. However, there are significant intra- and interspecies variations in the extent and quality of parental care provided (see Rosenblatt and Snowdon, 1996). Perhaps the biggest interspecies differences relate to the involvement of both parents in the care of the offspring. In the vast majority of species, males are seldom involved in rearing of the young and it is the mothers who take on the primary responsibility of parental care (Kinsley and Amori-Meyer, 2011; Numan and Insel, 2003; Mann and Bridges, 2001; Rosenblatt and Snowdon, 1996; Stern and Lonstein, 2001).

* Corresponding author at: Department of Psychology, University of Calgary, Canada.
E-mail address: vedran.lovic@ucalgary.ca (V. Lovic).

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Over several decades of research, we have examined the role of hormones, neural structures, and experience on maternal behavior. Early postpartum period is characterized by pronounced plasticity for the new mother but also for her offspring. Alterations in the mother-offspring relationship can produce acute and long-term changes in the offspring's behavior and physiology. Here we review findings from our laboratory, as well as by others, examining the effects of early life manipulations on brain and behavior. We provide evidence that early life manipulations of the quality and quantity of maternal care offspring receive from their mother subsequently alters the maternal behavior offspring show toward their own young. Therefore, we see a propagation of maternal behavior across generations. However, these early life experiences with one's mother not only alter future display of maternal behavior toward the next generation of young, but they also alter some general functions, such as impulsivity, attention, behavioral flexibility, and attraction to reward-related stimuli or cues (Lovic et al., 2001, 2006, 2011a; Lovic and Fleming, 2004). We argue that, although mothering alters mothering of the next generation, mothering also changes general cognitive-behavioral profile of the offspring and these changes in turn change maternal 'styles' in the offspring.

2. Rat maternal behavior

Rat maternal behavior is relatively stereotyped yet complex, as it consists of a constellation of behaviors that are influenced by numerous sensory, hormonal, and experiential factors. Typically, virgin female rats are not responsive to pups and will avoid them, bury them, or even attack them. Pregnant female rats become responsive to pups in the latter third of the 21-day pregnancy period. During parturition female rats will pull pups out of the vaginal canal, clean them by removing the placenta, and retrieve the pups to the nest site. Soon after, the female will crouch over the pups allowing them to nurse while keeping them warm and protected from the environment. New mothers will lick pups' anogential regions to stimulate urination and defecation. Mothers will also lick and groom pups non-anogential skin (see Rosenblatt and Snowdon, 1996). Given that pups are born blind and deaf, maternal licking is a major sensory stimulation for newborn pups (see Rosenblatt and Snowdon, 1996). However, it is important to note that in addition to receiving somatosensory stimulation from the mother, pups also receive considerable somatosensory from each other as well (e.g., Alberts, 1978). While virtually all postpartum rats show maternal behavior, there are significant individual differences in the amount of licking and grooming mothers provide to their pups. These differences have long-lasting effects on pups' physiology and behavior.

The change from the virgin, maternally non-responsiveness state, to the postpartum, maternally responsive state, is associated with hormonal alterations characterizing the end of pregnancy – namely, declining levels of progesterone and rising levels of estrogen and prolactin (see Bridges, 2008; Mann and Bridges, 2001). These hormones act on numerous brain areas, but the most relevant is their action on the medial preoptic area of the hypothalamus (MPOA) (Numan, 1974; Stern and Lonstein, 2001). The MPOA, along with several other brain areas, is the ultimate neural node controlling rat maternal behavior. Lesions of the MPOA rapidly abolish many feature of maternal behavior (Numan, 1974). The hormonal profile of postpartum females changes rapidly and within days their hormonal profile is similar to that of the virgin female (Orpen and Fleming, 1987). Hence, the importance of hormones diminishes and maternal behavior is maintained by sheer experience of being maternal. In fact, as little as 30 min of postpartum experience is enough to make the female rat responsive to pups for a long period of time (Orpen and Fleming, 1987). In a number of studies, we have demonstrated that maternal experience effect is dependent on the functional integrity of the nucleus accumbens (Li and Fleming, 2003a,b). This area of the ventral striatum receives rich dopamingergic input from the ventral tegmental area and dopaminergic blockade in the accumbens can block the maternal experience effect (Parada et al., 2008). Overall, rat maternal behavior, while stereotypic, is highly complex and is modulated by motivational, affective, and as will be evident below, cognitive processes.

3. From maternal separation to individual variations in maternal behavior

In 1956, Levine et al. (1956) made a surprising discovery. Their experiment examined the effects of early life 'trauma' on adult 'emotionality' (stress responses). The experimental group consisted of rat pups, removed daily from their mother and nest, and subsequently given mild electric shocks over a 3-min period. The control groups consisted of undisturbed pups and pups that were removed from the nest but not given mild shock. The pups were allowed to grow up and their 'emotionality' was assessed. Surprisingly, pups that were removed from their mother and electrically stimulated were not significantly different from the pups that were removed from their mothers but not given shocks. Importantly, both of these groups were less 'emotional' compared to the non-manipulated (control) group of rats. This was one the first studies showing that relatively brief separations from the mother can have long-term effects on offsprings' responses to stressor. However, the mechanisms by which these effects come to be were not known for some time.

Bell et al. (1971) found that manipulating or 'handling' pups altered their ultrasonic vocalizations and Levine (1975) proposed that handling of the pups alters the behavior of mother and pups and that this alteration in mother-pup interaction then produces the effects of handling. This turned out to be the case. Mothers of pups that have been handled show increased pup licking and arched-back nursing (Liu et al., 1997). Therefore, solely manipulating the pups can alter maternal behavior, which was hypothesized to then, in turn, alter the pups' long-term neurophysiology, such as expression of several biomarkers involved in stress responses (Meaney et al., 1996, 2000; Meaney, 2001).

If handling is mediated by alterations in mother-pup interactions, namely the amount of licking that pups receive and the type of nursing posture that the mother exhibits, then it is conceivable that naturally occurring differences in these two behaviors will produce effects associated with handling experiments. Liu et al. (1997) tested this hypothesis. They observed and recorded maternal behavior of rat mothers during the first ten days of the postpartum period. They separated the mothers, based on the mean of licking and arched-back nursing, into those that were one standard deviation above the mean (i.e., high licking arched-back nursing) and those that were one standard deviation below the mean (i.e., low licking arched-back nursing). Once the offspring of these animals reached adulthood their physiological responses to stress were assessed. They found a significant negative correlation between the amount of licking and arched-back nursing administered to the pups by dams and pups' physiological indicators of emotionality. That is, pups that are licked more are less 'emotional'. Furthermore, we and others have found that the amount licking and grooming mother rats provide to their offspring is correlated with the amount of licking grown offspring show toward their own offspring (Francis et al., 1999). Hence, there is a propagation of individual differences in maternal behavior across generations. However, the causal effects from these observational and correlational studies are not self-evident.