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Review article

Stress and parental behaviors

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ABSTRACT

In nearly all mammalian species, newborn pups are weak and vulnerable, relying heavily on care and protection from parents for survival. Thus, developmentally hardwired neural circuits are in place to ensure the timely expression of parental behaviors. Furthermore, several neurochemical systems, including estrogen, oxytocin, and dopamine, facilitate the emergence and expression of parental behaviors. However, stress can adversely affect these systems, impairing parental behaviors. In this review, we will summarize our current knowledge regarding the impact of stress on pup-directed behavior circuits that lead to infant neglect, abuse, and, in extreme cases, killing. We will discuss various stressors that influence parental behaviors at different life stages and how stress induces changes in the neurochemical systems that support parental care, ultimately leading to its poor performance.

1. Introduction

In the wild, natural conditions are harsh, especially for helpless newborns. Adverse weather, predators, hunger, and even minor temperature fluctuations can threaten their survival. Without parental care, it would be nearly impossible for infants to grow into adults in most mammalian species. Therefore, "hardwired" neural mechanisms are in place to ensure robust parental behaviors are expressed the moment newborns arrive (Kohl et al., 2017; Kohl and Dulac, 2018). However, the mechanisms supporting parental behaviors could be affected by various stressors, decreasing the quality of parental care. In particular, stress during early life and pregnancy appears to have a long-lasting impact on parental behaviors (Davis and Narayan, 2020; Lupien et al., 2009). Here, we will first summarize changes in parental behaviors induced by stressors at different life stages, including pre-birth, infancy, puberty, pregnancy, and lactation (**Fig. 1**). We will then discuss our current understanding regarding the neural mechanisms underlying the stress-induced decrease in parental behaviors (Fig. 2).

2. Stress-induced changes in parental behaviors

2.1. During early life

Exposure to severe stress during childhood — frequently referred to as early life stress (ELS) —has a profound and lasting negative impact across the life course (Baram et al., 2012; Bock et al., 2015; Fox, Levitt, and Nelson III, 2010; Gröger et al., 2016; Weinstock, 2008) (Fig. 1). Maltreated young are at risk of showing poor parental behaviors to their own young as adults, a phenomenon known as the "Cycle of abuse" (Michl-Petzing et al., 2019; Thornberry and Henry, 2013). This session discusses evidence supporting the intergenerational transmission of parental behaviors.

2.1.1. Before birth

Early life stress can be divided into stress experienced during the fetal stage and infancy. In the fetal stage, the stress experienced by the pregnant female can influence the developing fetus. In rats, exposing pregnant females to psychosocial and restraint stressors daily between days 4 and 10 of pregnancy significantly reduced the offspring's nursing behavior and the time spent with pups when they became mothers (Bosch et al., 2007). In another study, Champagne et al. found that the offspring of stressed mothers (placed in Plexiglas restrainers for 30 min,

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3 times/ day during the last 7 days of pregnancy) exhibited reduced licking and grooming toward their own offspring compared to the progeny of non-stressed dams (F. A. Champagne and Meaney, 2006).

2.1.2. *During infancy*

Stress during infancy caused by inadequate parental interaction also adversely affects later parental behaviors during adulthood. For example, compared with biparentally reared animals, monogamous prairie vole pups raised by the mother alone show lower levels of licking and grooming towards their young when they become parents (Ahern, Hammock, and Young, 2011). Kikusui et al. found that compared to the normally weaned mice, the early-weaned female mice show a lower frequency of pup licking/grooming and arched-back nursing when they become mothers (Kikusui, Isaka, and Mori, 2005). When parental care is completely deprived by raising the mouse pups in isolation via feeding tubes, the animals show markedly low levels of licking, sniffing, and retrieving behavior towards their offspring in adulthood (Afonso et al., 2011; Gonzalez et al., 2001). Similar phenomena were observed in non-human primates. Harlow et al. found that female rhesus monkeys separated from their mothers at birth and deprived of early peer interactions exhibit reduced maternal behaviors and sometimes are abusive towards their infants, such as refusing to nurse, pushing the young away, crushing them to the floor and even attacking unprovokedly (Arling and Harlow, 1967; Harlow et al., 1966). In humans, females who lose parents early in life or have strained relationships with their mothers tend to interact with their babies less (Hall and Pawlby, 1981; Minde et al., 1980). Individuals who were physically abused as infants are more likely to become abusive as parents (Parke and Collmer, 1975; Wolfe, 1987),

The quality of maternal care the infants receive also affects their future parental behaviors. In mice, individual females that exhibit high licking/grooming of pups and arched-back nursing (LG-ABN) are considered good mothers. A good mother's daughter is more likely to become a good mother. Specifically, female offspring of low LG-ABN dams reared by high LG-ABN mothers exhibit high frequencies of parental care behaviors as normal high LG-ABN offspring. In contrast, females born to high LG-ABN females but reared by low LG-ABN mothers show low parental care (F. A. Champagne et al., 2003; F. A. Champagne and Meaney, 2006; D. Francis et al., 1999; Umemura et al., 2015). Similarly, in non-human primates, female vervet monkeys who spent ample time interacting with their mothers as infants tend to behave the same way when becoming mothers (Fairbanks, 1989). These results suggest that early life experiences with mothers strongly influence an individual's parental behaviors later in life.

2.2. *During puberty*

Puberty marks the transition from a non-reproductive juvenile into a reproductively competent adult. In female rodents, the first external sign of ovarian activity, i.e., vaginal opening, marks the onset of puberty (~ 4 weeks), while the first reproductive cycle (estrous cycle) marks its offset (~6 weeks) (Ismail et al., 2011; Mayer et al., 2010).

Stressful experiences during puberty can disrupt the estrous cycle, affect sexual behaviors (Bentefour and Bakker, 2024), and increase anxiety (Yohn and Blendy, 2017). But interestingly, certain stressors in puberty appear to increase instead of decreasing future pup caring behaviors. For instance, male mice isolated for three weeks during puberty (5–8 weeks old) spent significantly more time interacting and crouching over pups and retrieved pups faster than group-housed males (Orikasa et al., 2015). Juvenile females exposed to trimethylthiazoline (TMT), a chemical found in fox feces, and an elevated platform under direct bright light show increased maternal aggression, as reflected by the decreased attack latency of an intruder during lactation (Cordero et al., 2013). However, given the limited research on the impact of stress during puberty on maternal behaviors, additional studies are needed to confirm the facilitating effect of puberty stress on caregiving behaviors in adulthood.

2.3. *During pregnancy*

Pregnancy is when the parental circuit undergoes many changes to support the emergence of parental behaviors during motherhood. As such, it is a sensitive period for experiences, both negative and positive, to influence later parental behaviors.

2.3.1. *Physical stress impairs parental behavior*

Restraint, which involves placing the pregnant females in Plexiglas restrainers for around 1–2 hours per day, in the late gestation (~days

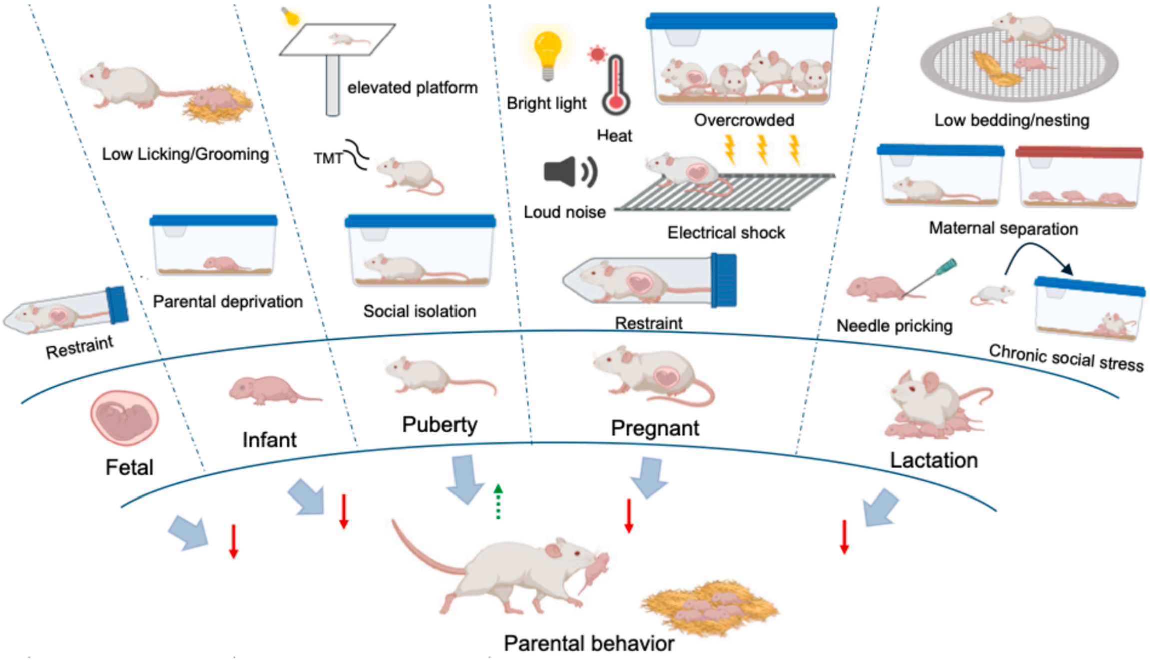

Fig. 1. Various stressors across life stages impact parental behaviors. The red and green arrows indicate impaired and enhanced parental behaviors, respectively.

10–20), is a commonly used procedure to induce stress (Baker et al., 2008; Smith, 2004; F. A. Champagne and Meaney, 2006). This paradigm consistently decreases parental behaviors, including licking/grooming (Baker et al., 2008; F. A. Champagne and Meaney, 2006; De Souza et al., 2012; Maccari et al., 1995), arched-back nursing (Smith, 2004), nesting/grouping pups (Smith, 2004), crouching (Herrenkohl and Whitney, 1976), pup contact (De Souza et al., 2012; Maccari et al., 1995) and pup retrieval (Herrenkohl and Whitney, 1976; Maccari et al., 1995). Exposure to stress during one pregnancy can impact parental behaviors for multiple litters, even if the females are not exposed to stress during later pregnancies (F. A. Champagne and Meaney, 2006).

Other stressors experienced during mid-pregnancy, such as foot shock or a combination of heat, bright light, and loud music, also decrease parental behaviors (Golub et al., 2016). Specifically, mice subjected to these conditions spend significantly less time in the nest grooming and nursing their pups (Meek et al., 2001). However, not all sensory stressors have the same impact. For example, Olga and colleagues found that daily exposure to variable frequency ultrasound (20–25 kHz, 25–40 kHz, 40–45 kHz) throughout the pregnancy did not affect maternal behavior (Abramova et al., 2021). This may suggest that the parental circuit can withstand mild stressors. It is worth noting that stress applied to pregnant mice will also affect the fetuses and change the infants' behaviors. Typically, stressed pups elicit stronger parental care (Walker et al., 2003). This may compensate for the mild stress-induced parental behavior deficits to some extent.

Overcrowding is another type of physical stressor that is likely to be experienced by animals under natural conditions. When pregnant females are housed in a small cage with 4 male mice from gestation day 14–21 (Moore and Power, 1986), the females show reduced anogenital licking of the pups compared to control females (Hillerer et al., 2011; Moore and Power, 1986). Consistently, the offspring survival rate is negatively affected by the population density in house mice (Ferrari et al., 2022; Lidicker, 1976; Southwick, 1955).

In humans, pregnant females in low-income countries face challenges such as overcrowding and poor housing conditions. Overcrowding is significantly associated with postpartum depression (Gupta et al., 2013), which is a risk factor for hostile young-directive behaviors and child neglect (Lovejoy et al., 2000; Cousons-Read, 2013; Goodman, 2007).

2.3.2. *Environmental enrichment (EE) has a positive impact on parental behavior*

While negative experiences during pregnancy impair parental behaviors, positive experiences have the opposite effect. Female rats living in a large arena containing stimulating objects, such as ramps, tubes, and balls, and other females during pregnancy exhibit significantly enhanced parental behaviors compared to females living in a standard lab cage. They spend twice as much time licking and grooming pups as control animals and more actively hover over pups during the first postpartum week. In the maternal defensive test, EE dams exhibit three times the level of aggressive behaviors compared to the control group. (Núñez-Murrieta et al., 2021). This beneficial effect of EE on parental behaviors is observed not only in normal rats but also in rats predisposed to anxiety and depression (Rosenfeld and Weller, 2012).

2.4. *During lactation*

After giving birth, parental behavior truly begins. We can divide the stressors in this period into two categories. The first category includes environmental factors unrelated to pups, such as resource availability. The second category involves the pups themselves. The suboptimal health state of pups or their mere absence can act as potent stressors, promoting parental behavior to ensure the safety and survival of the young.

2.4.1. *Pup-unrelated*

Low resource availability can be a potent stressor during the lactation period because high-quality parental care requires an adequate supply of food and nesting materials. The limited bedding/nesting materials (LBN) model, introduced by the Baram lab, is commonly used to study how environmental stress changes parental behavior in lactating mothers (Gilles, Schultz, and Baram, 1996; Molet et al., 2014; Walker et al., 2017). In this paradigm, the dams are transferred to cages with bedding and nesting material sparsely covering the wire mesh floor from PND 2–9 (Avishai-Eliner et al., 2001; Gilles, Schultz, and Baram, 1996; Walker et al., 2017). Variants of this model include using approximately 20 % of bedding material in a normal cage from PND 8–12 or intermittently from PND 1–7 (Moriceau et al., 2009; Raineki, Moriceau, and Sullivan, 2010; T. L. Roth and Sullivan, 2005; Walker et al., 2017). The most apparent consequence of LBN is the fragmentation of parental

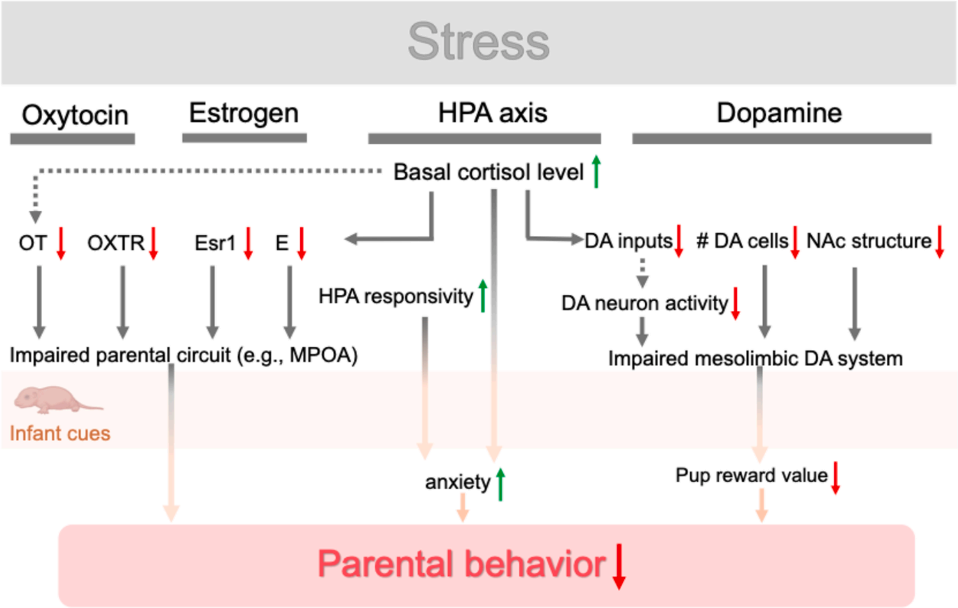

Fig. 2. Summary of stress-induced dysfunction in the oxytocin, estrogen and dopamine systems and HPA axis that impair parental behaviors. Green and red arrows indicate increase and decrease, respectively.

behaviors, as reflected by the shorter bouts of pup-directed caring behaviors. The mother leaves the nest frequently (Brunson et al., 2005; Demaestri et al., 2022; Gallo et al., 2019; Ivy et al., 2008; Lapp and Moore, 2020; Pardo et al., 2023; Rice et al., 2008) and spends limited time nursing, licking and grooming the pups even when in the nest (Dalle Molle et al., 2012; Demaestri et al., 2022; Gallo et al., 2019; Pardo et al., 2023). Resource-limited mothers also show longer latency to retrieve pups back to the nest and, in some cases, show abusive behaviors towards pups, including aggressive grooming and kicking, stepping or jumping on pups, and transporting pups by gripping a limb (Blaze et al., 2015; Gallo et al., 2019; Rincón-Cortés and Grace, 2022; T. L. Roth and Sullivan, 2005; Walker et al., 2017).

Beyond limited resource-induced stress, chronic social stress (CSS) also affects the parental behavior of mothers. In one CSS model in mice, a novel male was introduced into the dam's home cage for 1 hour each day from lactating day 2–16. The repeated home intrusion attenuates maternal care during mid-lactation and promotes maternal aggression toward a novel male intruder (Nephew and Bridges, 2011; Rosinger et al., 2021).

In humans, limited resources, i.e., financial hardship and social conflict (within the family or in workplaces), are major risk factors for postpartum depression (Pawluski et al., 2017; Westdahl et al., 2007), which is often associated with a weak mother-infant bond (Tietz et al., 2014) and poor maternal care (Field, 2018).

2.4.2. *Pup-related*

The goal of parental behaviors is to ensure the well-being of the young. Thus, deprivation of pup access is a unique stressor, prompting the mother to search for the young and show compensatory caring behavior after the reunion, especially towards the missing pup (Burenkova et al., 2020; Zimmerberg et al., 2003). While acute maternal separation promotes parental behavior, chronic or repeated separation can negatively impact parental behavior. For instance, after 4–5 days of daily maternal separation, mothers frequently leave the nest and spend less time nursing the young (Demaestri et al., 2022) and crouching (Burenkova et al., 2020).

Mothers also adjust their parental behaviors based on the state and needs of their pups. When the pups are under stress, mothers enhance their parental behavior to relieve their discomfort. In the repeated neonatal pain model, the neonatal rats (P2-P14) are separated from their mothers for 15 minutes daily, and their rear heel is pricked with a 30-G needle. After the pup is returned, mothers lick the pricked pups significantly more than handled-only pups during the first 10 min of reunion and, to a lesser extent, over the 90 min following reunion (Walker et al., 2003).

Altogether, these studies revealed that stress experienced in nearly all life stages can impact parental behaviors. It could impair not only current parental behaviors, i.e., low LBN during lactation, but also those that will happen in the future, i.e., early life stress. However, pup-related stress is unique as it tends to increase instead of decreasing parental behaviors to improve the well-being of the young.

3. Mechanisms behind stress-induced changes in parenting behaviors

Parental behavior is supported by a developmentally wired neural circuit, with the medial preoptic area (MPOA) being a key node of this circuit (Kohl et al, 2017; Yu et al., 2020; Kohl and Dulac, 2018). The maternal circuit is under the modulation of several neurochemical systems to ensure rapid onset and robust expression of maternal care (Fig. 2). Specifically, sex hormones, such as estrogen and progesterone, are vital for refining the circuit during pregnancy for maternal behavior initiation. Neuropeptides, such as oxytocin, boost the maternal care circuit to ensure behavior expression under challenging conditions. The mesolimbic dopamine reinforces the behavior by signaling the positive valence of pup interaction. In this section, we will discuss the importance of estrogen, oxytocin, and mesolimbic dopamine in promoting parental behaviors and review the impact of stress on these systems that leads to long-lasting changes in parental behaviors.

3.1. *Estrogen*

Virgin female rodents typically show aversion towards pups. During late pregnancy or lactation, females reduce pup avoidance and start to show pup-caring behaviors, such as grooming, crouching, and retrieving (F. Champagne et al., 2001; Numan and Sheehan, 1997; A. S. Fleming, O'Day, and Kraemer, 1999). This transformation is strongly influenced by sex hormone changes during pregnancy, with estrogen playing a particularly important role (Rosenblatt, 1994). Seminal studies by Rosenblatt and colleagues demonstrated that estrogen surge during late pregnancy enables the fast onset of maternal behaviors (Harold I. Siegel and Rosenblatt, 1975; H.I. Siegel and Rosenblatt, 1975), and later studies showed that parental behavior can be elicited in virgin rats by mimicking estradiol rise during pregnancy (Bridges, 1984; Doerr, Siegel, and Rosenblatt, 1981).

Numerous studies established the central role of MPOA in parental behaviors (Lee, Clancy, and Fleming, 1999; Numan, 1974; Numan et al., 1988; Wu et al., 2014; Fang et al., 2018; Wei et al., 2018; Kohl et al., 2018; Yoshihara et al., 2021). MPOA expresses abundant estrogen receptor alpha (Esr1) – a nuclear receptor that acts as a transcription factor upon binding to estrogen. During pregnancy, estrogen acts on Esr1 to induce molecular, morphological, and physiological changes in MPOA cells, resulting in enhanced cell responses to pups and, ultimately, efficient expression of maternal behaviors (Ammari et al., 2023). When Esr1 expression in MPOA is knocked down using siRNA, the maternal behavior is almost abolished, and in extreme cases, manipulated females display infanticidal behaviors (Ribeiro et al., 2012). Conversely, bilateral estrogen implants in the MPOA hasten the onset of maternal behavior in pregnancy-terminated primigravid (Numan et al., 1977) or ovariectomized and virgin female rats (Fahrbach and Pfaff, 1986). Optogenetic activation of Esr1-expressing cells in MPOA (MPOA-Esr1) is sufficient to promote parental behaviors acutely in virgin female mice (Fang et al., 2018; Wei et al., 2018).

Stress can modulate Esr1 expression in multiple parental behavior-related regions. Compared to offspring from high-LG mothers, females raised by low-LG dams express less Esr1 in the MPOA, and show decreased neuronal responses to estrogen (F. A. Champagne et al., 2003; F. Champagne et al., 2001). Similarly, post-weaning social isolation reduces Esr1 expression in the MPOA of prairie voles (Ruscio et al., 2009). Chronic stress also causes reduced Esr1 expression in the nucleus accumbens (NAc), another brain region indicated in maternal behaviors (Numan, 2007; Lorsch et al., 2018). Beyond decreased Esr1 level, early life stress can also lower estradiol levels. Restraint stress (Ordyan et al., 2013; Reynaert et al., 2016) and lipopolysaccharide-induced immune stress in mothers (Izvolskaia et al., 2016) decrease estradiol levels in female offspring once they reach adulthood. Given the critical role of estrogen in the onset of maternal behaviors, the early life stress-induced Esr1 and estradiol decrease is expected to dampen the activation of the maternal circuit, resulting in poor maternal behaviors in adulthood.

3.2. *Oxytocin*

Although not absolutely required, oxytocin (OT) has been found to enhance parental behaviors consistently. Intracerebroventricular (i.c.v.) (Pedersen and Prange, 1979; Pedersen et al., 1982) or intraperitoneal (i.p.) (Marlin et al., 2015) injection of OT can shorten the latency to express parental behaviors in virgin female rodents. Similarly, optogenetic activation of OT neurons in the paraventricular hypothalamus (PVH) increases pup retrieval in virgin female mice (Marlin et al., 2015). Conversely, disrupting brain oxytocin signaling pharmacologically or genetically impairs maternal behavior (Jin et al., 2007; Leengoed et al., 1987). Specifically, i.c.v. injection or local infusion of oxytocin receptor antagonist (OTA) into the MPOA, ventral tegmental area (VTA), and medial prefrontal area (mPCF) all impair parental behaviors in lactating females (Sabihi et al., 2014; Pedersen et al., 1994). Furthermore, *CD38* knockout that results in impaired oxytocin secretion disrupts maternal care, which can be restored by subcutaneous injection of OT (Jin et al., 2007). Recent studies using conditioning OT or OXTR knockout, optogenetic and chemogenetic OT cell activation and inactivation reached essentially a similar conclusion: although OT is not absolutely required for maternal behaviors, deficits in OT system could delay the behavior onset in inexperienced virgin females or impair the performance of mothers in a stressful environment (Ng et al., 2023; Ragnauth et al., 2005; Carcea et al., 2021). Similar effects have also been reported in male mice. Knockout of the OT gene in the PVH or genetic ablation of PVH-OT neurons significantly decreases retrieving behaviors and the duration of paternal care exhibited by fathers. Conversely, chemogenetic activation of PVH OT neurons blocks infanticidal behaviors and promotes caregiving behaviors in sexually naïve male mice (Inada et al., 2022). Oxytocin could exert its influence on the maternal circuit in multiple ways, including directly changing the excitability of OXTR-expressing cells (first-order modulation) (Osakada et al., 2024), changing the local circuit elements (e.g., inhibitory interneurons) that influence the principal output cells (second-order modulation) (Owen et al., 2013; Sato et al., 2020), or changing activities of other neuromodulatory systems (third-order modulation) (Froemke and Young, 2021; Dölen et al., 2013; Xiao et al., 2017).

In humans, oxytocin levels during early pregnancy and the postpartum period have been correlated to maternal behaviors, including gaze, vocalizations, positive affect, and affectionate touch (Feldman et al., 2007). Additionally, higher oxytocin levels are associated with attachment-related thoughts and frequent infant checking (Feldman et al., 2010; Feldman et al., 2007). Thus, oxytocin represents an evolutionarily conserved mechanism to promote parental behaviors in both males and females of various mammalian species.

Stress can suppress the oxytocin system at both the neuropeptide and receptor levels. In primates, for example, rhesus macaques raised by human caregivers without maternal interaction exhibit low central oxytocin levels (Winslow et al., 2003). Women who experienced early childhood abuse or neglect have significantly lower levels of OT in their CSF compared to women without such experiences (Heim et al., 2009). In rodents, female offspring of low-LG dams show reduced OXTR binding in several brain regions, including the MPOA (F. A. Champagne and Meaney, 2007; D. D. Francis et al., 2002). Offspring of high-LG mothers with post-weaning isolation display impaired maternal behaviors and a 16 % reduction in oxytocin receptor binding in the MPOA. In contrast, social enrichment enhances maternal behaviors and OXTR binding in the MPOA of low-LG offspring by nearly 20 % (F. A. Champagne and Meaney, 2007). The stress-induced changes in OXTR expression may be due to epigenetic modifications, such as methylation of OXTR gene (Perkeybile et al., 2019; Danoff et al., 2021; Hammock, 2015). These results support that stress experienced early in life can shape the oxytocin system and impair parenting behavior in adulthood.

3.3. Mesolimbic dopamine system

Parenting behavior is modulated by the mesolimbic dopamine (DA) system, which signals the positive value of offspring (Pereira and Morrell, 2011; Stolzenberg and Numan, 2011). Dopamine levels in the NAc increase during maternal interactions, and the quality of maternal care correlates with these elevated DA levels (Dai et al., 2022; Shnitko et al., 2017; Hansen, Bergvall, and Nyiredi, 1993; F. A. Champagne et al., 2004). Lesions or inactivation of the VTA or NAc, as well as injecting dopamine antagonists into the NAc, all significantly impaired maternal behavior in rodents (Numan et al., 2009; Hansen et al., 1991; Numan et al., 2005). Optogenetic inhibition of VTA dopamine cells at the onset of pup contact slows down the emergence of maternal care, suggesting that dopamine signals the reward value of pup interaction and reinforces the behavior (Xie et al., 2023).

Stress can impair the development of the mesolimbic dopamine system. For example, Peña et al. found that early life stress induces long-lasting changes in the expression of *Otx2*, a developmental transcription factor implicated in dopamine neuron development (Catherine J. Peña et al., 2017). Similarly, adult female offspring of low-LG rat dams show low expression of the LIM homeobox transcription factor 1 beta (Lmx1b) and brain-derived neurotrophic factor (BDNF), two essential genes for the development and survival of dopaminergic neurons, and correspondingly, the number of tyrosine hydroxylase (TH)-immunoreactive dopamine neurons in the VTA decreases (Catherine Jensen Peña et al., 2014). In adult female rats reared with dams with limited bedding and nesting materials, the number of spontaneously active VTA DA neurons decreases by 75 % compared to control animals reared with dams with abundant resources (Rincón-Cortés and Grace, 2022). In postpartum female rats that experience repeated restraint stress during pregnancy, NAc shell cells show approximately 30 % reduction in dendritic length, branching, and spine density (Haim et al., 2014). Human studies also suggest dysregulation of the mesolimbic dopamine system under stress-induced disease conditions. For example, mothers with postpartum depression (PPD) show reduced brain activation in the mesolimbic system in response to infant-related cues (Moses-Kolko et al., 2011; Post and Leuner, 2019; Duan et al., 2017). Altogether, stress can induce molecular, electrophysiological, and structural changes in the mesolimbic dopamine system, reducing dopamine release to pups, diminishing and rewarding the value of pups, and ultimately impairing parental care behaviors.

3.4. The HPA axis in stress-induced maternal behavior impairment

How does stress alter dopamine, oxytocin, and estrogen systems? The hypothalamic-pituitary-adrenal (HPA) axis is at the core of orchestrating stress responses. In detail, corticotropin-releasing hormone (CRH)-expressing cells in the PVH comprise the first responders of the HPA axis (Antoni, 1986). These cells are activated by various stressors. Upon activation, CRH is released into the hypophysial portal plexus at the median eminence, binding to receptors in the anterior pituitary and triggering the release of adrenocorticotropic hormone (ACTH). ACTH then stimulates the adrenal cortex to synthesize and secrete glucocorticoids, the stress hormone, including cortisol in humans and corticosterone (CORT) in rodents (James P. Herman et al., 2016). Glucocorticoids cause a wide range of bodily changes, such as increasing glucose levels to fuel the muscle and brain and suppressing immune systems (Hostinar et al., 2014; Coutinho and Chapman, 2011; Exton, 1979; Chourpiliadis and Narothama, 2024). Glucocorticoid also provides negative feedback to the PVH CRH cells to prevent over-activation of the HPA axis (J. P. Herman et al., 2012).

In the context of parental behavior, adequate caregiving is essential for the normal development of HPA axis. Parents act as social buffers to shield their offspring from stressors, keeping HPA activity low during early development (Wiedenmayer et al., 2003; Coe et al., 1982; Stanton and Levine, 1985; Shionoya et al., 2007). When the shield fails due to either inadequate care or excessive stress, the HPA axis in the pups becomes hyper-active, reflected by 3–4 folds increase in basal plasma CORT and ACTH levels and exaggerated and prolonged CORT and ACTH responses to subsequent stressors (Avishai-Eliner et al., 2001; Gilles et al., 1996; Suchecki et al., 2008). At the PVH, glucocorticoid receptor expression drastically decreases, indicating reduced negative feedback (Avishai-Eliner et al., 2001; Gilles et al., 1996; Suchecki et al., 2008). PVH CRH levels reportedly decrease in some studies but increase in others, likely depending on the type and duration of the stress (Plotsky et al., 2005; Owens and Nemeroff, 1991; Darlene D Francis and Meaney, 1999; Swanson and Simmons, 1989). These changes persist in adulthood and thus permanently alter the stress responses. Consistent with animal studies, children who experience early life adversity, such as poverty and poor parental care, show increased basal cortisol levels and heightened emotional reactivity (Mehta et al., 2009; Tottenham et al., 2010; Holochwost et al., 2020).

The long-lasting change in the basal CORT level could contribute to the altered function of the dopamine, oxytocin, and estrogen systems. In support, dopamine neurons express abundant glucocorticoid receptors (Härfstrand et al., 1986). Chronic CORT administration in drinking water in adolescent male mice decreases excitability and excitatory synaptic transmission onto VTA dopamine neurons (Peng et al., 2021). CORT treatment also decreases dopamine release in the dorsal striatum in females and impairs the function of dopamine transporter in male mice (Holloway et al., 2023). Behaviorally, the CORT-treated animals show higher anxiety and reduced reward-seeking behaviors (Peng et al., 2021). In addition to CORT, CRH can also reduce VTA dopamine release and motivation to work for food rewards (Wanat et al., 2013). Thus, a basal elevation of stress hormones due to early-life stress or stress during pregnancy and lactation likely dampens the dopamine system function, reducing parental motivation and the rewarding value of pups.

Elevated glucocorticoids can disrupt the estrogen system by interfering with the hypothalamic-pituitary-gonadal (HPG) axis, which regulates estrogen secretion (Breen and Karsch, 2006). In the HPG axis, gonadotropin-releasing hormone (GnRH) from the hypothalamus induces the release of luteinizing hormone (LH) and follicle-stimulating hormone (FSH), which then control the release of estrogen (Albert and Newhouse, 2019). Glucocorticoid receptors are abundantly expressed in hypothalamic areas critical for GnRH neuron regulation (Dufourny and Skinner, 2002; Takumi et al., 2012). Early studies showed that cortisol can inhibit hypothalamic GnRH release. For example, in gonadectomized rhesus monkeys and pigs, chronic glucocorticoid administration suppressed LH and FSH secretion without affecting pituitary responsiveness to GnRH (Breen and Mellon, 2014; Dubey and Plant, 1985; Estienne et al., 1991). In sheep, high cortisol levels suppress estradiol levels and prevent the LH surge during the follicular phase (Macfarlane et al., 2000). Similarly, chronic exposure to stress also impairs estrous cyclicity and reduces GnRH-induced LH synthesis and secretion in diestrus female mice (Breen et al., 2012). In adult male rats, chronic treatment with CORT significantly reduces serum LH levels and decreases hypothalamic GnRH mRNA expression by 35–40 % compared to vehicle-treated animals (Gore et al., 2006). Furthermore, glucocorticoid receptors can displace Esr1 and its co-activator from their DNA binding sites to suppress Esr1-medicated transcription activation (Karmakar et al., 2013). Thus, chronic elevation of CORT could counter-act the effect of estrogen on activating the parental circuits.

The relationship between HPA axis activation and oxytocin system is not straightforward. Some studies support the suppressive role of glucocorticoids on oxytocin. Specifically, glucocorticoid was found to reduce OXT release by inhibiting glutamatergic inputs while enhancing GABAergic inputs to OXT cells (Di et al., 2005; 2003). Dexamethasone, a potent glucocorticoid, has been indicated to reduce the synthesis of OXT mRNA in the PVH and SON in rats (Ruginsk et al., 2009). However, several human studies found CORT level is positively correlated with oxytocin (Tops et al., 2007, 2007a; Taylor et al., 2006; Li et al., 2019). Additionally, adrenalectomized animals show decreased OXTR binding, while corticosterone implants increase OXTR binding in the hippocampus, suggesting that glucocorticoid promotes OXTR expression (Liberzon and Young, 1997; Liberzon et al., 1994).Overall, whether HPA axis activation is responsible for stress-induced oxytocin system deficiency that leads to impaired parental behaviors remains to be investigated in future studies.

Lastly, HPA axis overactivation could also directly impair parental behaviors (Fig. 2). Newborn pups themselves could be a source of stressors. For instance, aversive or distress-related calls from pups induce place aversion (Lecca et al., 2023), and female mice will actively press a lever to turn off pup USV calls (Schiavo et al., 2020). In humans, infant crying can activate the HPA axis, increasing cortisol levels and heart rate (Swain, Kim, and Ho, 2011; Alison S. Fleming et al., 2002; Giardino et al., 2008). As parental behaviors are often prompted by stress signals from infants, e.g., cries (Bornstein et al., 2017), parenting behaviors, in many cases, could be considered a stress-coping process. In rats that experienced chronic stress, such as repeated cold exposure, the animals become more passive in dealing with stressors, reflected in their decreased burying behavior and increased immobility in the shock probe test and their increased latency to feed in a novelty suppressed feeding test (M. K. Roth et al., 2012). Thus, stressed parents may become less responsive to pup stress signals and show reduced active stress coping behaviors, i.e., parental care. Consistent with this hypothesis, in rodents, anxious lactating females display reduced licking and grooming of pups (Mir et al., 2022; Perani and Slattery, 2014).

Thus, chronic stress, especially during critical developmental periods, can cause long-lasting dysregulation of the HPA axis. On the one hand, the heightened stress hormone may negatively affect multiple neurochemical systems that support maternal behaviors. On the other hand, an over-activated HPA axis may compromise active maternal behaviors in response to pup stress signals.

4Concluding remarks

It is important to note that while we review these systems separately, they are heavily interconnected. For instance, the OXTR gene contains estrogen response elements, enabling the Esr1 signaling to modulate OXTR expression (Young et al., 1998; 1997; Rozen et al., 1995). Thus, a decrease in Esr1 expression in the MPOA will not only reduce the effect of estrogen on MPOA properties but also reduce the cell sensitivity to oxytocin (de Kloet et al., 2008). VTA dopamine neurons express both Esr1 and OXTR, and hence stress-induced decrease in Esr1 and OXTR will also change estrogen and oxytocin modulation in dopamine cells, causing reduced dopamine responses to pups in mothers (Peris et al., 2017; Vandegrift et al., 2020). Lastly, oxytocin has been shown to suppress HPA responses to stressors (Pati et al., 2020; Takahashi, 2021). Interestingly, baby cries can induce oxytocin release in new mothers, which may help dampen the stress response induced by the cry normally (Bornstein et al., 2017; Valtcheva et al., 2023). A deficit in the oxytocin system may worsen the HPA activation to pup-related stress signals.

Overall, estrogen, dopamine, oxytocin, and HPA axis function in concert to support the emergence and expression of parental behaviors. While sex hormones prepare the maternal circuit to engage, oxytocin boosts maternal performance, whereas dopamine reinforces the behaviors by signaling the positive valence of pup interaction. CRH neurons, on the other hand, are being kept in check in both mothers and pups under normal conditions. Stress, either occurring in early life or during pregnancy and lactation, can sensitize HPA responses and reduce the efficacy of estrogen, dopamine, and oxytocin systems by influencing both receptor expression and neurochemical release. These changes could lead to decreased maternal circuit responses to pups and exaggerated HPA activation in response to pup stress cues, collectively causing poor parental behaviors (Fig. 2). It is worth noting that although not discussed here, other modulatory systems, e.g., prolactin, can also influence parental behaviors (Stagkourakis et al., 2020) and be affected by stress. Lastly, recent studies have started to reveal a separate circuit mediating negative pup-directed behaviors, specifically infanticide, which antagonizes the maternal circuit (Tsuneoka et al., 2015; Mei et al., 2023). Stress may also compromise parental behaviors by enhancing the responses of infanticidal circuits, a possibility that remains to be investigated in future studies.

Competing interests statement

The authors declare no competing interest.

CRediT authorship contribution statement

Yifan Wang: Investigation, Writing – original draft, Writing – review & editing. **Dayu Lin:** Conceptualization, Funding acquisition, Investigation, Supervision, Writing – review & editing.

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