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How stress can influence brain adaptations to motherhood

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ABSTRACT

Research shows that a woman's brain and body undergo drastic changes to support her transition to parenthood during the perinatal period. The presence of this plasticity suggests that mothers' brains may be changed by their experiences. Exposure to severe stress may disrupt adaptive changes in the maternal brain and further impact the neural circuits of stress regulation and maternal motivation. Emerging literature of human mothers provides evidence that stressful experience, whether from the past or present environment, is associated with altered responses to infant cues in brain circuits that support maternal motivation, emotion regulation, and empathy. Interventions that reduce stress levels in mothers may reverse the negative impact of stress exposure on the maternal brain. Finally, outstanding questions regarding the timing, chronicity, types, and severity of stress exposure, as well as study design to identify the causal impact of stress, and the role of race/ethnicity are discussed.

1. Introduction

Pregnancy and new parenthood bring excitement and joy in developing a close relationship with a new baby. During this period, a mother's brain undergoes dynamic changes to support the important transition to providing care for a child (Brunton and Russell, 2008; Kim, 2016; Lonstein et al., 2015; Numan and Insel, 2003). Brain plasticity is adaptive in terms of supporting this transition to parenthood, but may also increase a woman's neural vulnerability to negative experiences such as exposure to severe stress. Beyond the typical demands associated with parenting, some mothers are exposed to severe stress in their environments such as marital conflict, low income, or unsafe neighborhoods (Belsky and Jaffee, 2006; Crnic and Low, 2002; Kettinger et al., 2000). Mothers also may have been abused or neglected in their childhood, and this adverse early experience can compromise their ability to develop close emotional bonds with their children (Conger et al., 2003; Van Ijzendoorn, 1992). Recent studies suggest that these stressful experiences are associated with variations found in the maternal brain, which further influence parenting and the mother–child relationship (Azhari et al., 2019; Feldman et al., 2019; Kim et al., 2014; Levy et al., 2019b; Olsavsky et al., 2019; Schechter et al., 2012).

Stress that negatively influences mothers' adjustment to parenthood can be categorized into three groups. First, early experiences of child neglect and abuse can compromise mothers' mental health and parenting quality (Conger et al., 2003; Pears and Capaldi, 2001; Simons et al., 1991). This has been suggested as one of the pathways by which stress is transmitted across generations (Buss et al., 2017; Kaufman and Zigler, 1989). Second, environmental stress during the perinatal period such as exposure to violence, marital conflicts, and living in poverty presents significant burdens to mothers in managing their own negative emotions, and providing sensitive care for their children (Crnic and Low, 2002; Goyal et al., 2010; Raver and Leadbeater, 1999). Third, there are relatively acute stressors that are more specifically associated with childbirth and parenting such as a difficult birth and parenting stress. These stressors that are specific to the perinatal experience have also been negatively related to mothers' moods and their relationships with their children (Deater-Deckard, 2008; Simpson and Catling, 2016; Singer et al., 1999).

A better understanding of the neurobiological mechanisms by which stress influences a mother's transition to parenthood can inform current interventions and treatments for new mothers (Kim and Watamura, 2015; Phu et al., 2020). Understanding the maternal brain is important not only for mothers but for the generations that follow because mothers play a critical role in supporting their children's long-term health outcomes and life potentials (Bornstein, 2002). While reviews of non-human animal studies on the role of stress exposure in the maternal brain already exist (for example, please see Hillerer et al., 2012; Klampfl and Bosch, 2019; Slattery and Hillerer, 2016), such a review of studies with human mothers is relatively absent.

The following is a review of the emerging literature on the role of

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stress in human mothers' brain adjustment during the perinatal period. First, I describe the normative changes in the maternal brain during pregnancy and the postpartum period. Second, I review current evidence for the associations between stress exposure and human maternal brain function. The current literature on the maternal brain focuses on childhood adversity, environmental stress, and childbirth- or parenting-specific stress. Third, I discuss potential neurobiological mechanisms by which stress influences brain adaptation to motherhood. Fourth, I review evidence suggesting that interventions to help mothers cope with stress may impact maternal brain responses to their children. Last, I discuss outstanding questions and implications for future studies such as timing, intensity, and types as well as a causality of stress effects.

2. Neural adaptation to motherhood

Since the earliest publication on human mothers' brain responses to infant cues using functional magnetic resonance imaging (fMRI) in 2002 (Lorberbaum et al., 2002), the number of neuroimaging studies of human mothers has rapidly increased. Several different neuroimaging methods including MRI (magnetic resonance imaging), fMRI (functional MRI), PET (positron emission tomography), MEG (magnetoencephalography), EEG (electroencephalogram), and fNIRS (functional near-infrared spectroscopy) have been used to understand the structural and functional basis of the maternal brain. The majority of work done with human mothers to date uses the MRI/fMRI method, but if a study has implemented a different method, it is noted throughout the paper.

2.1. Structural plasticity

Several longitudinal studies have revealed plasticity in brain structure during ~~before and after~~ pregnancy and beyond. In a study of 24 first-time mothers, structural scans were performed twice - first before pregnancy, then at 2–3 months postpartum (Hoekzema et al., 2017). Reduction in grey matter volumes from the first scan to the second was observed in brain regions including the medial prefrontal cortex (PFC) and inferior frontal gyrus (IFG), superior temporal sulcus, precuneus, and fusiform gyrus (Hoekzema et al., 2017). These brain regions are involved in aspects of social cognition such as the theory of mind and perspective taking (Spreng et al., 2009; Van Overwalle, 2009; Van Overwalle and Baetens, 2009). A similar reduction in grey matter volume was observed in the ventral striatum, a key reward and motivation region, among first-time mothers (Carmona et al., 2019). Interestingly, the greater the amount of structural reduction in these brain regions, the greater a mother's functional brain response to pictures of her own infant postnatally (Hoekzema et al., 2017; Hoekzema et al., 2020).

After a child's birth, however, several studies have shown a widespread increase in brain structure in human mothers, at least during the first several months postpartum. In a study of 19 women, structural images of mothers' brains were compared between 2–4 weeks and 12–16 weeks postpartum (Kim et al., 2010a). Between these two time points, several large brain regions involved in maternal motivation exhibited increases in gray matter volume, including the striatum, amygdala, hypothalamus, and the substantia nigra (Kim et al., 2010a). Increases in gray matter volume were also observed in areas involved in sensory and social information processing, including the superior temporal gyrus, thalamus, and pre- and post-central gyri. Finally, the inferior and medial frontal gyri, insula, inferior parietal lobe, precuneus, as well as the anterior cingulate gyrus, regions that are associated with emotion regulation and empathy, also showed gray matter volume increase. Another longitudinal study of a separate cohort of 14 women examined changes in brain structure from the first two days after childbirth to 4–6 weeks postpartum (Luders et al., 2020). A significant increase in grey matter volume was observed in several brain regions that are largely overlapping with the brain regions identified in Kim et al. (2010). These brain regions include the striatum, thalamus, hypothalamus, the pre- and postcentral gyrus, superior parietal lobe, the temporal pole, middle and inferior frontal gyrus, inferior parietal lobe, and insula (Luders et al., 2020). Using the same sample, the researchers estimated changes in the brain age (i.e. anatomical correlates of aging in the brain) between the first few days and 4–6 weeks postpartum (Luders et al., 2018). The results suggest that the brains at 4–6 weeks postpartum were estimated to be 5 years younger than the brains right after the childbirth. Because the significant structural increase was also observed during the same postpartum period in the same sample (Luders et al., 2020), the structural increase is likely to be associated with the decrease in the brain age among mothers (Luders et al., 2018). Together, the findings from these two studies show a structural increase in many maternal brain regions that are involved in parenting, from immediately after childbirth to 3–4 months postpartum.

Another study reported the associations between postpartum months and greater cortical thickness during the first 6 months postpartum in 39 mothers with relatively diverse socioeconomic backgrounds (Kim et al., 2018a). While the two previously-mentioned studies included both first-time and multiparous mothers (those with previous children), this research included only first-time mothers (Kim et al., 2010a; Luders et al., 2020). The study did not use a longitudinal design, but found that later postpartum months were positively associated with cortical thickness in many of the same brain regions reported in Kim et al. (2010) and Luders et al (2020). These included the medial PFC, orbitofrontal gyrus, precentral gyrus, the middle temporal gyri, inferior parietal lobe, and fusiform gyri (Kim et al., 2018a). Furthermore, greater cortical thickness in the superior frontal gyrus including medial PFC and orbitofrontal gyrus was associated with a higher parental self-efficacy score (Kim et al., 2018a), which reflects a mother's belief in her capacity to effectively manage parenting-related tasks (Teti and Gelfand, 1991).

While it is not about brain structure, using an overlapping sample from Kim et al. (2018), a separate study examined the associations between postpartum months and intrinsic functional connectivity (Dufford et al., 2019). Among 47 first-time mothers, later postpartum months were associated with an increase in resting-state functional connectivity of the amygdala with the anterior cingulate cortex, nucleus accumbens, and caudate (Dufford et al., 2019). Greater functional connectivity between the amygdala and anterior cingulate cortex was further associated with more positive parenting behaviors – specifically, appropriate scaffolding during interactions with infants (Dufford et al., 2019). In contrast to the findings observed during pregnancy, these four studies conducted during the postpartum period showed no negative associations between postpartum months and structural size or functional connectivity.

MRI methods used across the studies above do not provide direct evidence of the cellular mechanisms of these structural changes. It has been speculated, however, that structural reduction is driven by drastic hormonal changes during pregnancy, whereas structural increase during the early postpartum period may be driven by both hormonal levels and experience-dependent plasticity. During pregnancy, levels of progesterone and estradiol increase at an unparalleled rate (Brunton and Russell, 2008). There also is an increase in cortisol (or corticosterone in rodents). These kinds of hormonal changes have been associated with structural changes in the brain via reduced cell proliferation, dendritic remodeling, spine density, and astrocytic density (Pawluski et al., 2016). Hoekzema and colleagues have argued that the structural decrease during pregnancy is similar to the structural decrease during puberty that is driven in part by synaptic pruning and remodeling (Carmona et al., 2019; Hoekzema et al., 2017). In support of this speculation, similar patterns of structural decrease have been observed in first-time mothers during pregnancy and adolescent girls during two years of pubertal development (Carmona et al., 2019). As in adolescence, structural reorganization during pregnancy may be part of the normal developmental process of women's brains that supports the efficiency of the brain network (Carmona et al., 2019).

During the postpartum period, estrogen levels drop significantly while oxytocin and prolactin levels increase (Numan, 2020; Rosenblatt,

2002). Rodent studies demonstrated that elevated oxytocin and prolactin levels during the postpartum period have been associated with cell proliferation and increase in synaptic and dendritic densities in some of the brain regions that support maternal behaviors (Larsen and Grattan, 2012; Leuner and Sabihi, 2016; Numan, 2020). During pregnancy and the postpartum period, cell proliferation in the hippocampus is suppressed but spine density increases (Pawluski et al., 2016). Rodent studies have also reported dendritic growth of pyramidal neurons in the medial PFC (Leuner et al., 2010; Leuner and Sabihi, 2016) and increased neurogenesis in the subventricular zone where proliferating cells migrate to the olfactory bulb (Larsen and Grattan, 2010). In addition to the structural changes related to hormones, structural increase may reflect experience-dependent plasticity. The maternal brain receives a rich array of visual, auditory and tactile cues from her infant during the postpartum period, which in turn activates the brain regions that are involved in parenting. Thus, high levels of interaction with the infant may structurally augment these brain areas (Lonstein et al., 2015). Last, while hormonal changes and input from the infant are considered to drive postpartum structural growth, some of the increase in human maternal brain structure may reflect recovery from structural reduction during pregnancy. In a study of 9 women, a reduction in total brain size was observed during pregnancy, but brain size was fully recovered at six weeks postpartum (Oatridge et al., 2002).

It is unclear whether and how long structural growth during the postpartum period may last, and until there is a study that examines the morphological changes from before pregnancy to every few months during the postpartum period, we will not have a full understanding of changes in the maternal brain. It is worth noting that studies focused on the first few months postpartum found significant structural increase (Kim et al., 2010a, Luders et al., 2020, Kim et al., 2018a), while the study by Hoekzema et al. (2017) did not see an increase in brain structure from after pregnancy to a 2-year follow-up scan. Structural reduction in most of the identified brain regions remained after 2 years, but in the hippocampus, grey matter volume returned to the pre-pregnancy levels. One possibility is that after the early postpartum period, brain structure may be reduced again due to a decrease in hormonal levels such as oxytocin, or the reduced amount of time spent with a child as a child becomes older. The hippocampus, in particular, is a region that maintains capability of generating new neurons throughout the lifespan, and non-human animal studies provide evidence that pregnancy and parity have been associated with later increases in cell proliferation in the hippocampus in response to hormone replacement in middle-aged females (Barha and Galea, 2011).

Indeed, the complex relationships between pregnancy, parenthood and brain structure continue across lifespan. Recent studies that examine the associations between parity and brain structure in older women provide insight into the impact of pregnancy, childbirth, and parenting on women's brain structure across the lifespan (Orchard et al., 2020). In a sample of more than 10,000 middle-aged women, the number of childbirths was associated with fewer signs of brain aging, which also reflects greater brain structure for the age at the time of the scan (de Lange et al., 2019). In another large sample-size study of both middle- and older-aged women, parity was again associated with fewer signs of brain aging in specific brain regions including the accumbens, putamen, thalamus, hippocampus, and amygdala – key brain regions involved in maternal motivation (De Lange et al., 2020). In a study of 220 healthy older-aged women, the number of children was associated with intrinsic functional connectivity patterns that were further associated with less age-related cognitive decline, again suggesting that motherhood can protect the brain from the negative impacts of aging (Orchard et al., 2020). Therefore, the evidence together suggests that maternal brain structure waxes and wanes throughout the lifespan, but more prospective studies with a wide time window will be critical to track the longitudinal changes in women's brains due to pregnancy and motherhood.

2.2. Functional plasticity

Functionally, mothers' brains exhibit heightened behavioral and neural sensitivity to infant cues (Barba-Müller et al., 2019; Barrett et al., 2012; Cárdenas et al., 2019; Kim et al., 2016b; Kim and Strathearn, 2016; Rutherford et al., 2018). During pregnancy, EEG rather than fMRI is typically used as a neuroimaging technique. Mothers' greater behavioral attentional bias toward distressed infant faces during late pregnancy is associated with more positive mother-infant relationships after the child's birth (Pearson et al., 2011). Increased neural response to infant faces from the prenatal to postnatal periods is also prospectively associated with stronger emotional bonding between new mothers and their own infants (Dudek et al., 2020). This increased neural sensitivity to infant cues during pregnancy may support increased feelings of emotional attachment toward the fetus during late pregnancy (Levine et al., 2007).

The postpartum period is when new mothers show an enhanced neural function to respond to their own infant's cues, which are further associated with sensitive parenting (Atzil et al., 2011; Elmadih et al., 2016; Kim et al., 2011a; Kim et al., 2015b; Musser et al., 2012; Wan et al., 2014). The following studies have used the fMRI neuroimaging technique. Several meta-analyses show that, across many studies, infant cues activate brain regions that comprise the mesocorticolimbic dopaminergic reward/maternal motivation circuit including the midbrain (hypothalamus, ventral tegmental area, nucleus accumbens, and substantia nigra) and the medial PFC, as well as the salience network including the amygdala, anterior insula, and the anterior cingulate cortex (Paul et al., 2019; Rigo et al., 2019b; Rocchetti et al., 2014). The brain networks are also critically involved in maternal motivation and parenting behaviors in other female mammals (Numan, 2012; Numan, 2020), suggesting they may be the most evolutionarily conserved to support a basis of maternal behavior.

While maternal motivation is critical, human parenting is a complex task, thus, also requires higher-order social and cognitive function (Corter and Fleming, 1990; Crandall et al., 2015; Lonstein et al., 2015). Therefore, across studies with human mothers, we see evidence that a wide network of cortical brain regions is activated by infant cues. New mothers exhibit enhanced neural activation in the emotion regulation and cognitive control circuit including the anterior cingulate cortex, and the medial and lateral PFC (Barrett and Fleming, 2011; Kim et al., 2011b; Rutherford et al., 2015). Effective emotion regulation especially in the context of distressful interactions with a child is important for sensitive parenting (Hajal and Paley, 2020; Morelen et al., 2016; Shaffer and Obradović, 2017). PFC regions have strong functional connectivity to the amygdala, with the PFC acting to downregulate amygdala activation in the case of threats and negative stimuli (Kalisch, 2009). This downregulation of the amygdala helps to reduce anxiety and negative emotions (Etkin et al., 2015; Ochsner et al., 2012). In addition to emotion regulation, PFC regions are involved in cognitive control and executive function (Braun et al., 2015; Braver, 2012; Kouneiher et al., 2009). Thus, PFC activation among mothers is considered to also support a wide range of planning and decision making for appropriate responses to various infant cues (Krawczyk, 2002).

In response to infant cues, new mothers exhibit increased neural activation in the sensorimotor areas and auditory and visual social and emotional information circuit which includes the precentral gyri, supplementary motor area, superior temporal gyrus, fusiform gyrus, occipital lobe, and cerebellum (Bornstein et al., 2017; Witteman et al., 2019). Activation of this circuit supports processing and sending sensory information to other brain networks as well as visually mapping the motor responses to infants (Rayson et al., 2017). Increased connectivity within and between the brain regions involved in motor-sensory-auditory networks has been observed in mothers over the postpartum period (Rutherford et al., 2019).

Empathy is an important component of human parenting. There are two aspects of empathy: (1) emotional empathy refers to the ability to

share feelings that others feel and (2) cognitive empathy refers to the ability to understand what others feel and think. Cognitive empathy is characterized as social cognition, theory of mind, mentalizing, or perspective-taking (Shamay-Tsoory et al., 2009). Emotional empathy regions primarily include IFG, anterior insula, and ACC whereas cognitive empathy regions include the temporoparietal junction, the superior temporal sulcus, medial PFC including ventromedial PFC and dorsomedial PFC, frontopolar cortex and precuneus (Shamay-Tsoory et al., 2009; Yu and Chou, 2018). Both emotional and cognitive empathy is critically involved in sensitive caregiving, and increased activation in both networks is consistently observed in response to infant cues (Abraham et al., 2018; Hipwell et al., 2015; Ho et al., 2014).

Generally speaking, increased activation and connectivity in and between the brain regions listed above are considered to indicate increased neural sensitivity to infant cues, and to support sensitive parenting behaviors (Abraham et al., 2016; Elmadih et al., 2016; Kim et al., 2015b; Wan et al., 2014). However, that assumption varies for certain brain regions, particularly the amygdala and insula. The amygdala is involved in both stress reactivity and reward processing (Feder et al., 2009). Therefore, depending on the context and its connectivity to other brain regions, increased amygdala response to infant cues can be associated with sensitive parenting but can also be associated with stress reactivity and intrusive parenting (Atzil et al., 2011; Kim et al., 2017a). The anterior insula is a key region involved in emotional empathy and a mother's ability to share the experience of her child's distress. Therefore, while too little activation in this region can indicate a lack of emotional empathy, too much activation can lead to too-high levels of distress in a mother, which can in turn compromise the mother's ability to respond to her child's distress (Li et al., 2018; Musser et al., 2012).

Neuroimaging studies with human mothers typically use a paradigm that presents either visual cues, primarily an infant's emotional faces, or auditory cues, primarily an infant's cry sounds. The brain areas involved in processing sensory information such as thalamus and striatum and the empathy network such as insula and IFG are commonly activated by both auditory and visual infant cues. However, findings of several recent meta-analyses suggest differences in maternal brain responses to visual vs. auditory infant cues. One of the most noticeable differences is that visual cues more robustly activate reward processing regions such as the hypothalamus, ventral tegmental area, nucleus accumbens, and substantia nigra (Rigo et al., 2019a; Rocchetti et al., 2014). Activation in these maternal motivation regions is particularly strong toward visual cues from one's own infant compared to a control infant (Paul et al., 2019; Rocchetti et al., 2014). In contrast, activation in the reward processing regions is not consistently observed in response to infant cry sounds. The most likely reason for this difference is that compared to visual cues, auditory cues elicit fewer differences in response to own vs. control child stimuli (Witteman et al., 2019). This may be due to the likelihood that it is easier to recognize one's own visual infant cues compared to auditory cues. Because infant cry sounds are likely to convey more urgency than visual cues (Joosen et al., 2013), it may also be adaptive that the maternal brain has elevated sensitivity to infant cry sounds, regardless of the identity of the infant.

Another reason why infant cry sounds do not elicit consistently strong responses in the brain's reward areas can be that cry sounds are distressing, whereas visual cues can include both positive and distressing stimuli, such as smiling and crying faces. While visual child cues more robustly activate the reward and motivation regions in the brain, infant cry sounds more robustly activate brain regions involved in processing emotional auditory stimuli such as superior temporal gyrus and somatosensory and motor areas such as supplementary motor area and precentral gyrus (Rigo et al., 2019a; Witteman et al., 2019). In a study that included mothers from three different countries (US, Italy, China), increased responses to infant cry sounds in regions across several brain networks including the supplementary motor area and superior temporal gyrus were found among mothers across cultures (Bornstein et al., 2017). Given the urgency that can be elicited by infant cry sounds, these sounds may strongly engage the brain circuits involved in mentalizing how to care for the distressed infant, which can lead to increased activation in the brain regions involved in planning for complex movements (Bornstein et al., 2017; Witteman et al., 2019).

3. How stress exposure is associated with brain adjustment to motherhood

As mentioned earlier, there are three categories of stressful experience that are linked to maternal brain outcomes: first, stress experienced in a mother's own childhood which can have a long-term impact on her brain, second, psychosocial and environmental stress that are experienced during the perinatal period, and third, stressors specific to the perinatal period that are related to childbirth or parenting. Below I discuss existing studies that examine the question of how these stressful experiences are linked to mothers' brain responses to infant cues. Table 1 summarizes the findings of the studies reviewed in this section.

3.1. Childhood adversity

New mothers' parenting behaviors have been related to the trauma they experienced in their own childhoods (Belsky et al., 2005; van IJzendoorn et al., 1995). In both rodents and nonhuman primates, low-quality maternal care leads to reduced nurturing in the next generation (Maestripieri, 2005; Roth et al., 2009). In human mothers, childhood adversity has been assessed primarily based on mothers' retrospective reports of childhood experience. A mother's insecure attachment style that is assessed using the Adult Attachment Interview (George et al., 1996) has also been considered to reflect negative childhood experience in close social relationships (Kim et al., 2014; Lyons-Ruth et al., 1999) and has been associated with a less nurturing parenting style for her own child (Iyengar et al., 2014; Van Ijzendoorn, 1995).

Childhood adversity may lead to long-term structural changes in brain regions that are involved in empathy and social information processing. In 24 mothers with childhood maltreatment and 28 without that history, childhood maltreatment was associated with less behavioral maternal sensitivity while interacting with their children at ages 7–8 (Mielke et al., 2016). In mothers with childhood maltreatment, maternal sensitivity was further associated with greater grey matter volume in the superior temporal sulcus and temporal pole, regions involved in cognitive empathy. On the other hand, in the control mothers, maternal sensitivity was associated with greater grey matter volume in the anterior insula, a region involved in emotional empathy (Mielke et al., 2016). While emotional empathy is an important aspect of mothers' relationships with children (Abraham et al., 2014), the findings suggest that mothers with childhood adversity may rely on cognitive empathy rather than emotional empathy in responding to their children. In another study of 22 neglectful and 22 control mothers of children at age 2, mothers who were neglected in childhood and were neglectful of their own daughters had more disrupted interior fronto-temporo-occipital structural connectivity (Rodrigo et al., 2016). This connectivity is important for processing faces, therefore aberrant activity for face processing may contribute to neglectful parenting (Inmaculada et al., 2019).

Childhood adversity has also been associated with mothers' altered functional responses to infant cues. In one study, 42 first-time mothers were asked about unresolved attachment-related trauma from their childhood (Kim et al., 2014). Mothers who reported unresolved trauma exhibited a more blunted amygdala response to their own infant's distress images compared to happy images at 11 months postpartum. Mothers who did not report trauma exhibited the reverse of this brain response pattern (Kim et al., 2014). In a study of 45 first-time mothers at 4 months postpartum, those who reported experiencing childhood neglect and maltreatment exhibited blunted amygdala response to infant images across emotionality (sad, happy and neutral faces) (Olsavsky et al., 2019). The discrepancies between these two studies may reflect

Table 1
Brain networks and regions that support parenting in human mothers and changes in these brain networks that are associated with different types of stress exposure. The arrows indicate a direction of changes such as increased/decreased brain responses to infant cues or increased/decreased brain structure or brain-to-brain synchrony with own child. PFC = prefrontal cortex.

Brain Network	Brain Regions	Childhood Adversity	Environmental Stress	Childbirth/Parenting Stress
Maternal Motivation/ Reward	hypothalamus, ventral tegmental area, nucleus accumbens, substantia nigra, striatum, medial PFC, orbitofrontal cortex	↓ (positive and negative cues)		↓ (parenting stress - positive and negative cues), ↓ (maternal cortisol - negative cues),
Salience	amygdala, anterior insula, anterior cingulate cortex	↓ (positive and negative cues)	↓ (positive cues), ↑ (negative cues)	
Stress Regulation	hippocampus	↑ (negative cues)		
Emotional and Cognitive Control	medial and lateral PFC, anterior cingulate cortex	↓ (negative cues)	↓ (negative cues)	↓ (brain-to-brain synchrony), ↓ (maternal cortisol - negative cues),
Sensorimotor	thalamus, precentral gyrus, supplementary motor area, superior temporal gyrus, fusiform gyrus, occipital lobe, cerebellum	↑ (negative cues), ↑ (structural size), ↓ (structural connectivity)	↓ (negative cues)	↑ (childbirth - positive and negative cues)
Emotional Empathy	inferior frontal gyrus, anterior insula, anterior cingulate cortex	↑ (negative cues)	↓ (negative cues)	↑ (childbirth - positive and negative cues), ↓ (maternal cortisol - negative cues),
Cognitive Empathy	superior temporal sulcus, medial PFC, frontopolar cortex, precuneus	↑ (structural size)		↓ (parenting stress - negative cues)

that the latter study did not include images of the mother's own baby, thus the finding may reflect blunted amygdala responses to infant cues more generally. Mothers' insecure attachment style has also been associated with reduced nucleus accumbens response to positive images of one's own infant (Strathearn et al., 2009). These dampened neural responses in the amygdala and nucleus accumbens regions may reflect disrupted brain function in salience and reward processing.

In addition to the blunted amygdala and nucleus accumbens responses to infant images, first-time mothers who reported their own mothers to be less warm and caring have exhibited reduced activation in response to infant cry sounds in regions involved in the regulation of emotions and social information processing, including the superior frontal gyrus, the orbitofrontal gyrus, the superior and middle temporal gyri, and the fusiform gyrus (Kim et al., 2010b). However, in contrast to the reduced responses to infant cry sounds in the cortical regions, the hippocampus showed increased activation among the mothers who reported their own mothers to be less caring (Kim et al., 2010b). The hippocampus regulates HPA axis activity and the stress response (McEwen, 2001), and this finding may reflect higher distress in response to infant cry sounds among these mothers. Increased neural responses to infants' distress cues have been found in other studies with mothers who report negative childhood experiences. In a study of 22 first-time mothers of 18-months-old infants, mothers who indicated emotional neglect in their own childhoods exhibited increased insula and anterior cingulate cortex responses to cry sounds from their own infant (Wright et al., 2016). The insula is activated by distress in others and is involved in both personal and empathetic distress (Zaki et al., 2012). Thus, negative childhood experiences may be related to a mother's increased distress in response to her infant's distressed cues.

Poverty in childhood increases the likelihood of exposure to adversities such as violence, harsh parenting, and separations from family members (Bradley and Corwyn, 2002; Conger and Donnellan, 2007; Evans, 2004). In a small sample of young adult women who did not have children, childhood poverty was associated with increased brain response to baby cry sounds in the posterior insula, striatum, hippocampus and fusiform gyrus compared to young adult women who were not exposed to poverty in childhood (Kim et al., 2015a). The increased brain response was further correlated with more negative emotional responses to infant cry sounds such as being annoyed (Kim et al., 2015a). In another study of 23 women without children, women with insecure attachment exhibited increased activation in several brain regions including the hippocampus and lateral IFG in response to infant images (Lenzi et al., 2013). On the other hand, women with secure attachment exhibited activation in brain regions associated with reward processing including medial PFC and striatum, and amygdala (Lenzi et al., 2013). Together, these findings suggest that overall childhood adversity is linked to increased brain responses to infant distress in the regions that regulate stress responses, but dampened brain responses to infants' positive cues in the regions that detect salient and rewarding information. These brain response patterns may negatively influence a mother's ability to manage her own negative emotions in response to her distressed infant, and sensitively respond to her infant's needs.

Similar neural response patterns have been observed among mothers with older children. In a study of 22 mothers with a history of physical and/or sexual abuse and 25 control mothers with children ages 7 to 11, participants watched video clips of conflictual vs. pleasant interactions with their own child vs. an unfamiliar child (Neukel et al., 2018). While viewing conflictual interactions with their own child, mothers with a history of childhood abuse showed greater activation in several regions including the hippocampus, insula, supplementary motor area, and middle frontal gyrus, but no brain region responded more strongly to pleasant interactions. On the other hand, mothers without a history of childhood abuse showed greater activation in the same brain regions in response to pleasant interactions with their own child.

In sum, the findings of these studies suggest a potential neural pathway by which adverse experience in childhood influences later parenting behaviors and may be transmitted intergenerationally (Table 1). This understanding can provide insight into intervention efforts for mothers who experienced childhood adversities by supporting them to reduce distressing feelings in response to difficult interactions with their children and to enhance positive feelings in parenting.

3.2. Environmental stress

Environmental stress such as poverty, marital conflicts, violence, and racism during pregnancy, the postpartum period, and beyond are significant risk factors for maternal mental health, as well as negative parenting (Abdou et al., 2010; Barnett, 2008; Crnic and Low, 2002; Raver and Leadbeater, 1999). While mothers who are exposed to these environmental risk factors are frequently targeted for interventions to reduce stress and improve parenting skills (Beeber et al., 2008; Miller et al., 2014; Morris et al., 2017; Olds et al., 2007), understanding of the mechanisms by which stress influences parenting quality remains relatively limited.

One of the environmental stressors that has been examined in relation to the maternal brain is poverty. Poverty environments are characterized as chaotic and unpredictable and are more likely to be accompanied by stressful conditions for pregnant women and new mothers (Braveman et al., 2010; Fell et al., 2004; Goyal et al., 2010; Rich-Edwards et al., 2006; Wells and Harris, 2007). In a study of 39 first-

time mothers in the first 6 months postpartum, low income was associated with differential amygdala sensitivity to infant emotional cues (Kim et al., 2017a). Mothers experiencing low income exhibited dampened amygdala response to happy infant cues but enhanced amygdala response to distressed infant cues. This enhanced amygdala response to distressed infant cues was further associated with more intrusive behaviors observed during mother-infant interactions at home (Kim et al., 2017a). The amygdala is involved in detecting salient social cues, so the increased amygdala response, particularly to happy infant cues, is considered important for sensitive parenting. However, in the context of a high stress environment, neural hypervigilance to distress cues among low income mothers may be adaptive for protecting infants from potential threats. Because intrusive parenting behaviors tend to be associated with more negative infant outcomes including risks for mood disorders (Feldman et al., 2009; Smith and Pederson, 1988), long-term follow-up work is needed to examine whether the neural responses to negative infant faces and intrusive parenting behaviors among low-income mothers can be prospectively linked to infants' developmental outcomes at a later age.

In an overlapping sample with the previous study (Kim et al., 2016a), low income was associated with decreased neural responses to infant cry sounds in the medial and lateral PFC (Kim et al., 2016a). Supporting the hypothesis that psychological stress associated with the experience of living in poverty can contribute to differences in neural response, the associations between income and lateral PFC response to infant cry sounds were mediated by increased levels of perceived stress reported by new mothers (Kim et al., 2016a). Among many other functions, the lateral PFC is involved in emotional and cognitive controls, thus reduced PFC activation in response to emotional cues can be associated with difficulties in managing mothers' own emotions, as similar neural patterns are observed in other populations with mood dysregulation (Kim et al., 2016a). In a follow-up study of 53 first-time mothers, a range of socioeconomic, physical environmental, and psychosocial stressors e.g. low income, financial stress, substandard housing, crowding at home, marital dissatisfaction, and violence were assessed (Kim et al., 2020). A higher number of stressors was associated with dampened brain responses to infant cry sounds in the insula, IFG, and superior temporal gyrus. Thus, there is evidence that exposure to poverty and other environmental stress during the postpartum period is associated with dampened brain responses to negative infant cues in brain regions that are involved in empathy and emotion regulation, which can negatively influence mothers' ability to respond to their infants appropriately. Indeed, the reduced brain response to infant cry sounds was further associated with lower maternal sensitivity in mothers (Kim et al., 2020).

Mothers who experience other severely stressful experiences have been shown to exhibit patterns of brain activation similar to those who experience poverty. Mothers exhibited greater activation in limbic regions including the amygdala and reduced brain activation in the PFC (the superior frontal gyrus) while seeing their own children at ages 12–42 months distressed during separation (Schechter et al., 2012). The perceived stress levels in response to separation from their children was further associated with reduced PFC activation (Schechter et al., 2012). In another study using MEG and including mothers with older children, mothers who were living in a war zone exhibited a lack of the brain response associated with empathy to other's pain (Levy et al., 2019b). While the study did not include child cues, the reduced brain response to others' pain was further associated with less sensitivity in mothers' interactions with their adolescent children (Levy et al., 2019b).

Taken together, these findings provide evidence for the potential neural mechanisms by which exposure to severe stress can negatively influence parenting quality (Table 1). The findings provide support for the prevention and intervention approaches that target mothers who are exposed to severe stress. Moreover, they suggest that stress exposure may impact maternal brain activations that are important for empathy and emotion regulation, thus mothers may need support for understanding their children's feelings and thoughts as well as help to address difficulties in regulating their own negative emotions, particularly in response to negative child cues.

3.3. Stress in the context of child-birth and parenting

Preterm birth and associated hospitalization of preterm infants can be a traumatic experience for mothers (Hynan et al., 2013). Having a preterm infant is a risk factor for maternal depressive symptoms, higher levels of parenting stress, and more intrusive parenting behaviors (Bilgin and Wolke, 2015; Chertok et al., 2014; Greene et al., 2015; Neri et al., 2015). In a study at 3 months of infant age (corrected for gestational age for preterm infants), 10 first-time mothers of preterm infants and 11 first-time mothers of full-term infants viewed happy, neutral, and distressed images of their own and control infants (Montirosso et al., 2017). Preterm infant mothers showed greater activation in brain regions including the IFG in response to both distressed and happy faces, and the insula in response to their own infant's happy faces compared to full-term infant mothers. The increased brain responses to positive infant faces among preterm infant mothers appear to be opposite from the findings associated with other types of stress. One interpretation is that the greater neural responses in preterm mothers indicate the mother's enhanced attention and effort to understand her infant's emotional cues (Montirosso et al., 2017). Elevated neural activation may be necessary, as studies suggest that preterm infants are less responsive to social cues, which provides more challenges for mothers to read their cues appropriately (Bozzette, 2007).

Another related interpretation is that preterm infants' cry sounds may have atypical characteristics that require additional neural processing (Friedman et al., 1982). Infant cues that are more aversive than the normal range or are difficult to interpret can be associated with elevated brain responses, which reflect increased mental efforts to understand the cues. For example, during their first year, autistic children have atypical cry sounds that are perceived to be more aversive by both parents and non-parents (Venuti et al., 2012). Compared to typically developing infants' cry sounds, autistic infants' cry sounds elicit greater brain responses in the superior temporal gyrus, insula, IFG, and supramarginal gyrus, regions that are involved in social and emotional information processing (Venuti et al., 2012). Thus, preterm infants may require a similarly heightened level of information processing and attention in the brains of their mothers.

In addition to preterm birth, other difficult birth experiences and related trauma (McDonald et al., 2011; Molloy et al., 2020), as well as difficult infant temperament (Mills-Koonce et al., 2007; Oddi et al., 2013), can negatively influence a mother's mental health and parenting. Exploration of the impact of these factors on the maternal brain remains very limited. In one pilot study of 8 mothers, higher amygdala activation during recall of childbirth-related trauma was associated with less positive parenting behaviors (Berman et al., 2020). Neural and emotional reactivity to trauma may increase mothers' difficulties in developing positive bonds with their infants.

Parenting stress refers to physiological and psychological reactions to the demands, stress, and challenges arising from caring for a child (Deater-Deckard, 2008). While a certain level of parenting stress is considered normal, high levels suggest difficulties in adjusting to parenthood, and have been associated with negative maternal outcomes such as maternal depression and harsh parenting styles (Deater-Deckard, 2008; Rutherford and Mayes, 2019). Parenting stress has been associated with reduced orbitofrontal gyrus activation in first-time mothers watching videos of their 2–3 year-old child's feeding behavior (Noriuchi et al., 2019). Parenting stress was also associated with reduced amygdala responses to positive facial expressions from one's own infant vs. a control infant at 3 months postpartum (Barrett et al., 2012). Thus, parenting stress was associated with dampened responses to one's own infant in the brain regions that are part of the reward and motivation circuits.

Parenting stress can further impact neural synchrony between

mothers and children. Brain-to-brain synchrony is a measure of the temporal correlation between brain activations in two or more people and is considered to reflect the attunement of the emotional, social, and physiological states of another person (Hasson et al., 2012; Reindl et al., 2018). Thus, brain-to-brain synchrony has been proposed as an underlying neural mechanism for behavioral synchrony between mothers and their children, which plays an important role in a child's positive development (Bell, 2020; Reindl et al., 2018). A recent study assessed brain-to-brain synchrony between mothers and their children at ages 3–4 and its association with parenting stress using fNIRS (Azhari et al., 2019). A total of 31 mother–child dyads viewed movie clips together while their PFC activations were recorded. Higher parenting stress reported by mothers was associated with reduced brain-to-brain synchrony between mothers and children in brain regions including the IFG and dorsolateral PFC. The results indicate that mothers who report high levels of parentings stress exhibit brain activation that is less synchronized with their children, potentially due to their difficulties in regulating their own emotions and less attunement to their children's emotions during interactions (Azhari et al., 2019).

Most neuroimaging studies with human mothers have assessed stress based on maternal report. However, one study directly measured HPA axis reactivity to a stressful situation and its association with maternal brain responses to infants (Laurent et al., 2011). Cortisol reactivity to a stressful situation in the context of parenting (i.e. the Strange Situation that includes separation and reunion between mothers and children) was assessed among 22 first-time mothers of infants ages 15–18 months (Laurent et al., 2011). Greater cortisol reactivity was associated with reduced responses to a mother's own infant's cry sounds in the brain regions that are involved in maternal motivation, empathy, and emotion regulation including the thalamus, striatum, orbitofrontal gyrus, medial PFC, anterior cingulate cortex and insula.

In sum, studies that examined the impact of stressful experience on maternal brain activity suggest different patterns of brain responses to children depending on the type of stress (Table 1). For distress and difficulties that are caused by the nature of infant cues, mothers exhibited increased brain responses that reflect enhanced efforts to process and understand those cues (Montirosso et al., 2017). However, stress that mothers feel in the context of parenting was generally associated with dampened brain responses to both their infants' positive and negative cues (Barrett et al., 2012; Noriuchi et al., 2019). Furthermore, a mother's physical stress regulation as assessed by cortisol reactivity to a stressful situation was associated with reduced brain responses to her own infant's cry (Laurent et al., 2011). The findings highlight the importance of supporting mothers who have infants with developmental delays or difficult temperaments. Moreover, while parenting is stressful from time to time, an atypical range of parenting stress and physiological stress reactivity should receive more attention, as they may limit parenting capacity via changes in the brain responses to infant cues.

4. Neurobiological mechanisms by which stress exposure impacts maternal brain adaptation

Due to the correlational nature of human mother studies, understanding of the neurobiological mechanisms by which stress impacts the maternal brain is primarily based on non-human animal studies. Non-human animal studies have investigated what happens in the maternal brain when a mother experiences severe stress during pregnancy and/or the postpartum period. Compared to acute stress exposure, chronic and repeated exposure, particularly multiple types, and unpredictable exposure to stress more reliably elicit anxious or depressive-like behaviors in rodents (Antoniuk et al., 2019; Gururajan et al., 2019) and impair maternal neural adaptation and behaviors (Hillerer et al., 2011; Slattery and Hillerer, 2016). Paradigms that use social stress such as social defeat, the resident-intruder paradigm (Klampfl et al., 2018), social instability (rotating periods of social isolation and overcrowding), and frequent housing mobility (Brunton, 2013; Gururajan et al., 2019; Haim et al., 2014; Hillerer et al., 2011) have particularly significant impacts on maternal behaviors. Providing limited materials to build a nest, similar to material deprivation or poverty in humans, has also led to impaired maternal behaviors in rodents (Gallo et al., 2019; Moussaoui et al., 2016; Perry et al., 2018) and further impacts on offspring outcomes (Walker et al., 2017). To study the impact of early adversity, variations in maternal care such as low vs. high licking and grooming behaviors, maternal deprivation, and prolonged maternal separation (Champagne et al., 2003; Gonzalez and Fleming, 2002; Lovic et al., 2001) have been used in rodent models.

The research using these paradigms provides robust evidence for the causal relationships between stress exposure, the maternal brain, and suboptimal parenting behaviors (Bosch et al., 2007; Hillerer et al., 2012; Klampfl and Bosch, 2019; Slattery and Hillerer, 2016; Zoubovsky et al., 2020). Stress impacts maternal brain adaptation in multiple ways. Below I review some of the potential mechanisms by which stress – first, stress exposure during the perinatal period, and second, childhood stress - impact the maternal brain.

4.1. Impact of stress on the neurobiological system of emotion regulation

Stress exposure at any point in the lifespan impacts brain structure and function in both non-human animals and humans. Brain regions that are particularly important in the context of stress exposure are the amygdala, hippocampus, and prefrontal cortex (McEwen et al., 2016). Among many functions that the regions have, these brain regions are involved in the regulation of the hypothalamic–pituitaryadrenal (HPA) axis. When an individual perceives actual or anticipated threats, the amygdala signals the paraventricular nucleus of the hypothalamus which then activates the HPA axis, which then triggers corticotropin-releasing factor (CRF), adrenocorticotropic hormone (ACTH) and glucocorticoids (Rodrigues et al., 2009). While the amygdala rapidly activates the HPA axis, the hippocampus plays a regulatory role by providing negative feedback control and decreasing glucocorticoid secretion (Jacobson and Sapolsky, 1991; McEwen, 2001). This in turn leads to recovery of the HPA axis activation to baseline. PFC activation has an effect of suppressing amygdala activation, which in turn can inhibit the HPA axis response (Kalisch et al., 2006; Radley et al., 2006; Sullivan and Gratton, 2002). However, severe and chronic exposure to stress such as the environmental stress reviewed earlier impairs the microstructure, function, and connectivity of these brain regions due to elevated glucocorticoid levels, suppressed neuronal proliferation, and reduced dendritic spine density (Davidson and McEwen, 2012; McEwen, 2001; Tottenham and Sheridan, 2010). The alteration in these brain regions can lead to difficulties in regulating negative emotions such as elevated levels of anxiety and depressive mood (Gianaros et al., 2008; Gianaros et al., 2011; Lupien et al., 2009; Taylor et al., 2006).

Pregnancy and the postpartum period are unique in that there are drastic changes in how the HPA axis is regulated to support pregnancy and parenting (Brunton and Russell, 2008; Brunton et al., 2008). In human mothers, placental corticotropin-releasing hormone (CRH) and cortisol levels increase drastically during pregnancy as the high levels of cortisol concentration support normal fetal growth and the maintenance of pregnancy (Almanza-Sepulveda et al., 2020; Dickens and Pawluski, 2018). Despite the higher cortisol levels, pregnancy and lactation have been linked to highly dampened HPA axis reactivity to acute stressors in rodents and humans (Altemus et al., 2001; Klampfl and Bosch, 2019; Neumann et al., 1998; Schulte et al., 1990). The suppression of HPA reactivity to stress is considered to be an adaptive mechanism to protect the fetus from adverse programming by maternal stress and increased corticosterone levels (Brunton and Russell, 2008; Hillerer et al., 2014; Lonstein et al., 2014).

However, in the context of severe stress, this adaptive suppression of cortisol reactivity may not occur. As a result, women may have high levels of cortisol in their system which may present a risk for both mothers themselves and their fetus/infant development (Seth et al.,

2016). For example, stress exposure leads to HPA axis dysregulation, indicated by a high concentration of corticosterone and upregulation in the CRF system in the maternal brain of rodents (Bosch et al., 2007; Herzog et al., 2009; Hillerer et al., 2012; Hillerer et al., 2011). HPA axis dysregulation leads to impaired maternal behaviors such as decreased time spent on nursing and more time away from the nest (Brummelte and Galea, 2010). In primates, high cortisol levels lead to neglectful maternal behaviors (Bahr et al., 1998; Klampfl and Bosch, 2019). The high concentration of corticosterone leads to morphological and functional alterations in the brain such as decreased dendritic remodeling in the hippocampus (Pawluski et al., 2016) and reduced dendritic spine density in the medial PFC in the maternal brain (Leuner et al., 2014; Sabihi et al., 2014).

As part of normative changes in the maternal brain, oxytocin and prolactin levels increase during late pregnancy and the postpartum period (Brunton and Meddle, 2011; Levine et al., 2007; Numan, 2020). The oxytocin and prolactin system contribute to reducing the HPA axis activity. Both oxytocin and prolactin have an anxiolytic effect and are involved in the blunted reactivity to acute stressors in the HPA axis as well as in the brain such as the amygdala (Bosch and Neumann, 2012; Kirsch et al., 2005; Slattery and Neumann, 2008; Torner and Neumann, 2002; Torner et al., 2001). Thus, while the oxytocin and prolactin systems are important to protect the maternal brain from the negative impact of stress, exposure to chronic stress can disrupt the adaptive changes in the oxytocin and prolactin systems and reduces the anxiolytic effect of these hormones in the brain (Hillerer et al., 2011; Torner, 2016). Furthermore, another system that chronic stress can influence is the central serotonergic system which is involved in mood regulation (Canli and Lesch, 2007). Pregnancy and postpartum stress impact the maternal central serotonin system, such as increased serotonin and reduced serotonin 1A receptor expressions in the PFC and hippocampus (Lonstein, 2019; Pawluski et al., 2019).

The neurobiological mechanisms by which stress exposure can impact the brain and neuroendocrine systems that regulate stress responsiveness provide insight into how mood dysregulation such as high depressive mood or anxiety symptoms can increase risks for suboptimal parenting quality (Nguyen et al., 2019; O'Hara and McCabe, 2013; Pawluski et al., 2017). The perinatal period is when risks for maternal depression and anxiety disorders significantly increase (Goyal et al., 2010; Segre et al., 2007). Increased symptoms of maternal anxiety and depression are closely linked to the experience of stress including childhood and current adversity and parenting stress (Goyal et al., 2010; Guintivano et al., 2017; Leach et al., 2017; Thomason et al., 2014). Depression and anxiety disorders as well as increased symptoms during the postpartum period have been further associated with altered neural responses to infant cues (Bjertrup et al., 2019; Pawluski et al., 2017). Although there are exceptions (Wonch et al., 2015), depressed mothers exhibit dampened PFC activity in response to cry sounds from their own infant (Laurent and Ablow, 2011) and reduced orbitofrontal cortex and precuneus in response to infant images (Lenzi et al., 2016), and mothers with higher depressive symptoms also show reduced connectivity between the amygdala and nucleus accumbens in response to infant cry sounds (Ho and Swain, 2017). Anxiety symptoms have also been associated with reduced amygdala responses to images of one's own infant (Barrett et al., 2012). These neural patterns overlap with the overall neural patterns associated with stress exposure reviewed in this paper. Thus, negative maternal mood and anxiety that are impacted by disrupted brain adaptation during the perinatal period may mediate the link between stress exposure and parenting behaviors. However, in human mothers, little is known about the links between stress exposure and brain responses to infant cues among mothers with mood or anxiety disorders, thus future work is needed.

In sum, during pregnancy and the postpartum period, the maternal brain has an adaptive process of HPA axis hyporeactivity to stress. However, exposure to severe stress can disrupt this adaptive process and lead to HPA axis dysregulation and morphological and functional impairment in the brain regions that are involved in stress and emotion regulation including the amygdala, hippocampus, and PFC. Changes in the HPA axis system and brain system due to stress exposure can lead to heightened risks for mood dysregulation such as depression and anxiety, and further impaired maternal behaviors.

4.2. Impact of stress on the neurobiological system of maternal motivation

The expression of oxytocin receptors is another mechanism by which stress impacts the maternal brain. Under normal circumstances, oxytocin receptor expression is upregulated in the midbrain and striatum of pregnant dams (Numan, 2012; Numan, 2020). As discussed earlier, the midbrain and striatum are parts of the mesocorticolimbic dopamine pathway that are critically involved in caregiving motivation in non-human animal and human mothers (Ferris et al., 2005; Numan and Insel, 2003; Strathearn et al., 2008; Swain et al., 2011). In dams, upregulated oxytocin receptor expression sensitizes these brain regions to support the onset of maternal behaviors as soon as pups arrive. (Bell et al., 2014; Pedersen et al., 1994; Russell and Leng, 1998). After parturition, pup cues strongly activate the oxytocin system in the brain, which leads to increased neural sensitivity to the cues. However, prenatal stress leads to reduced oxytocin receptor expression in the mesocorticolimbic dopamine pathway (Haim et al., 2014; Hillerer et al., 2011), which in turn leads to reduced maternal behaviors during the postpartum period (Herzog et al., 2009; Hillerer et al., 2011; Smith et al., 2004).

Human mothers also show an increase in oxytocin levels during pregnancy and before and after interaction with their own infants during the postpartum period (Feldman et al., 2010; Gordon et al., 2010a,b; Levine et al., 2007). Higher levels of oxytocin during late pregnancy have been associated with a stronger emotional attachment of mothers with their infants (Levine et al., 2007). Higher oxytocin levels have also been associated with greater brain responses to mothers' own infants in key brain regions for sensitive parenting including the amygdala, nucleus accumbens, insula, anterior cingulate gyrus, inferior parietal lobule and superior temporal gyrus in mothers (Atzil et al., 2012). However, mothers' insecure attachment, which may reflect childhood stress, has been associated with lower oxytocin levels (Strathearn et al., 2009). The lower oxytocin levels were further associated with reduced responses to mothers' own infant images in the ventral striatum and nucleus accumbens, a part of the mesocorticolimbic dopamine pathway (Strathearn et al., 2009).

4.3. Impact of early life stress on the neural system of emotion regulation and maternal motivation

Exposure to stress as early as the prenatal period can influence the neural system that later supports maternal behaviors. Prenatal stress disrupts the development of hypothalamic and dopaminergic circuits in the fetal brain (Champagne and Curley, 2016). An increase in estrogen during pregnancy stimulates the release of oxytocin and prolactin and is important in priming the medial preoptic area of the hypothalamus (MPOA) that is critically involved in maternal motivation (Numan, 2020; Numan and Insel, 2003). Infant cues stimulate MPOA projections to the ventral tegmental area, a key region of the mesolimbic dopamine system. Activation in mesolimbic dopamine neurons from the ventral tegmental area to the nucleus accumbens, as well as dopamine release in the nucleus accumbens and subsequent brain areas in the mesolimbic dopaminergic pathway, support maternal motivation and behaviors (Numan, 2020; Numan and Insel, 2003). Lower levels of estrogen, reduced estrogen receptors in the MPOA, as well as altered expressions of transcription factors involved in dopaminergic neurons are detected in prenatally stressed female offspring (Champagne and Curley, 2016).

Postnatally, abusive and less nurturing parenting behaviors lead to reduced expression of estrogen receptors in the MPOA via epigenetic mechanisms, which further impairs parenting behaviors in female

offspring in their adulthood (Peña et al., 2012; Peña et al., 2013). Adversity such as prolonged maternal separation has also been shown to reduce estrogen receptors and oxytocin receptors in the brain (Stamatakis et al., 2015). Exposure to low-quality parenting also influences the maternal brain's dopaminergic system. Early adversity such as lower levels of licking and grooming from mothers or maternal deprivation lead to reduced dopaminergic neuron projections from the ventral tegmental area and reduced dopaminergic levels induced by pups in the nucleus accumbens (Afonso et al., 2011; Peña et al., 2014).

In addition to the impact on the maternal motivation neural circuit, childhood adversity also impacts the brain system that regulates the HPA axis. Low quality maternal care such as low licking and grooming in rodents leads to increased glucocorticoid receptor expression which in turn leads to lower levels of glucocorticoid in the hippocampus (Meaney, 2010; Weaver et al., 2004). This disrupts the negative feedback loop of the HPA axis system which leads to chronically high levels of corticosterone in rodents (Meaney, 2010; Weaver et al., 2004). Chronically high glucocorticoid levels impair the brain system that underlies stress reactivity and regulation through the mechanisms I explained earlier. In humans, early adversity such as maternal deprivation has a long-term impact on the brain including higher reactivity to threats in the amygdala and ineffective regulation of the amygdala activation by the PFC (Gee et al., 2013; Tottenham and Sheridan, 2009). Moreover, prenatally stressed female offspring do not exhibit normative adaptations in terms of dampened stress responsiveness during pregnancy (Bosch et al., 2007). These findings present evidence that childhood stress starting from the prenatal period can disrupt later normative adaptation in the maternal brain for both stress regulation and maternal motivation.

5. Mitigating the impact of stress exposure on the maternal brain

The increase in neural plasticity during pregnancy and the early postpartum period suggests that the brain is susceptible to not only negative experiences such as stress, but also positive experiences during this time. Moreover, this time period is when women express higher levels of motivation for positive health behaviors such as lower rates of substance use (Hotham et al., 2008). Thus, the perinatal period has been identified as an important opportunity for interventions involving both neural and behavioral modifications that can have positive impacts on mothers and their infants (Glynn et al., 2018; Kim and Watamura, 2015; Saxbe et al., 2018).

Recent findings from intervention studies suggest the positive role of reduced psychological stress on mothers' brain responses to infants, as well as their parenting behaviors. Mothers participated in a "Mom Power" intervention that focused on parenting skills as well as self-care and emotion regulation skills (Muzik et al., 2015). In response to infant cry sounds, among mothers who received an intervention and had young children at age around 2, decreased psychological stress was associated with enhanced functional connectivity between the amygdala and temporal pole as well as subgenual anterior cingulate cortex and precuneus, regions that are involved in self-reflective functions and mood regulation (Swain et al., 2017). In another study, low-income mothers of children age four or younger participated in an intervention called Filming Interactions to Nurture Development (FIND), a video coaching program to improve parenting behaviors (Fisher et al., 2016). The intervention was associated with increased PFC and insula activation during inhibitory control (Giuliani et al., 2019). Inhibitory control supports cognitive functioning and decision making, which are important aspects of parenting (Giuliani et al., 2019).

The work of examining the impact of the interventions on the maternal brain is currently very limited, and much more work is needed. Breastfeeding has been linked to reduced reactivity to stress and more positive mood states (Heinrichs et al., 2001; Mezzacappa and Katlin, 2002; Mezzacappa et al., 2005). Breastfeeding has also been associated with elevated brain response to infant cry sounds among first-time new mothers (Kim et al., 2011a). However, mothers who are exposed to high levels of environmental stress less likely to breastfeed and more likely to terminate breastfeeding early (Maleki-Saghooni et al., 2017). This may be related to the finding that psychological stress can lead to reduced breastmilk production and more difficulties in nursing (Chatterton et al., 2000; Farideh Bastani et al., 2008). Skin to skin contact, particularly with preterm infants, has also been associated with increased oxytocin levels, which can promote deeper emotional bonds with mothers who are in stressful conditions (Cong et al., 2015; Feldman, 2007). Other interventions including cognitive behavioral stress management and mindfulness-based programs have also been related to reduction in psychological stress and negative mood, and reduced cortisol levels among mothers (Urizar and Muñoz, 2011; Vieten and Astin, 2008). The positive effects of interventions to support breastfeeding, skin-to-skin contact, and emotion regulation skills may be based in part on changes in mothers' brains, and future studies are needed to confirm this hypothesis.

In addition to interventions, it is important to consider social policies that support a mother's transition to parenthood. Paid parental leave reduces stress among new mothers and has positive impacts on maternal and infant health (Isaacs et al., 2017; Jou et al., 2018). However, according to 2018 data from the Organization for Economic Cooperation and Development (OECD), of 41 countries, the US alone had no policy mandating paid leave for new parents (Livingston and Thomas, 2019, December 16). Moreover, mothers who are single and low-income experience the greatest decrease in income after the child's birth, which can put them in more stressful environments (Stanczyk, 2016). Therefore, it is imperative to consider changes in policies to support the financial, psychological, and physical well-being of new mothers, which can help prevent their exposure to severe levels of stress and empower them to provide supportive environments for their children.

6. Looking ahead – Outstanding questions

Evidence for the role of stress exposure on the human maternal brain is still scarce, and much more research is needed to support a detailed understanding. In this section, I discuss directions that can advance our knowledge of the role of stress in maternal brain adaption, and inform prevention and intervention efforts to support mothers who are exposed to stress.

Several important aspects of stress exposure need to be studied in more depth. First, little is known about when a human mother's brain is most vulnerable to stress exposure. It is generally considered that when the brain is rapidly developing and highly plastic, the brain is also more susceptible to stress and adversities (Dunn et al., 2019; Hertzman and Boyce, 2010; Lupien et al., 2009; Nelson Iii et al., 2019; Tottenham, 2020). For the maternal brain, there is evidence that stress starting from the woman's own prenatal period impacts later maternal brain function (Champagne and Curley, 2016). The brain is also highly plastic during pregnancy and the postpartum period, which can lead to high vulnerability to stress (Hillerer et al., 2014; Pawluski et al., 2016). Exposure to stress at different timing in life may have different impacts on maternal brain function. In this review, childhood adversity seems to have a greater impact on the hippocampus the brain region that is involved in the HPA axis regulation and on the midbrain regions that are involved in maternal motivation compared to concurrent environmental stress (Table 1). Childhood adversity was also associated with dampened amygdala response to both positive and negative infant cues (Table 1) which may reflect a more severe impact of childhood adversity on the amygdala compared to concurrent environmental stress in mothers.

However, one of the main challenges to delineating the separate effects of stress exposure at different time points in human mothers is that psychosocial and environmental stress tends to be chronic (Evans and Kim, 2010; Kim et al., 2018b). Thus, a significant percentage of mothers who have experienced childhood adversity are at risk of being exposed to stress such as poverty or interpersonal violence during the

perinatal period as well (Mahenge et al., 2018; Mersky and Janczewski, 2018; Mezey et al., 2005). Chronic and repeated exposure to stress, compared to acute and short-term exposure, can lead to more significant injures in brain morphology and function (Lupien et al., 2018; McEwen, 2012). Thus, stress may impact the maternal brain in a complex way based on both timing and chronicity. A better understanding of the relative impact of stress exposure during different time points and durations will be highly informative to prevention and intervention efforts. With the information, we can consider investing more in prevention and intervention strategies that target time periods when stress exposure is most likely to lead to short- and long-term impacts on mothers' brains. Also, the understanding of the accumulative impact of stress will help to identify mothers who are chronically exposed to stress, thus are more vulnerable to the negative brain and perinatal outcomes.

In addition to the timing and chronicity, the severity of stress is another aspect that is not well understood. As discussed earlier, non-human animal studies suggest that the normal range of stress provides protective mechanisms for mothers such as blunted stress reactivity, however, exposure to severe stress disrupts this adaptive system in the brain and significantly degrades maternal behaviors (Hillerer et al., 2012; Klampfl and Bosch, 2019; Numan, 2020; Slattery and Hillerer, 2016). While stress exposure is typically associated with negative maternal outcomes in human mothers, there is evidence that mild exposure to psychosocial stress during pregnancy is prospectively associated with more positive interactions with infants (Wolf et al., 2017). Furthermore, some mothers are more susceptible to stressful experiences than other mothers based on individual characteristics such as genetic predisposition. Evidence suggests that the impact of childhood adversity on later parenting style is moderated by genetic variations in hormonal receptor expressions (Fujiwara et al., 2019; Hiraoka and Nomura, 2019; Reichl et al., 2019; Savelieva et al., 2019; Senese et al., 2017). For example, mothers who experienced an overprotective parenting style in their childhood were more likely to exhibit a harsh parenting style with their own children if they carried the G allele on the oxytocin receptor gene (Fujiwara et al., 2019). For the serotonin transporter genotype that regulates serotonin level, the short (S)-allele is associated with greater susceptibility to environmental stress on the brain and depression (Flasbeck et al., 2019). Among individuals exposed to childhood or current stressful life events, individuals with the S-allele exhibit more depressive symptoms and greater amygdala and hippocampal reactivity to negative emotional stimuli (Canli et al., 2006; Caspi et al., 2003; Karg et al., 2011). Thus, to move the field forward, it will be important to investigate whether the severity of stress leads to more positive or negative changes in the maternal brain, as well as how individual characteristics such as genetics can interact with the impact of stress. Such understanding will help to explain why some mothers may be more vulnerable to stress exposure and whether some levels of stress exposure can have positive aspects for mothers.

The unique and overlapping effects of different types of stressors also warrant further investigation. As reviewed earlier, the neurobiological mechanisms as well as the impact of stress exposure on the maternal brain seem to overlap across different stressors (see Table 1). Some of the differences may be due to the limited amount of studies available. However, recently there also are increased efforts to identify the unique effects of different types of stressors that are related to threats (such as child abuse) vs. deprivation (such as child neglect) on brain outcomes (McLaughlin and Sheridan, 2016; Sheridan and McLaughlin, 2014). Testing the unique effects of stressors in humans is challenging, as individuals living in a stressful environment tend to be exposed to multiple stressors. However, the effort to understand the unique vs. overlapping effects of stressors on the maternal brain can further advance our understanding of which stressors may have particularly adverse impacts on the transition to parenthood and on parenting behaviors.

Related to different types of stressors, it would also be important to examine other factors that can interact with stress exposure. Due to the physical demands of pregnancy and child care during the early postpartum period, the perinatal period has been linked to lower sleep quality and sleep deprivation (Hagen et al., 2013; Sedov et al., 2018), which further increases risks for depression (Dørheim et al., 2009; Skouteris et al., 2009). Stress can negatively influence already-compromised sleep quality among pregnant women and new mothers during this time. Moreover, stress can increase risks for substance use (Marcenko et al., 2000; Mezick et al., 2008; Tanya Nagahawatte and Goldenberg, 2008) and inflammatory dysregulation (Coussons-Read et al., 2007), which can disrupt mothers' brain and psychological adaptations to parenthood (Corwin et al., 2008; Kim et al., 2017b; Landi et al., 2011; Lowell et al., 2020; Swain et al., 2019).

When studying the associations between stress exposure and the maternal brain in human mothers, one of the major limitations is that the observational research design does not directly support understanding causal relationships between stress and brain outcomes. This is significant in terms of providing supportive arguments for intervention efforts to reduce mothers' stress. For example, some may argue that mothers who exhibit poor parenting behaviors may also have a genetic predisposition to make poor decisions, and therefore cause higher levels of stress in their lives. Therefore, stressful conditions may be correlated with more difficulties in the transition to parenthood, but do not cause them.

In studies with human mothers, there are several ways to support the causal link. First, non-human animal studies using experimental manipulations provide strong evidence for the causal relationships between stress and changes in the maternal brain (Lambert and Byrnes, 2019). Thus, a cross-species approach that directly compares the impact of the same stressor in rodents and humans, such as poor quality maternal care received in childhood (Davis et al., 2017), can help to strengthen the directionality of the relationships between stress and maternal outcomes. Second, intervention studies to lower mothers' psychological stress or remove environmental stress can provide information on how reduced stress is associated with effects on the mother's brain. Third, a research design that allows a comparison of maternal brain structure and function before and after exposure to a significantly stressful event such as the COVID-19 pandemic (Lebel et al., 2020) can provide support for causal associations between stress exposure and brain outcomes. Last, longitudinal studies can clarify the directionality of the associations between stress exposure, maternal mood, and brain responses to infant cues during pregnancy and the early postpartum period, as well as further associations with mothers' relationships with their infants.

To improve understanding of the neurobiological mechanisms by which stress impacts the maternal brain, studying the relationships between hormones and maternal brain responses to infants are needed. Women's brains and bodies experience drastic changes in hormone levels during pregnancy and the postpartum period (Almanza-Sepulveda et al., 2020; Feldman and Bakermans-Kranenburg, 2017; Lonstein et al., 2015). As discussed earlier, these hormonal changes play an important role in both brain and behavioral adjustment to motherhood, but the influence of stress exposure on the associations between hormone levels and maternal brain responses to children has not been extensively examined in human mothers. A careful approach is needed due to complex associations among stress, maternal mood, and cortisol levels. For example, the link between high cortisol levels and the maternal depressive mood is not consistent across studies, and low levels of cortisol have also been linked to depression (Seth et al., 2016). One possibility is that higher cortisol reactivity to stress is more evident among mothers with comorbid depression and anxiety (Evans et al., 2008).

Another area that should receive more attention is the neurobiological and neuroendocrine mechanisms by which stress exposure influences brain networks involved in cognitive and emotional empathic processes. The function of the brain regions involved in emotion regulation including the amygdala, hippocampus, and PFC is also involved in social cognition, thus the neurobiological mechanisms of emotion dysregulation may further influence empathic processes in the brain

(Beadle et al., 2013; Grimm et al., 2017; Levy et al., 2019a). However, more research is needed to provide a detailed understanding of how the two networks may interact to support parenting and how stress exposure may interrupt the connectivity between the two networks.

Throughout the consideration of all these factors, it is critical to examine how different racial and ethnic backgrounds and cultural differences may interact with the impact of stress exposure. Currently, mothers with immigrant or minority backgrounds are underrepresented in the human maternal brain literature. However, mothers with immigrant or minority status on average are more vulnerable to childhood adversity and environmental stressors (Liu et al., 2016; Maguire-Jack et al., 2020). In addition, women with immigrant or minority backgrounds are vulnerable to racism or discrimination in both their childhood and adulthood, and this experience is a significant stressor for mothers (Dunkel Schetter, 2011; Engle et al., 1990). Therefore, greater efforts must be made to increase the representation of mothers with minority backgrounds, so the research findings can reflect unique and common risk and protective factors for mothers with different racial and ethnic backgrounds.

While the research on resilience factors is very limited, the current literature suggests certain factors are important, including appropriate social support and adaptive coping strategies. Having a supportive partner or relatives for both emotional support (such as receiving emotional comfort) or instrumental support (such as child care assistance) helps to protect mothers from the negative impacts of stress – both normative as well as severe levels of stress exposure – during pregnancy and the postpartum period (Collins et al., 1993; Razurel et al., 2012). Increased levels of oxytocin that were induced by social support were particularly effective to reduce anxiety and cortisol levels among women who were exposed to childhood adversity (Riem et al., 2020). Thus, while all mothers can benefit, mothers under stress may benefit more from social support. It is important to note that while fathers are key figures to provide the support that mothers need, fathers also undergo neurobiological and psychological changes in the adaptation to parenthood (Kim et al., 2013; Kim et al., 2015b). Thus, future studies may consider including both mothers and fathers in order to develop an understanding of how stress differentially or similarly influences mothers' and fathers' neural adaptations to parenthood. Adaptive coping strategies may also be an important resilience factor that can help mothers reduce the negative impacts of stress exposure, particularly on maternal mood (George et al., 2013; Goletzke et al., 2017; Guardino and Dunkel Schetter, 2014). Among other brain regions, PFC function supports adaptive cognitive strategies such as cognitive reappraisal and active coping (Frank et al., 2014); however, the associations among stress, PFC function, and coping strategies during the perinatal period are not well understood. Therefore, neuroimaging studies focused on protective and resilience factors would be particularly informative for interventions and treatments for pregnant and postpartum women.

7. Conclusions

The adverse impacts of stress on the brain are now well recognized in the scientific literature due to consistent findings across the lifespan (Lupien et al., 2018; McEwen, 2012). Emerging literature reviewed here now provides evidence that stress impacts the brains of new mothers and the perinatal period may be a window of vulnerabilities and opportunities. During pregnancy and the postpartum period, a woman's brain undergoes changes that support her role as a parent. An increase in brain plasticity suggests that this is a period when women are particularly vulnerable to stress and adversity, but also sensitive to positive interventions and social supports. The success of the adaptation to motherhood can significantly impact mothers' own wellbeing as well as the development of their children (Buss et al., 2010; Glynn and Baram, 2019; Moog et al., 2018), however, the importance of supporting a woman's optimal transition to parenthood may not be sufficiently recognized at the societal level.

Therefore, in this paper, I have reviewed available evidence that exposure to different types of stress, from childhood to the perinatal period, is associated with disrupted brain adaptation to motherhood, which can further increase risks for difficulties in developing sensitive parenting behaviors among new mothers. Non-human animal research points to the neurobiological mechanisms by which exposure to severe stress can disrupt the normative adaptation of the maternal brain for enhanced maternal motivation and stress regulation. This understanding can impact our approach to supporting mother-infant dyads who face the challenges of stressful environments. Reducing stress exposure and providing support for mothers to cope with stress and regulate depressive mood and anxiety can help them build more positive perspectives toward their relationships with their own infants and children, as well as their role as parents.

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References

Abdou, C.M., Schetter, C.D., Jones, F., Roubinov, D., Tsai, S., Jones, L., Lu, M., Hobel, C., 2010. Community perspectives: Mixed-methods investigation of culture, stress, resilience, and health. Ethn. Dis. 20, S2–S48.

Abraham, E., Hendler, T., Shapira-Lichter, I., Kanat-Maymon, Y., Zagoory-Sharon, O., Feldman, R., 2014. Father's brain is sensitive to childcare experiences. Proc. Natl. Acad. Sci. U S A. 111, 9792–9797. https://doi.org/10.1073/pnas.1402569111.

Abraham, E., Hendler, T., Zagoory-Sharon, O., Feldman, R., 2016. Network integrity of the parental brain in infancy supports the development of children's social competencies. Soc. Cogn. Affect. Neurosci. 11, 1707–1718. https://doi.org/10.1093/scan/nsw090.

Abraham, E., Raz, G., Zagoory-Sharon, O., Feldman, R., 2018. Empathy networks in the parental brain and their long-term effects on children's stress reactivity and behavior adaptation. Neuropsychologia. 116, 75–85. https://doi.org/10.1016/j.neuropsychologia.2017.04.015.

Afonso, V.M., King, S.J., Novakov, M., Burton, C.L., Fleming, A.S., 2011. Accumbal dopamine function in postpartum rats that were raised without their mothers. Horm. Behav. 60, 632–643. https://doi.org/10.1016/j.yhbeh.2011.08.016.

Almanza-Sepulveda, M.L., Fleming, A.S., Jonas, W., 2020. Mothering revisited: A role for cortisol? Horm. Behav. 121, 104679. https://doi.org/10.1016/j.yhbeh.2020.104679.

Altemus, M., Redwine, L.S., Leong, Y.-M., Frye, C.A., Porges, S.W., Carter, C.S., 2001. Responses to laboratory psychosocial stress in postpartum women. Psychosom. Med. 63, 814–821.

Antoniuk, S., Bijata, M., Ponimaskin, E., Wlodarczyk, J., 2019. Chronic unpredictable mild stress for modeling depression in rodents: Meta-analysis of model reliability. Neurosci. Biobehav. Rev. 99, 101–116. https://doi.org/10.1016/j.neubiorev.2018.12.002.

Atzil, S., Hendler, T., Feldman, R., 2011. Specifying the neurobiological basis of human attachment: brain, hormones, and behavior in synchronous and intrusive mothers. Neuropsychopharmacol. 36, 2603–2615. https://doi.org/10.1038/npp.2011.172.

Atzil, S., Hendler, T., Zagoory-Sharon, O., Winetraub, Y., Feldman, R., 2012. Synchrony and specificity in the maternal and the paternal brain: relations to oxytocin and vasopressin. J. Am. Acad. Child Adolesc. Psychiatry 51, 798–811. https://doi.org/10.1016/j.jaac.2012.06.008.

Azhari, A., Leck, W.Q., Gabrieli, G., Bizzego, A., Rigo, P., Setoh, P., Bornstein, M.H., Esposito, G., 2019. Parenting stress undermines mother-child brain-to-brain synchrony: A hyperscanning study. Sci. Rep. 9, 11407. https://doi.org/10.1038/s41598-019-47810-4.

Bahr, N.I., Pryce, C.R., Dobeli, M., Martin, R.D., 1998. Evidence from urinary cortisol that maternal behavior is related to stress in gorillas. Physiol. Behav. 64, 429–437.

Barha, C.K., Galea, L.A., 2011. Motherhood alters the cellular response to estrogens in the hippocampus later in life. Neurobiol. Aging 32, 2091–2095.

Barba-Müller, E., Craddock, S., Carmona, S., Hoekzema, E., 2019. Brain plasticity in pregnancy and the postpartum period: links to maternal caregiving and mental health. Arch. Womens Ment. Health. 22, 289–299.

Barnett, M.A., 2008. Economic disadvantage in complex family systems: Expansion of family stress models. Clin. Child. Fam. Psychol. Rev. 11, 145–161.

Barrett, J., Fleming, A.S., 2011. Annual Research Review: All mothers are not created equal: neural and psychobiological perspectives on mothering and the importance of individual differences. J. Child Psychol. Psychiatry 52, 368–397. https://doi.org/10.1111/j.1469-7610.2010.02306.x.

Barrett, J., Wonch, K.E., Gonzalez, A., Ali, N., Steiner, M., Hall, G.B., Fleming, A.S., 2012. Maternal affect and quality of parenting experiences are related to amygdala response to infant faces. Soc. Neurosci. 7, 252–268. https://doi.org/10.1080/17470919.2011.609907.

Beadle, J.N., Tranel, D., Cohen, N.J., Duff, M., 2013. Empathy in hippocampal amnesia. Front. Psychol. 4, 69. https://doi.org/10.3389/fpsyg.2013.00069.

Beeber, L.S., Perreira, K.M., Schwartz, T., 2008. Supporting the mental health of mothers raising children in poverty - How do we target them for intervention studies? Ann. N. Y. Acad. Sci. 1136, 86–100. https://doi.org/10.1196/annals.1425.008.

Bell, A.F., Erickson, E.N., Carter, C.S., 2014. Beyond labor: the role of natural and synthetic oxytocin in the transition to motherhood. J. Midwifery Womens Health. 59, 35–42. https://doi.org/10.1111/jmwh.12101.

Bell, M.A., 2020. Chapter six - mother-child behavioral and physiological synchrony. Adv. Child Dev. Behav. 58, 163–188.

Belsky, J., Jaffee, S., 2006. The multiple determinants of parenting. In: Cohen, D.J., Cicchetti, D. (Eds.), Developmental psychopathology: Risk, Disorder, and Adaptation. John Wiley & Sons, Hoboken, NJ, pp. 38–85.

Belsky, J.J., S R;Sligo, J; Woodward, L; Silva, P A., 2005. Intergenerational transmission of warm-sensitive-stimulating parenting: a prospective study of mothers and fathers of 3-year-olds. Child Dev. 76, 384–396.

Berman, Z., Kaim, A., Reed, T., Felicione, J., Hinojosa, C., Oliver, K., Rutherford, H., Mayes, L., Shin, L., Dekel, S., 2020. Amygdala response to traumatic childbirth recall is associated with impaired bonding behaviors in mothers with childbirth-related PTSD symptoms: preliminary findings. Biol. Psychiatry 87, S142. https://doi.org/10.1016/j.biopsych.2020.02.378.

Bilgin, A., Wolke, D., 2015. Maternal sensitivity in parenting preterm children: a meta-analysis. Pediatrics 136, e177–e193.

Bjertrup, A.J., Friis, N.K., Miskowiak, K.W., 2019. The maternal brain: Neural responses to infants in mothers with and without mood disorder. Neurosci. Biobehav. Rev. 107, 196–207. https://doi.org/10.1016/j.neubiorev.2019.09.011.

Bornstein, M.H., 2002. Parenting Infants. In: Bornstein, M.H. (Ed.), Handbook of Parenting. Erlbaum, Mahwah, N.J., pp. 3–43

Bornstein, M.H., Putnick, D.L., Rigo, P., Esposito, G., Swain, J.E., Suwalsky, J.T.D., Su, X., Du, X., Zhang, K., Cote, L.R., De Pisapia, N., Venuti, P., 2017. Neurobiology of culturally common maternal responses to infant cry. PNAS 114, E9465–E9473. https://doi.org/10.1073/pnas.1712022114.

Bosch, O.J., Musch, W., Bredewold, R., Slattery, D.A., Neumann, I.D., 2007. Prenatal stress increases HPA axis activity and impairs maternal care in lactating female offspring: implications for postpartum mood disorder. Psychoneuroendocrinology 32, 267–278. https://doi.org/10.1016/j.psyneuen.2006.12.012.

Bosch, O.J., Neumann, I.D., 2012. Both oxytocin and vasopressin are mediators of maternal care and aggression in rodents: From central release to sites of action. Horm. Behav. 61, 293–303. https://doi.org/10.1016/j.yhbeh.2011.11.002.

Bozzette, M., 2007. A review of research on premature infant-mother interaction. Newborn Infant. Nurs. Rev. 7, 49–55.

Bradley, R.H., Corwyn, R.F., 2002. Socioeconomic status and Child Dev. Annu. Rev. Psychol. 53, 371–399. https://doi.org/10.1146/annurev.psych.53.100901.135233.

Braun, U., Schäfer, A., Walter, H., Erk, S., Romanczuk-Seiferth, N., Haddad, L., Schweiger, J.I., Grimm, O., Heinz, A., Tost, H., Meyer-Lindenberg, A., Bassett, D.S., 2015. Dynamic reconfiguration of frontal brain networks during executive cognition in humans. PNAS 112, 11678–11683. https://doi.org/10.1073/pnas.1422487112.

Braveman, P., Marchi, K., Egerter, S., Kim, S., Metzler, M., Stancil, T., Libet, M., 2010. Poverty, near-poverty, and hardship around the time of pregnancy. Matern. Child Health J. 14, 20–35.

Braver, T.S., 2012. The variable nature of cognitive control: a dual mechanisms framework. Trends Cogn. Sci. 16, 106–113. https://doi.org/10.1016/j.tics.2011.12.010.

Brummelte, S., Galea, L.A., 2010. Depression during pregnancy and postpartum: contribution of stress and ovarian hormones. Prog. Neuro-Psychoph Biol. Psychiatry. 34, 766–776.

Brunton, P.J., 2013. Effects of maternal exposure to social stress during pregnancy: consequences for mother and offspring. Reproduction 146, R175–R189. https://doi.org/10.1530/rep-13-0258.

Brunton, P.J., Meddle, S.L., 2011. Parenthood and Changing Brains. J. Neuroendocrinol. 23, 957–960. https://doi.org/10.1111/j.1365-2826.2011.02218.x.

Brunton, P.J., Russell, J.A., 2008. The expectant brain: adapting for motherhood. Nat. Rev. Neurosci. 9, 11–25.

Brunton, P.J., Russell, J.A., Douglas, A.J., 2008. Adaptive responses of the maternal hypothalamic-pituitary-adrenal axis during pregnancy and lactation. J. Neuroendocrinol. 20, 764–776. https://doi.org/10.1111/j.1365-2826.2008.01735.x.

Buss, C., Davis, E.P., Muftuler, L.T., Head, K., Sandman, C.A., 2010. High pregnancy anxiety during mid-gestation is associated with decreased gray matter density in 6–9-year-old children. Psychoneuroendocrinology. 35, 141–153.

Buss, C., Entringer, S., Moog, N.K., Toepfer, P., Fair, D.A., Simhan, H.N., Heim, C.M., Wadhwa, P.D., 2017. Intergenerational transmission of maternal childhood maltreatment exposure: implications for fetal brain development. J. Am. Acad. Child Adolesc. Psychiatry 56, 373–382. https://doi.org/10.1016/j.jaac.2017.03.001.

Canli, T., Lesch, K.-P., 2007. Long story short: the serotonin transporter in emotion regulation and social cognition. Nat. Neurosci. 10, 1103–1109.

Canli, T., Qiu, M., Omura, K., Congdon, E., Haas, B.W., Amin, Z., Herrmann, M.J., Constable, R.T., Lesch, K.P., 2006. Neural correlates of epigenesis. PNAS 103, 16033–16038.

Cárdenas, E.F., Kujawa, A., Humphreys, K.L., 2019. Neurobiological changes during the peripartum period: implications for health and behavior. Soc. Cogn. Affect. Neurosci. https://doi.org/10.1093/scan/nsz091.

Carmona, S., Martínez-García, M., Paternina-Die, M., Barba-Müller, E., Wierenga, L.M., Alemán-Gómez, Y., Pretus, C., Marcos-Vidal, L., Beumala, L., Cortizo, R., Pozzobon, C., Picado, M., Lucco, F., García-García, D., Soliva, J.C., Tobeña, A., Peper, J.S., Crone, E.A., Ballesteros, A., Vilarroya, O., Desco, M., Hoekzema, E., 2019. Pregnancy and adolescence entail similar neuroanatomical adaptations: A comparative analysis of cerebral morphometric changes. Hum. Brain Mapp. 40, 2143–2152. https://doi.org/10.1002/hbm.24513.

Caspi, A., Sugden, K., Moffitt, T.E., Taylor, A., Craig, I.W., Harrington, H., McClay, J., Mill, J., Martin, J., Braithwaite, A., 2003. Influence of life stress on depression: moderation by a polymorphism in the 5-HTT gene. Science 301, 386–389.

Champagne, F.A., Curley, J.P., 2016. Plasticity of the maternal brain across the lifespan. New Dir. Child Adolesc. Dev. 2016, 9–21.

Champagne, F.A., Weaver, I.C., Diorio, J., Sharma, S., Meaney, M.J., 2003. Natural variations in maternal care are associated with estrogen receptor alpha expression and estrogen sensitivity in the medial preoptic area. Endocrinology 144, 4720–4724.

Chatterton Jr., R.T., Hill, P.D., Aldag, J.C., Hodges, K.R., Belknap, S.M., Zinaman, M.J., 2000. Relation of plasma oxytocin and prolactin concentrations to milk production in mothers of preterm infants: influence of stress. J. Clin. Endocrinol. Metab. 85, 3661–3668. https://doi.org/10.1210/jcem.85.10.6912.

Chertok, I.R.A., McCrone, S., Parker, D., Leslie, N., Catlin, A., 2014. Review of interventions to reduce stress among mothers of infants in the NICU. Adv Neonatal Care. 14, 30–37.

Collins, N.L., Dunkel-Schetter, C., Lobel, M., Scrimshaw, S.C., 1993. Social support in pregnancy: psychosocial correlates of birth outcomes and postpartum depression. J. Pers. Soc. Psychol. 65, 1243–1258.

Cong, X., Ludington-Hoe, S.M., Hussain, N., Cusson, R.M., Walsh, S., Vazquez, V., Briere, C.-E., Vittner, D., 2015. Parental oxytocin responses during skin-to-skin contact in pre-term infants. Early Hum Dev. 91, 401–406. https://doi.org/10.1016/j.earlhumdev.2015.04.012.

Conger, R.D., Donnellan, M.B., 2007. An interactionist perspective on the socioeconomic context of human development. Annu. Rev. Psychol. 58, 175–199.

Conger, R.D., Neppl, T., Kim, K.J., Scaramella, L., 2003. Angry and aggressive behavior across three generations: a prospective, longitudinal study of parents and children. J. Abnorm. Child Psychol. 31, 143–160. https://doi.org/10.1023/a:1022570107457.

Corter, C.M., Fleming, A.S., 1990. Maternal responsiveness in humans: emotional, cognitive, and biological factors. In: Slater, P.J.B., Rosenblatt, J.S., Beer, C. (Eds.), Advances in the Study of Behavior. Academic Press, pp. 83–136.

Corwin, E.J., Johnston, N., Pugh, L., 2008. Symptoms of postpartum depression associated with elevated levels of interleukin-1 beta during the first month postpartum. Biol. Res. Nurs. 10, 128–133.

Coussons-Read, M.E., Okun, M.L., Nettles, C.D., 2007. Psychosocial stress increases inflammatory markers and alters cytokine production across pregnancy. Brain Behav. Immun. 21, 343–350. https://doi.org/10.1016/j.bbi.2006.08.006.

Crandall, A., Deater-Deckard, K., Riley, A.W., 2015. Maternal emotion and cognitive control capacities and parenting: A conceptual framework. Dev. Rev. 36, 105–126.

Crnic, K., Low, C., 2002. Everyday stresses and parenting. Handbook of parenting volume 5 practical issues in parenting. 242.

Davidson, R.J., McEwen, B.S., 2012. Social influences on neuroplasticity: stress and interventions to promote well-being. Nat. Neurosci. 15, 689–695. https://doi.org/10.1038/nn.3093.

Davis, E.P., Stout, S.A., Molet, J., Vegetabile, B., Glynn, L.M., Sandman, C.A., Heins, K., Stern, H., Baram, T.Z., 2017. Exposure to unpredictable maternal sensory signals influences cognitive development across species. PNAS 114, 10390–10395.

De Lange, A.-M.G., Barth, C., Kaufmann, T.G., Anatürk, M., Suri, S., Ebmeier, K.P., Westlye, L.T., 2020. History of childbirths relates to region-specific brain aging patterns in middle and older-aged women. bioRxiv.

de Lange, A.-M.G., Kaufmann, T., van der Meer, D., Maglanoc, L.A., Alnæs, D., Moberget, T., Douaud, G., Andreassen, O.A., Westlye, L.T., 2019. Population-based neuroimaging reveals traces of childbirth in the maternal brain. PNAS 116, 22341–22346. https://doi.org/10.1073/pnas.1910666116.

Deater-Deckard, K., 2008. Parenting Stress. Yale University Press.

Dickens, M.J., Pawluski, J.L., 2018. The HPA axis during the perinatal period: implications for perinatal depression. Endocrinology 159, 3737–3746.

Dørheim, S.K., Bondevik, G.T., Eberhard-Gran, M., Bjorvatn, B., 2009. Sleep and depression in postpartum women: a population-based study. Sleep 32, 847–855.

Dudek, J., Colasante, T., Zuffianò, A., Haley, D.W., 2020. Changes in cortical sensitivity to infant facial cues from pregnancy to motherhood predict mother-infant bonding. Child Dev. 91, e198–e217. https://doi.org/10.1111/cdev.13182.

Dufford, A.J., Erhart, A., Kim, P., 2019. Maternal brain resting-state connectivity in the postpartum period. J. Neuroendocrinol. 31, e12737 https://doi.org/10.1111/jne.12737.

Dunkel Schetter, C., 2011. Psychological science on pregnancy: stress processes, biopsychosocial models, and emerging research issues. Annu Rev of Psychol. 62, 531–558.

Dunn, E.C., Soare, T.W., Zhu, Y., Simpkin, A.J., Suderman, M.J., Klengel, T., Smith, A.D., Ressler, K.J., Relton, C.L., 2019. Sensitive periods for the effect of childhood adversity on DNA methylation: results from a prospective, longitudinal study. Biol. Psychiatry 85, 838–849.

Elmadih, A., Wan, M.W., Downey, D., Elliott, R., Swain, J.E., Abel, K.M., 2016. Natural variation in maternal sensitivity is reflected in maternal brain responses to infant stimuli. Behav. Neurosci. https://doi.org/10.1037/bne0000161.
Engle, P.L., Scrimshaw, S.C., Zambrana, R.E., Dunkel-Schetter, C., 1990. Prenatal and postnatal anxiety in Mexican women giving birth in Los Angeles. Health Psychol. 9, 285.
Etkin, A., Büchel, C., Gross, J.J., 2015. The neural bases of emotion regulation. Nat. Rev. Neurosci. 16, 693.
Evans, G.W., 2004. The environment of childhood poverty. Am. Psychol. 59, 77–92.
Evans, G.W., Kim, P., 2010. Multiple risk exposure as a potential explanatory mechanism for the socioeconomic status–health gradient. Ann. N. Y. Acad. Sci. 1186, 174–189.
Evans, L.M., Myers, M.M., Monk, C., 2008. Pregnant women's cortisol is elevated with anxiety and depression - but only when comorbid. Arch Womens Ment Health. 11, 239–248. https://doi.org/10.1007/s00737-008-0019-4.
Bastani, Farideh, Rahmatnejad, Leili, Jahdi, Fereshteh, Haghani, Hamid, 2008. Breastfeeding Self Efficacy and Perceived Stress in Primiparous Mothers. Iran J Nurs. 21, 9–24.
Feder, A., Nestler, E.J., Charney, D.S., 2009. Psychobiology and molecular genetics of resilience. Nat. Rev. Neurosci. 10, 446–457.
Feldman, R., 2007. Maternal-infant contact and Child Dev: Insights from the kangaroo intervention. Low-cost approaches to promote physical and mental health: Theory, research, and practice. Springer Science + Business Media, New York, NY, US, pp. 323–351.
Feldman, R., Bakermans-Kranenburg, M.J., 2017. Oxytocin: a parenting hormone. Curr Opin Psychol. 15, 13–18. https://doi.org/10.1016/j.copsyc.2017.02.011.
Feldman, R., Braun, K., Champagne, F.A., 2019. The neural mechanisms and consequences of paternal caregiving. Nat. Rev. Neurosci. 1.
Feldman, R., Gordon, I., Schneiderman, I., Weisman, O., Zagoory-Sharon, O., 2010. Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent–infant contact. Psychoneuroendocrinology. 35, 1133–1141. https://doi.org/10.1016/j.psyneuen.2010.01.013.
Feldman, R., Granat, A., Pariente, C., Kanety, H., Kuint, J., Gilboa-Schechtman, E., 2009. Maternal depression and anxiety across the postpartum year and infant social engagement, fear regulation, and stress reactivity. J. Am. Acad. Child Adolesc. Psychiatry 48, 919–927.
Fell, D.B., Dodds, L., King, W.D., 2004. Residential mobility during pregnancy. Paediatr. Perinat. Epidemiol. 18, 408–414.
Ferris, C.F., Kulkarni, P., Sullivan Jr., J.M., Harder, J.A., Messenger, T.L., Febo, M., 2005. Pup suckling is more rewarding than cocaine: evidence from functional magnetic resonance imaging and three-dimensional computational analysis. J. Neurosci. 25, 149–156. https://doi.org/10.1523/jneurosci.3156-04.2005.
Fisher, P.A., Frenkel, T.I., Noll, L.K., Berry, M., Yockelson, M., 2016. Promoting healthy Child Dev via a two-generation translational neuroscience framework: the Filming Interactions to Nurture Development video coaching program. Child Dev Perspect. 10, 251–256.
Flasbeck, V., Moser, D., Pakusch, J., Kumsta, R., Brüne, M., 2019. The association between childhood maltreatment and empathic perspective taking is moderated by the 5-HTT linked polymorphic region: Another example of "differential susceptibility". PLoS One 14, e0226737.
Frank, D., Dewitt, M., Hudgens-Haney, M., Schaeffer, D., Ball, B., Schwarz, N., Hussein, A., Smart, L., Sabatinelli, D., 2014. Emotion regulation: quantitative meta-analysis of functional activation and deactivation. Neurosci. Biobehav. Rev. 45, 202–211.
Friedman, S.L., Zahn-Waxler, C., Radke-Yarrow, M., 1982. Perceptions of cries of full-term and preterm infants. Infant. Behav. Dev. 5, 161–173. https://doi.org/10.1016/S0163-6383(82)80025-8.
Fujiwara, T., Weisman, O., Ochi, M., Shirai, K., Matsumoto, K., Noguchi, E., Feldman, R., 2019. Genetic and peripheral markers of the oxytocin system and parental care jointly support the cross-generational transmission of bonding across three generations. Psychoneuroendocrinology. 102, 172–181.
Gallo, M., Shleifer, D.G., Godoy, L.D., Ofray, D., Olaniyan, A., Campbell, T., Bath, K.G., 2019. Limited bedding and nesting induces maternal behavior resembling both hypervigilance and abuse. Front. Behav. Neurosci. 13 https://doi.org/10.3389/fnbeh.2019.00167.
Gee, D.G., Gabard-Durnam, L.J., Flannery, J., Goff, B., Humphreys, K.L., Telzer, E.H., Hare, T.A., Bookheimer, S.Y., Tottenham, N., 2013. Early developmental emergence of human amygdala–prefrontal connectivity after maternal deprivation. PNAS 110, 15638–15643. https://doi.org/10.1073/pnas.1307893110.
George, A., Luz, R.F., De Tychey, C., Thilly, N., Spitz, E., 2013. Anxiety symptoms and coping strategies in the perinatal period. BMC Pregnancy Childbirth. 13, 233. https://doi.org/10.1186/1471-2393-13-233.
George, C., Kaplan, N., Main, M., 1996. Adult attachment interview.
Gianaros, P.J., Horenstein, J.A., Hariri, A.R., Sheu, L.K., Manuck, S.B., Matthews, K.A., Cohen, S., 2008. Potential neural embedding of parental social standing. Soc. Cogn. Affect. Neurosci. 3, 91–96. https://doi.org/10.1093/scan/nsn003.
Gianaros, P.J., Manuck, S.B., Sheu, L.K., Kuan, D.C.H., Votruba-Drzal, E., Craig, A.E., Hariri, A.R., 2011. Parental education predicts corticostriatal functionality in adulthood. Cereb. Cortex 21, 896–910. https://doi.org/10.1093/cercor/bhq160.
Giuliani, N.R., Beauchamp, K.G., Noll, L.K., Fisher, P.A., 2019. A Preliminary study investigating maternal neurocognitive mechanisms underlying a child-supportive parenting intervention. Front. Behav. Neurosci. 13 https://doi.org/10.3389/fnbeh.2019.00016.
Glynn, L.M., Baram, T.Z., 2019. The influence of unpredictable, fragmented parental signals on the developing brain. Front. Neuroendocrinol. 53, 100736. https://doi.org/10.1016/j.yfrne.2019.01.002.
Glynn, L.M., Howland, M.A., Fox, M., 2018. Maternal programming: Application of a developmental psychopathology perspective. Dev. Psychopathol. 30, 905–919. https://doi.org/10.1017/S0954579418000524.
Goletzke, J., Kocalevent, R.D., Hansen, G., Rose, M., Becher, H., Hecher, K., Arck, P.C., Diemert, A., 2017. Prenatal stress perception and coping strategies: Insights from a longitudinal prospective pregnancy cohort. J Psychosomatic Res. 102, 8–14. https://doi.org/10.1016/j.jpsychores.2017.09.002.
Gonzalez, A., Fleming, A.S., 2002. Artificial rearing causes changes in maternal behavior and c-fos expression in juvenile female rats. Behav. Neurosci. 116, 999–1013.
Gordon, I., Zagoory-Sharon, O., Leckman, J.F., Feldman, R., 2010a. Oxytocin and the development of parenting in humans. Biol. Psychiatry 68, 377–382. https://doi.org/10.1016/j.biopsych.2010.02.005.
Gordon, I., Zagoory-Sharon, O., Leckman, J.F., Feldman, R., 2010b. Oxytocin, cortisol, and triadic family interactions. Physiol. Behav. No Pagination Specified. https://doi.org/10.1016/j.physbeh.2010.08.008.
Goyal, D., Gay, C., Lee, K.A., 2010. How much does low socioeconomic status increase the risk of prenatal and postpartum depressive symptoms in first-time mothers? Womens Health Issues. 20, 96–104 doi: S1049-3867(09)00136-4 [pii]10.1016/j.whi.2009.11.003.
Greene, M.M., Rossman, B., Patra, K., Kratovil, A.L., Janes, J.E., Meier, P.P., 2015. Depressive, anxious and perinatal post-traumatic distress in mothers of very low birth weight infants in the NICU. J. Dev. Behav. Pediatr. 36, 362–370.
Grimm, S., Wirth, K., Fan, Y., Weigand, A., Gärtner, M., Feeser, M., Dziobek, I., Bajbouj, M., Aust, S., 2017. The interaction of corticotropin-releasing hormone receptor gene and early life stress on emotional empathy. Behav. Brain Res. 329, 180–185.
Guardino, C.M., Dunkel Schetter, C., 2014. Coping during pregnancy: a systematic review and recommendations. Health Psychol. Rev. 8, 70–94.
Guintivano, J., Sullivan, P.F., Stuebe, A.M., Penders, T., Thorp, J., Rubinow, D.R., Meltzer-Brody, S., 2017. Adverse life events, psychiatric history, and biological predictors of postpartum depression in an ethnically diverse sample of postpartum women. Psychol. Med. 48, 1190–1200. https://doi.org/10.1017/S0033291717002641.
Gururajan, A., Reif, A., Cryan, J.F., Slattery, D.A., 2019. The future of rodent models in depression research. Nat. Rev. Neurosci. 20, 686–701. https://doi.org/10.1038/s41583-019-0221-6.
Hagen, E.W., Mirer, A.G., Palta, M., Peppard, P.E., 2013. The sleep-time cost of parenting: Sleep duration and sleepiness among employed parents in the Wisconsin Sleep Cohort Study. Am. J. Epidemiol. 177, 394–401.
Haim, A., Sherer, M., Leuner, B., 2014. Gestational stress induces persistent depressive-like behavior and structural modifications within the postpartum nucleus accumbens. Eur. J. Neurosci. 40, 3766–3773.
Hajal, N.J., Paley, B., 2020. Parental emotion and emotion regulation: A critical target of study for Res and intervention to promote child emotion socialization. Dev. Psychol. 56, 403.
Hasson, U., Ghazanfar, A.A., Galantucci, B., Garrod, S., Keysers, C., 2012. Brain-to-brain coupling: a mechanism for creating and sharing a social world. Trends Cogn Sci. 16, 114–121.
Heinrichs, M., Meinlschmidt, G., Neumann, I., Wagner, S., Kirschbaum, C., Ehlert, U., Hellhammer, D.H., 2001. Effects of suckling on hypothalamic-pituitary-adrenal axis responses to psychosocial stress in postpartum lactating women. J. Clin. Endocrinol. Metab. 86, 4798–4804.
Hertzman, C., Boyce, T., 2010. How Experience Gets Under the Skin to Create Gradients in Developmental Health. In: Fielding, J.E., Brownson, R.C., Green, L.W. (Eds.), Annual Review of Public Health, vol. 31. Annual Reviews, Palo Alto, pp. 329–347.
Herzog, C., Czéh, B., Corbach, S., Wuttke, W., Schulte-Herbrüggen, O., Hellweg, R., Flügge, G., Fuchs, E., 2009. Chronic social instability stress in female rats: a potential animal model for female depression. Neuroscience 159, 982–992.
Hillerer, K.M., Jacobs, V.R., Fischer, T., Aigner, L., 2014. The maternal brain: an organ with peripartal plasticity. Neural Plast. 2014, 574159. https://doi.org/10.1155/2014/574159.
Hillerer, K.M., Neumann, I.D., Slattery, D.A., 2012. From stress to postpartum mood and anxiety disorders: how chronic peripartum stress can impair maternal adaptations. Neuroendocrinology 95, 22–38.
Hillerer, K.M., Reber, S.O., Neumann, I.D., Slattery, D.A., 2011. Exposure to chronic pregnancy stress reverses peripartum-associated adaptations: implications for postpartum anxiety and mood disorders. Endocrinology 152, 3930–3940. https://doi.org/10.1210/en.2011-1091.
Hipwell, A.E., Guo, C., Phillips, M.L., Swain, J.E., Moses-Kolko, E.L., 2015. Right frontoinsular cortex and subcortical activity to infant cry is associated with maternal mental state talk. J. Neurosci. 35, 12725–12732. https://doi.org/10.1523/jneurosci.1286-15.2015.
Hiraoka, D., Nomura, M., 2019. Maternal childhood adversity, OXTR genotype and cognitive load impact on perceptual and behavioral responses to infant crying. Psychoneuroendocrinology. 104, 195–202. https://doi.org/10.1016/j.psyneuen.2019.03.005.
Ho, S.S., Konrath, S., Brown, S., Swain, J.E., 2014. Empathy and stress related neural responses in maternal decision making. Front. Neurosci. 8, 152. https://doi.org/10.3389/fnins.2014.00152.
Ho, S.S., Swain, J.E., 2017. Depression alters maternal extended amygdala response and functional connectivity during distress signals in attachment relationship. Behav. Brain Res. 325, 290–296. https://doi.org/10.1016/j.bbr.2017.02.045.
Hoekzema, E., Barba-Müller, E., Pozzobon, C., Picado, M., Lucco, F., García-García, D., Soliva, J.C., Tobeña, A., Desco, M., Crone, E.A., 2017. Pregnancy leads to long-lasting changes in human brain structure. Nat. Neurosci. 20, 287–296.

Hoekzema, E., Tamnes, C.K., Berns, P., Barba-Müller, E., Pozzobon, C., Picado, M., Lucco, F., Martínez-García, M., Desco, M., Ballesteros, A., Crone, E.A., Vilarroya, O., Carmona, S., 2020. Becoming a mother entails anatomical changes in the ventral striatum of the human brain that facilitate its responsiveness to offspring cues. Psychoneuroendocrinology. 112, 104507 https://doi.org/10.1016/j.psyneuen.2019.104507.

Hotham, E., Ali, R., White, J., Robinson, J., 2008. Pregnancy-related changes in tobacco, alcohol and cannabis use reported by antenatal patients at two public hospitals in South Australia. Aust N Z J Obstet and Gynaecol. 48, 248–254. https://doi.org/10.1111/j.1479-828X.2008.00827.x.

Hynan, M., Mounts, K., Vanderbilt, D., 2013. Screening parents of high-risk infants for emotional distress: rationale and recommendations. J. Perinatol. 33, 748–753.

Inmaculada, L., Rodrigo, M.J., El-Deredy, W., Cristián, M., Hernández-Cabrera, J.A., Ileana, Q., 2019. Limbic-visual attenuation to crying faces underlies neglectful mothering. Sci. Rep. (Nature Publisher Group) 9.

Isaacs, J., Healy, O., Peters, H.E., 2017. Paid Family Leave in the United States. Urban Institute.

Iyengar, U., Kim, S., Martinez, S., Fonagy, P., Strathearn, L., 2014. Unresolved trauma in mothers: intergenerational effects and the role of reorganization. Front. Psychol. 5, 966.

Jacobson, L., Sapolsky, R., 1991. The Role of the Hippocampus in Feedback Regulation of the Hypothalamic-Pituitary-Adrenocortical Axis. Endocr Revs. 12, 118–134.

Joosen, K.J., Mesman, J., Bakermans-Kranenburg, M.J., Pieper, S., Zeskind, P.S., van Ijzendoorn, M.H., 2013. Physiological reactivity to infant crying and observed maternal sensitivity. Infancy. 18, 414–431. https://doi.org/10.1111/j.1532-7078.2012.00122.x.

Jou, J., Kozhimannil, K.B., Abraham, J.M., Blewett, L.A., McGovern, P.M., 2018. Paid maternity leave in the United States: Associations with maternal and infant health. Matern. Child Health J. 22, 216–225.

Kalisch, R., 2009. The functional neuroanatomy of reappraisal: time matters. Neurosci. Biobehav. Rev. 33, 1215–1226. https://doi.org/10.1016/j.neubiorev.2009.06.003.

Kalisch, R., Wiech, K., Critchley, H.D., Dolan, R.J., 2006. Levels of appraisal: a medial prefrontal role in high-level appraisal of emotional material. NeuroImage. 30, 1458–1466. https://doi.org/10.1016/j.neuroimage.2005.11.011.

Karg, K., Burmeister, M., Shedden, K., Sen, S., 2011. the serotonin transporter promoter variant (5-HTTLPR), stress, and depression meta-analysis revisited: evidence of genetic moderation. Arch. Gen. Psychiatry 68, 444–454. https://doi.org/10.1001/archgenpsychiatry.2010.189.

Kaufman, J., Zigler, E., 1989. The intergenerational transmission of child abuse. Child maltreatment: Theory and research on the causes and consequences of child abuse and neglect. pp. 129–150.

Kettinger, L.A., Nair, P., Schuler, M.E., 2000. Exposure to environmental risk factors and parenting attitudes among substance-abusing women. Am. J. Drug Alcohol Abuse 26, 1–11. https://doi.org/10.1081/ADA-100100586.

Kim, P., 2016. Human maternal brain plasticity: adaptation to parenting. New Dir. Child Adolesc. Dev. 2016, 47–58.

Kim, P., Capistrano, C., Congleton, C., 2016a. Socioeconomic disadvantages and neural sensitivity to infant cry: role of maternal distress. Soc Cogn Affect Neurosci. 11, 1597–1607.

Kim, P., Capistrano, C.G., Erhart, A., Gray-Schiff, R., Xu, N., 2017a. Socioeconomic disadvantage, neural responses to infant emotions, and emotional availability among first-time new mothers. Behav. Brain Res. 325, 188–196. https://doi.org/10.1016/j.bbr.2017.02.001.

Kim, P., Dufford, A.J., Tribble, R.C., 2018a. Cortical thickness variation of the maternal brain in the first 6 months postpartum: associations with parental self-efficacy. Brain Struct. Funct. 223, 3267–3277. https://doi.org/10.1007/s00429-018-1688-z.

Kim, P., Evans, G.W., Chen, E., Miller, G.E., Seeman, T.E., 2018b. How socioeconomic disadvantages get under the skin and into the brain across the lifespan. In: Halfon, N., Forrest, C., Lerner, R., Faustman, E. (Eds.), The Handbook of Life Course Health Development. Springer, New York, NY, pp. 463–497.

Kim, P., Feldman, R., Mayes, L.C., Eicher, V., Thompson, N., Leckman, J.F., Swain, J.E., 2011. Breastfeeding, brain activation to own infant cry, and maternal sensitivity. J. Child Psychol. Psychiatry 52, 907–915.

Kim, P., Ho, S.S., Evans, G.W., Liberzon, I., Swain, J.E., 2015a. Childhood social inequalities influences neural processes in young adult caregiving. Dev. Psychobiol. 57, 948–960.

Kim, P., Leckman, J.F., Mayes, L.C., Feldman, R., Wang, X., Swain, J.E., 2010a. The plasticity of human maternal brain: longitudinal changes in brain anatomy during the early postpartum period. Behav. Neurosci. 124, 695.

Kim, P., Leckman, J.F., Mayes, L.C., Newman, M.A., Feldman, R., Swain, J.E., 2010b. Perceived quality of maternal care in childhood and structure and function of mothers' brain. Dev Sci. 13, 662–673.

Kim, P., Mayes, L., Feldman, R., Leckman, J.F., Swain, J.E., 2013. Early postpartum parental preoccupation and positive parenting thoughts: Relationship with parent–infant interaction. Infant Ment Health J. 34, 104–116.

Kim, P., Rigo, P., Leckman, J.F., Mayes, L.C., Cole, P.M., Feldman, R., Swain, J.E., 2015b. A prospective longitudinal study of perceived infant outcomes at 18–24 months: neural and psychological correlates of parental thoughts and actions assessed during the first month postpartum. Front. Psychol. 6, 1772.

Kim, P., Strathearn, L., Swain, J.E., 2016b. The maternal brain and its plasticity in humans. Horm. Behav. 77, 113–123.

Kim, P., Tribble, R., Olsavsky, A.K., Dufford, A.J., Erhart, A., Hansen, M., Grande, L., Gonzalez, D.M., 2020. Associations between stress exposure and new mothers' brain responses to infant cry sounds. Neuroimage. 223, 117360. https://doi.org/10.1016/j.neuroimage.2020.117360.

Kim, P., Watamura, S.E., 2015. Two Open Windows: Infant and Parent Neurobiologic Change. The Aspen Institute, Ascend.

Kim, S., Fonagy, P., Allen, J., Strathearn, L., 2014. Mothers' unresolved trauma blunts amygdala response to infant distress. Soc. Neurosci. 9, 352–363.

Kim, S., Iyengar, U., Mayes, L.C., Potenza, M.N., Rutherford, H.J.V., Strathearn, L., 2017b. Mothers with substance addictions show reduced reward responses when viewing their own infant's face. Hum. Brain Mapp. 38, 5421–5439. https://doi.org/10.1002/hbm.23731.

Kim, S., Strathearn, L., 2016. Oxytocin and maternal brain plasticity. New Dir. Child Adolesc. Dev. 2016, 59–72.

Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., Gruppe, H., Mattay, V.S., Gallhofer, B., Meyer-Lindenberg, A., 2005. Oxytocin modulates neural circuitry for social cognition and fear in humans. J. Neurosci. 25, 11489–11493. https://doi.org/10.1523/jneurosci.3984-05.2005.

Klampfl, S.M., Bosch, O.J., 2019. Mom doesn't care: When increased brain CRF system activity leads to maternal neglect in rodents. Front. Neuroendocrinol. 53, 100735. https://doi.org/10.1016/j.yfrne.2019.01.001.

Klampfl, S.M., Schramm, M.M., Gaßner, B.M., Hübner, K., Seasholtz, A.F., Brunton, P.J., Bayerl, D.S., Bosch, O.J., 2018. Maternal stress and the MPOA: Activation of CRF receptor 1 impairs maternal behavior and triggers local oxytocin release in lactating rats. Neuropharmacology 133, 440–450.

Kouneiher, F., Charron, S., Koechlin, E., 2009. Motivation and cognitive control in the human prefrontal cortex. Nat. Neurosci. 12, 939–945. https://doi.org/10.1038/nn.2321.

Krawczyk, D.C., 2002. Contributions of the prefrontal cortex to the neural basis of human decision making. Neurosci. Biobehav. Rev. 26, 631–664.

Lambert, K.G., Byrnes, E.M., 2019. Challenges to the parental brain: Neuroethological and translational considerations. Front. Neuroendocrinol. 53, 100747. https://doi.org/10.1016/j.yfrne.2019.04.004.

Landi, N., Montoya, J., Kober, H., Rutherford, H.J., Mencl, W.E., Worhunsky, P.D., Potenza, M.N., Mayes, L.C., 2011. Maternal neural responses to infant cries and faces: relationships with substance use. Front. Psychiatry 2, 32. https://doi.org/10.3389/fpsyt.2011.00032.

Larsen, C.M., Grattan, D., 2012. Prolactin, neurogenesis, and maternal behaviors. Brain Behav. Immun. 26, 201–209.

Larsen, C.M., Grattan, D.R., 2010. Prolactin-induced mitogenesis in the subventricular zone of the maternal brain during early pregnancy is essential for normal postpartum behavioral responses in the mother. Endocrinology 151, 3805–3814.

Laurent, H.K., Ablow, J.C., 2011. A cry in the dark: depressed mothers show reduced neural activation to their own infant's cry. Soc. Cogn. Affect. Neurosci. 7, 125–134 doi: nsq091 [pii]10.1093/scan/nsq091.

Laurent, H.K., Stevens, A., Ablow, J.C., 2011. Neural correlates of hypothalamic-pituitary-adrenal regulation of mothers with their infants. Biol. Psychiatry 70, 826–832 doi: S0006-3223(11)00610-X [pii]10.1016/j.biopsych.2011.06.011.

Leach, L.S., Poyser, C., Fairweather-Schmidt, K., 2017. Maternal perinatal anxiety: A review of prevalence and correlates. Clin. Psychol. 21, 4–19.

Lebel, C., MacKinnon, A., Bagshawe, M., Tomfohr-Madsen, L., Giesbrecht, G., 2020. Elevated depression and anxiety symptoms among pregnant individuals during the COVID-19 pandemic. J. Affect. Disord. 277, 5–13. https://doi.org/10.1016/j.jad.2020.07.126.

Lenzi, D., Trentini, C., Macaluso, E., Graziano, S., Speranza, A.M., Pantano, P., Ammaniti, M., 2016. Mothers with depressive symptoms display differential brain activations when empathizing with infant faces. Psychiatry Res. Neuroimag. 249, 1–11.

Lenzi, D., Trentini, C., Pantano, P., Macaluso, E., Lenzi, G.L., Ammaniti, M., 2013. Attachment models affect brain responses in areas related to emotions and empathy in nulliparous women. Hum. Brain Mapp. 34, 1399–1414.

Leuner, B., Fredericks, P.J., Nealer, C., Albin-Brooks, C., 2014. Chronic gestational stress leads to depressive-like behavior and compromises medial prefrontal cortex structure and function during the postpartum period. PLoS One 9.

Leuner, B., Glasper, E.R., Gould, E., 2010. Parenting and plasticity. Trends Neuroscis. 33, 465–473.

Leuner, B., Sabihi, S., 2016. The birth of new neurons in the maternal brain: hormonal regulation and functional implications. Front. Neuroendocrinol. https://doi.org/10.1016/j.yfrne.2016.02.004.

Levine, A., Zagoory-Sharon, O., Feldman, R., Weller, A., 2007. Oxytocin during pregnancy and early postpartum: individual patterns and maternal–fetal attachment. Peptides 28, 1162–1169.

Levy, J., Goldstein, A., Feldman, R., 2019a. The neural development of empathy is sensitive to caregiving and early trauma. Nat. Commun. 10, 1905. https://doi.org/10.1038/s41467-019-09927-y.

Levy, J., Yirmiya, K., Goldstein, A., Feldman, R., 2019b. Chronic trauma impairs the neural basis of empathy in mothers: Relations to parenting and children's empathic abilities. Dev. Cogn. Neurosci. 38, 100658. https://doi.org/10.1016/j.dcn.2019.100658.

Li, T., Horta, M., Mascaro, J.S., Bijanki, K., Arnal, L.H., Adams, M., Barr, R.G., Rilling, J. K., 2018. Explaining individual variation in paternal brain responses to infant cries. Physiol. Behav. 193, 43–54. https://doi.org/10.1016/j.physbeh.2017.12.033.

Liu, C.H., Giallo, R., Doan, S.N., Seidman, L.J., Tronick, E., 2016. Racial and Ethnic Differences in Prenatal Life Stress and Postpartum Depression Symptoms. Arch. Psychiatr. Nurs. 30, 7–12. https://doi.org/10.1016/j.apnu.2015.11.002.

Livingston, G., Thomas, D., 2019, December 16. Among 41 countries, only U.S. lacks paid parental leave.

Lonstein, J.S., 2019. The dynamic serotonin system of the maternal brain. Arch Womens Ment Health. 22, 237–243.

Lonstein, J.S., Lévy, F., Fleming, A.S., 2015. Common and divergent psychobiological mechanisms underlying maternal behaviors in non-human and human mammals. Horm. Behav. 73, 156–185.
Lonstein, J.S., Maguire, J., Meinlschmidt, G., Neumann, I.D., 2014. Emotion and mood adaptations in the peripartum female: complementary contributions of GABA and oxytocin. J. Neuroendocrinol. 26, 649–664.
Lorberbaum, J.P., Newman, J.D., Horwitz, A.R., Dubno, J.R., Lydiard, R.B., Hamner, M. B., Bohning, D.E., George, M.S., 2002. A potential role for thalamocingulate circuitry in human maternal behavior. Biolol. Psychiatry. 51, 431–445.
Lovic, V., Gonzalez, A., Fleming, A.S., 2001. Maternally separated rats show deficits in maternal care in adulthood. Dev. Psychobiol. 39, 19–33.
Lowell, A.F., Maupin, A.N., Landi, N., Potenza, M.N., Mayes, L.C., Rutherford, H.J.V., 2020. Substance use and mothers' neural responses to infant cues. Infant. Ment Health J. 41, 264–277. https://doi.org/10.1002/imhj.21835.
Luders, E., Gingnell, M., Poromaa, I.S., Engman, J., Kurth, F., Gaser, C., 2018. Potential brain age reversal after pregnancy: younger brains at 4–6 weeks postpartum. Neuroscience 386, 309–314. https://doi.org/10.1016/j.neuroscience.2018.07.006.
Luders, E., Kurth, F., Gingnell, M., Engman, J., Yong, E.-L., Poromaa, I.S., Gaser, C., 2020. From baby brain to mommy brain: Widespread gray matter gain after giving birth. Cortex. 126, 334–342.
Lupien, S.J., Juster, R.-P., Raymond, C., Marin, M.-F., 2018. The effects of chronic stress on the human brain: From neurotoxicity, to vulnerability, to opportunity. Front. Neuroendocrinol. 49, 91–105. https://doi.org/10.1016/j.yfrne.2018.02.001.
Lupien, S.J., McEwen, B.S., Gunnar, M.R., Heim, C., 2009. Effects of stress throughout the lifespan on the brain, behaviour and cognition. Nat. Rev. Neurosci. 10, 434–445 doi: nrn2639 [pii]10.1038/nrn2639.
Lyons-Ruth, K., Bronfman, E., Parsons, E., 1999. Maternal frightened, frightening, or atypical behavior and disorganized infant attachment patterns. Monogr. Soc. Res. Child Dev. 67–96.
Maestripieri, D., 2005. Early experience affects the intergenerational transmission of infant abuse in rhesus monkeys. PNAS 102, 9726–9729.
Maguire-Jack, K., Lanier, P., Lombardi, B., 2020. Investigating racial differences in clusters of adverse childhood experiences. Am. J. Orthopsychiatr. 90, 106–114. https://doi.org/10.1037/ort0000405.
Mahenge, B., Stöckl, H., Mizinduko, M., Mazalale, J., Jahn, A., 2018. Adverse childhood experiences and intimate partner violence during pregnancy and their association to postpartum depression. J. Affect. Disord. 229, 159–163. https://doi.org/10.1016/j.jad.2017.12.036.
Maleki-Saghooni, N., Amel Barez, M., Moeindarbari, S., Karimi, F.Z., 2017. Investigating the breastfeeding self-efficacy and its related factors in primiparous breastfeeding mothers. International. J. Pediatr. 5, 6275–6283.
Marcenko, M.O., Kemp, S.P., Larson, N.C., 2000. Childhood experiences of abuse, later substance use, and parenting outcomes among low-income mothers. Am. J. Orthopsychiatr. 70, 316.
McDonald, S., Slade, P., Spiby, H., Iles, J., 2011. Post-traumatic stress symptoms, parenting stress and mother-child relationships following childbirth and at 2 years postpartum. J. Psychosom. Obstet. Gynecol. 32, 141–146.
McEwen, B.S., 2001. Plasticity of the hippocampus: adaptation to chronic stress and allostatic load. Ann. N. Y. Acad. Sci. 933, 265–277.
McEwen, B.S., 2012. Brain on stress: How the social environment gets under the skin. PNAS 109, 17180–17185. https://doi.org/10.1073/pnas.1121254109.
McEwen, B.S., Nasca, C., Gray, J.D., 2016. Stress effects on neuronal structure: hippocampus, amygdala, and prefrontal cortex. Neuropsychopharmacology. 41, 3.
McLaughlin, K.A., Sheridan, M.A., 2016. Beyond cumulative risk: A dimensional approach to childhood adversity. Curr. Dir. Psychol Sci. 25, 239–245.
Meaney, M.J., 2010. Epigenetics and the Biological Definition of Gene x Environment Interactions. Child Dev. 81, 41–79.
Mersky, J.P., Janczewski, C.E., 2018. Adverse childhood experiences and postpartum depression in home visiting programs: prevalence, association, and mediating mechanisms. Matern. Child Health J. 22, 1051–1058. https://doi.org/10.1007/s10995-018-2488-z.
Mezey, G., Bacchus, L., Bewley, S., White, S., 2005. Domestic violence, lifetime trauma and psychological health of childbearing women. BJOG-Int. J. Obstet. Gynaecol. 112, 197–204. https://doi.org/10.1111/j.1471-0528.2004.00307.x.
Mezick, E.J., Matthews, K.A., Hall, M., Strollo Jr, P.J., Buysse, D.J., Kamarck, T.W., Owens, J.F., Reis, S.E., 2008. Influence of race and socioeconomic status on sleep: Pittsburgh Sleep SCORE project. Psychosom. Med. 70, 410.
Mezzacappa, E.S., Katlin, E.S., 2002. Breast-feeding is associated with reduced perceived stress and negative mood in mothers. Health Psychol. 21, 187–219.
Mezzacappa, E.S., Kelsey, R.M., Katkin, E.S., 2005. Breast feeding, bottle feeding, and maternal autonomic responses to stress. J. Psychosom. Res. 58, 351–365.
Mielke, E.L., Neukel, C., Bertsch, K., Reck, C., Möhler, E., Herpertz, S.C., 2016. Maternal sensitivity and the empathic brain: Influences of early life maltreatment. J. Psychiatr. Res. 77, 59–66. https://doi.org/10.1016/j.jpsychires.2016.02.013.
Miller, G.E., Brody, G.H., Yu, T., Chen, E., 2014. A family-oriented psychosocial intervention reduces inflammation in low-SES African American youth. PNAS 111, 11287–11292.
Mills-Koonce, W.R., Gariepy, J.-L., Propper, C., Sutton, K., Calkins, S., Moore, G., Cox, M., 2007. Infant and parent factors associated with early maternal sensitivity: A caregiver-attachment systems approach. Infant. Behav. Dev. 30, 114–126.
Molloy, E., Biggerstaff, D.L., Sidebotham, P., 2020. A phenomenological exploration of parenting after birth trauma: Mothers perceptions of the first year. Women and Birth. https://doi.org/10.1016/j.wombi.2020.03.004.
Montirosso, R., Arrigoni, F., Casini, E., Nordio, A., De Carli, P., Di Salle, F., Moriconi, S., Re, M., Reni, G., Borgatti, R., 2017. Greater brain response to emotional expressions of their own children in mothers of preterm infants: an fMRI study. J. Perinatol. 37, 716–722. https://doi.org/10.1038/jp.2017.2.
Moog, N.K., Entringer, S., Rasmussen, J.M., Styner, M., Gilmore, J.H., Kathmann, N., Heim, C.M., Wadhwa, P.D., Buss, C., 2018. Intergenerational effect of maternal exposure to childhood maltreatment on newborn brain anatomy. Biol. Psychiatry 83, 120–127. https://doi.org/10.1016/j.biopsych.2017.07.009.
Morelen, D., Shaffer, A., Suveg, C., 2016. Maternal emotion regulation: Links to emotion parenting and child emotion regulation. J. Fam. Issues 37, 1891–1916.
Morris, A.S., Robinson, L.R., Hays-Grudo, J., Claussen, A.H., Hartwig, S.A., Treat, A.E., 2017. Targeting parenting in early childhood: A public health approach to improve outcomes for children living in poverty. Child Dev. 88, 388–397.
Moussaoui, N., Larauche, M., Biraud, M., Molet, J., Million, M., Mayer, E., Taché, Y., 2016. Limited nesting stress alters maternal behavior and in vivo intestinal permeability in male wistar pup rats. PLoS One 11, e0155037. https://doi.org/10.1371/journal.pone.0155037.
Musser, E.D., Kaiser-Laurent, H., Ablow, J.C., 2012. The neural correlates of maternal sensitivity: An fMRI study. Dev. Cogn. Neurosci. 2, 428–436. https://doi.org/10.1016/j.dcn.2012.04.003.
Muzik, M., Rosenblum, K.L., Alfafara, E.A., Schuster, M.M., Miller, N.M., Waddell, R.M., Kohler, E.S., 2015. Mom Power: preliminary outcomes of a group intervention to improve mental health and parenting among high-risk mothers. Arch. Womens Ment Health. 18, 507–521. https://doi.org/10.1007/s00737-014-0490-z.
Nelson Iii, C.A., Zeanah, C.H., Fox, N.A., 2019. How early experience shapes human development: The case of psychosocial deprivation. Neural Plast. 2019 https://doi.org/10.1155/2019/1676285.
Neri, E., Agostini, F., Salvatori, P., Biasini, A., Monti, F., 2015. Mother-preterm infant interactions at 3 months of corrected age: influence of maternal depression, anxiety and neonatal birth weight. Front. Psychol. 6, 1234.
Neukel, C., Bertsch, K., Fuchs, A., Zietlow, A.-L., Reck, C., Moehler, E., Brunner, R., Bermpohl, F., Herpertz, S.C., 2018. The maternal brain in women with a history of early-life maltreatment: an imagination-based fMRI study of conflictual versus pleasant interactions with children. J. Psychiatr Neurosci. 43, 273–282.
Neumann, I., Johnstone, H., Hatzinger, M., Liebsch, G., Shipston, M., Russell, J., Landgraf, R., Douglas, A., 1998. Attenuated neuroendocrine responses to emotional and physical stressors in pregnant rats involve adenohypophysial changes. J. Physiol. 508, 289–300.
Nguyen, A.J., Hoyer, E., Rajhans, P., Strathearn, L., Kim, S., 2019. A tumultuous transition to motherhood: Altered brain and hormonal responses in mothers with postpartum depression. J. Neuroendocrinol. 31, e12794. https://doi.org/10.1111/jne.12794.
Noriuchi, M., Kikuchi, Y., Mori, K., Kamio, Y., 2019. The orbitofrontal cortex modulates parenting stress in the maternal brain. Sci. Rep. 9, 1–9.
Numan, M., 2012. Maternal behavior: neural circuits, stimulus valence, and motivational processes. Parenting. 12, 105–114.
Numan, M., 2020. The Parental Brain: Mechanisms, Development, and Evolution. Oxford University Press, New Yrok.
Numan, M., Insel, T.R., 2003. The Neurobiology of Parental Behavior. Springer, New York.
O'Hara, M.W., McCabe, J.E., 2013. Postpartum depression: current status and future directions. Annu. Rev. Clin. Psychol. 9, 379–407.
Oatridge, A., Holdcroft, A., Saeed, N., Hajnal, J.V., Puri, B.K., Fusi, L., Bydder, G.M., 2002. Change in brain size during and after pregnancy: study in healthy women and women with preeclampsia. Am. J. Neuroradiol. 23, 19–26.
Ochsner, K.N., Silvers, J.A., Buhle, J.T., 2012. Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion. Ann. N. Y. Acad. Sci. 1251, E1–E24. https://doi.org/10.1111/j.1749-6632.2012.06751.x.
Oddi, K.B., Murdock, K.W., Vadnais, S., Bridgett, D.J., Gartstein, M.A., 2013. Maternal and infant temperament characteristics as contributors to parenting stress in the first year postpartum. Infant. Child Dev. 22, 553–579.
Olds, D.L., Kitzman, H., Hanks, C., Cole, R., Anson, E., Sidora-Arcoleo, K., Luckey, D.W., Henderson Jr., C.R., Holmberg, J., Tutt, R.A., Stevenson, A.J., Bondy, J., 2007. Effects of nurse home visiting on maternal and child functioning: age-9 follow-up of a randomized trial. Pediatrics 120, e832–e845 doi: 120/4/e832 [pii]10.1542/peds.2006-2111.
Olsavsky, A.K., Stoddard, J., Erhart, A., Tribble, R., Kim, P., 2019. Neural processing of infant and adult face emotion and maternal exposure to childhood maltreatment. Soc. Cogn. Affect. Neurosci. 14, 997–1008.
Orchard, E.R., Chopra, S., Ward, P.G., Storey, E., Jamadar, S.D., Egan, G.F., 2020. Neuroprotective effects of motherhood on brain function in late-life: a resting state fMRI study. bioRxiv.
Paul, S., Austin, J., Elliott, R., Ellison-Wright, I., Wan, M.W., Drake, R., Downey, D., Elmadih, A., Mukherjee, I., Heaney, L., Williams, S., Abel, K.M., 2019. Neural pathways of maternal responding: systematic review and meta-analysis. Arch. Womens Ment Health. 22, 179–187. https://doi.org/10.1007/s00737-018-0878-2.
Pawluski, J.L., Lambert, K.G., Kinsley, C.H., 2016. Neuroplasticity in the maternal hippocampus: Relation to cognition and effects of repeated stress. Horm. Behav. 77, 86–97. https://doi.org/10.1016/j.yhbeh.2015.06.004.
Pawluski, J.L., Li, M., Lonstein, J.S., 2019. Serotonin and motherhood: From molecules to mood. Front. Neuroendocrinol. 53, 100742.
Pawluski, J.L., Lonstein, J.S., Fleming, A.S., 2017. The neurobiology of postpartum anxiety and depression. Trends Neurosci. 40, 106–120. https://doi.org/10.1016/j.tins.2016.11.009.
Pears, K.C., Capaldi, D.M., 2001. Intergenerational transmission of abuse: a two-generational prospective study of an at-risk sample. Child Abuse Negl. 25, 1439–1461. https://doi.org/10.1016/s0145-2134(01)00286-1.

Pearson, R.M., Lightman, S.L., Evans, J., 2011. Attentional processing of infant emotion during late pregnancy and mother–infant relations after birth. Arch. Womens Ment Health. 14, 23–31.
Pedersen, C.A., Caldwell, J.D., Walker, C., Ayers, G., Mason, G.A., 1994. Oxytocin activates the postpartum onset of rat maternal behavior in the ventral tegmental and medial preoptic areas. Behav. Neurosci. 108, 1163.
Peña, C.J., Monk, C., Champagne, F.A., 2012. Epigenetic effects of prenatal stress on 11β-hydroxysteroid dehydrogenase-2 in the placenta and fetal brain. PLoS One 7, e39791.
Peña, C.J., Neugut, Y.D., Calarco, C.A., Champagne, F.A., 2014. Effects of maternal care on the development of midbrain dopamine pathways and reward-directed behavior in female offspring. Eur. J. Neurosci. 39, 946–956.
Peña, C.J., Neugut, Y.D., Champagne, F.A., 2013. Developmental timing of the effects of maternal care on gene expression and epigenetic regulation of hormone receptor levels in female rats. Endocrinology 154, 4340–4351.
Perry, R.E., Finegood, E.D., Braren, S.H., Dejoseph, M.L., Putrino, D.F., Wilson, D.A., Sullivan, R.M., Raver, C.C., Blair, C., Investigators, F.L.P.K., 2018. Developing a neurobehavioral animal model of poverty: Drawing cross-species connections between environments of scarcity-adversity, parenting quality, and infant outcome. Dev. Psychopathol. 1–20.
Phu, T., Erhart, A., Kim, P., Watamura, S.E., 2020. Two Open Windows: Part II. The Aspen Institute, Ascend.
Radley, J.J., Arias, C.M., Sawchenko, P.E., 2006. Regional differentiation of the medial prefrontal cortex in regulating adaptive responses to acute emotional stress. J. Neurosci. 26, 12967–12976.
Raver, C.C., Leadbeater, B.J., 1999. Mothering under pressure: Environmental, child, and dyadic correlates of maternal self-efficacy among low-income women. J. Fam. Psychol. 13, 523.
Rayson, H., Bonaiuto, J.J., Ferrari, P.F., Murray, L., 2017. Early maternal mirroring predicts infant motor system activation during facial expression observation. Sci. Rep. 7, 11738. https://doi.org/10.1038/s41598-017-12097-w.
Razurel, C., Kaiser, B., Sellenet, C., Epiney, M., 2012. Relation between perceived stress, social support, and coping strategies and maternal well-being: A review of the literature. Women Health 53, 74–99. https://doi.org/10.1080/03630242.2012.732681.
Reichl, C., Kaess, M., Fuchs, A., Bertsch, K., Bödeker, K., Zietlow, A.-L., Dittrich, K., Hartmann, A.M., Rujescu, D., Parzer, P., Resch, F., Bermpohl, F., Herpertz, S.C., Brunner, R., 2019. Childhood adversity and parenting behavior: the role of oxytocin receptor gene polymorphisms. J. Neural Transm. 126, 777–787. https://doi.org/10.1007/s00702-019-02009-9.
Reindl, V., Gerloff, C., Scharke, W., Konrad, K., 2018. Brain-to-brain synchrony in parent-child dyads and the relationship with emotion regulation revealed by fNIRS-based hyperscanning. Neuroimage. 178, 493–502. https://doi.org/10.1016/j.neuroimage.2018.05.060.
Rich-Edwards, J.W., Kleinman, K., Abrams, A., Harlow, B.L., McLaughlin, T.J., Joffe, H., Gillman, M.W., 2006. Sociodemographic predictors of antenatal and postpartum depressive symptoms among women in a medical group practice. J Epidemiol Comm Health. 60, 221–227.
Riem, M.M.E., Kunst, L.E., Bekker, M.H.J., Fallon, M., Kupper, N., 2020. Intranasal oxytocin enhances stress-protective effects of social support in women with negative childhood experiences during a virtual Trier Social Stress Test. Psychoneuroendocrinology. 111, 104482. https://doi.org/10.1016/j.psyneuen.2019.104482.
Rigo, P., Esposito, G., Bornstein, M.H., De Pisapia, N., Manzardo, C., Venuti, P., 2019a. Brain processes in mothers and nulliparous women in response to cry in different situational contexts: A default mode network study. Parenting. 19, 69–85. https://doi.org/10.1080/15295192.2019.1555430.
Rigo, P., Kim, P., Esposito, G., Putnick, D.L., Venuti, P., Bornstein, M.H., 2019b. Specific maternal brain responses to their own child's face: an fMRI meta-analysis. Dev. Rev. 51, 58–69.
Rocchetti, M., Radua, J., Paloyelis, Y., Xenaki, L.A., Frascarelli, M., Caverzasi, E., Politi, P., Fusar-Poli, P., 2014. Neurofunctional maps of the "maternal brain" and the effects of oxytocin: A multimodal voxel-based meta-analysis. Psychiatr Clin Neurosci. 68, 733–751. https://doi.org/10.1111/pcn.12185.
Rodrigo, M.J., León, I., Góngora, D., Hernández-Cabrera, J.A., Byrne, S., Bobes, M.A., 2016. Inferior fronto-temporo-occipital connectivity: a missing link between maltreated girls and neglectful mothers. Soc. Cogn. Affect. Neurosci. 11, 1658–1665.
Rodrigues, S.M., LeDoux, J.E., Sapolsky, R.M., 2009. The influence of stress hormones on fear circuitry. Annu. Rev. Neurosci. 32, 289–313. https://doi.org/10.1146/annurev.neuro.051508.135620.
Rosenblatt, J.S., 2002. Hormonal bases of parenting in mammals. In: Handbook of Parenting. 2, pp. 31–60.
Roth, T., Lubin, F., Funk, A., Sweatt, J., 2009. Lasting epigenetic influence of early life adversity on the BDNF gene. Biol. Psychiatry 65, 760–769.
Russell, J., Leng, G., 1998. Sex, parturition and motherhood without oxytocin? J. Endocrinol. 157, 343–359.
Rutherford, H.J.V., Crowley, M.J., Gao, L., Francis, B., Schultheis, A., Mayes, L.C., 2018. Prenatal neural responses to infant faces predict postpartum reflective functioning. Infant Behav Dev. 53, 43–48. https://doi.org/10.1016/j.infbeh.2018.09.003.
Rutherford, H.J.V., Mayes, L.C., 2019. Parenting stress: A novel mechanism of addiction vulnerability. Neurobiol. Stress 11, 100172. https://doi.org/10.1016/j.ynstr.2019.100172.
Rutherford, H.J.V., Potenza, M.N., Mayes, L.C., Scheinost, D., 2019. The application of connectome-based predictive modeling to the maternal brain: implications for mother-infant bonding. Cereb. Cortex. https://doi.org/10.1093/cercor/bhz185.
Rutherford, H.J.V., Wallace, N.S., Laurent, H.K., Mayes, L.C., 2015. Emotion regulation in parenthood. Dev. Rev. 36, 1–14. https://doi.org/10.1016/j.dr.2014.12.008.
Sabihi, S., Dong, S.M., Durosko, N.E., Leuner, B., 2014. Oxytocin in the medial prefrontal cortex regulates maternal care, maternal aggression and anxiety during the postpartum period. Front. Behav. Neurosci. 8, 258. https://doi.org/10.3389/fnbeh.2014.00258.
Savelieva, K., Hintsanen, M., Dobewall, H., Jokela, M., Pulkki-Råback, L., Elovainio, M., Seppälä, I., Lehtimäki, T., Raitakari, O., Keltikangas-Järvinen, L., 2019. The role of oxytocinergic genes in the intergenerational transmission of parent–child relationship qualities. Horm. Behav. 114, 104540. https://doi.org/10.1016/j.yhbeh.2019.06.004.
Saxbe, D., Rossin-Slater, M., Goldenberg, D., 2018. The transition to parenthood as a critical window for adult health. Am. Psychol. 73, 1190–1200. https://doi.org/10.1037/amp0000376.
Schechter, D.S., Moser, D.A., Wang, Z.S., Marsh, R., Hao, X.J., Duan, Y.S., Yu, S., Gunter, B., Murphy, D., McCaw, J., Kangarlu, A., Willheim, E., Myers, M.M., Hofer, M.A., Peterson, B.S., 2012. An fMRI study of the brain responses of traumatized mothers to viewing their toddlers during separation and play. Soc Cogn Affect Neurosci. 7, 969–979. https://doi.org/10.1093/scan/nsr069.
Schulte, H.M., Weisner, D., Allolio, B., 1990. The corticotrophin releasing hormone test in late pregnancy: lack of adrenocorticotrophin and cortisol response. Clin. Endocrinol. 33, 99–106.
Sedov, I.D., Cameron, E.E., Madigan, S., Tomfohr-Madsen, L.M., 2018. Sleep quality during pregnancy: A meta-analysis. Sleep Med. Rev. 38, 168–176.
Segre, L.S., O'Hara, M.W., Arndt, S., Stuart, S., 2007. The prevalence of postpartum depression: the relative significance of three social status indices. Soc. Psychiatr Psychiatr Epidemiol. 42, 316–321. https://doi.org/10.1007/s00127-007-0168-1.
Senese, V.P., Shinohara, K., Esposito, G., Doi, H., Venuti, P., Bornstein, M.H., 2017. Implicit association to infant faces: Genetics, early care experiences, and cultural factors influence caregiving propensities. Behav. Brain Res. 325, 163–172. https://doi.org/10.1016/j.bbr.2016.09.040.
Seth, S., Lewis, A.J., Galbally, M., 2016. Perinatal maternal depression and cortisol function in pregnancy and the postpartum period: a systematic literature review. BMC Pregnancy Childbirth. 16, 124.
Shaffer, A., Obradović, J., 2017. Unique contributions of emotion regulation and executive functions in predicting the quality of parent–child interaction behaviors. J. Fam. Psychol. 31, 150.
Shamay-Tsoory, S.G., Aharon-Peretz, J., Perry, D., 2009. Two systems for empathy: a double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. Brain. 132, 617–627.
Sheridan, M.A., McLaughlin, K.A., 2014. Dimensions of early experience and neural development: deprivation and threat. Trends Cogn Sci. 18, 580–585. https://doi.org/10.1016/j.tics.2014.09.001.
Simons, R.L., Whitbeck, L.B., Conger, R.D., Wu, C.-I., 1991. Intergenerational transmission of harsh parenting. Dev. Psychol. 27, 159.
Simpson, M., Catling, C., 2016. Understanding psychological traumatic birth experiences: A literature review. Women Birth. 29, 203–207.
Singer, L.T., Salvator, A., Guo, S., Collin, M., Lilien, L., Baley, J., 1999. Maternal psychological distress and parenting stress after the birth of a very low-birth-weight infant. JAMA 281, 799–805.
Skouteris, H., Wertheim, E.H., Germano, C., Paxton, S.J., Milgrom, J., 2009. Assessing sleep during pregnancy: a study across two time points examining the Pittsburgh Sleep Quality Index and associations with depressive symptoms. Womens Health Issues. 19, 45–51.
Slattery, D.A., Hillerer, K.M., 2016. The maternal brain under stress: Consequences for adaptive peripartum plasticity and its potential functional implications. Front. Neuroendocrinol. 41, 114–128. https://doi.org/10.1016/j.yfrne.2016.01.004.
Slattery, D.A., Neumann, I.D., 2008. No stress please! Mechanisms of stress hyporesponsiveness of the maternal brain. J. Physiol. 586, 377–385.
Smith, J.W., Seckl, J.R., Evans, A.T., Costall, B., Smythe, J.W., 2004. Gestational stress induces post-partum depression-like behaviour and alters maternal care in rats. Psychoneuroendocrinology. 29, 227–244. https://doi.org/10.1016/S0306-4530(03)00025-8.
Smith, P.B., Pederson, D.R., 1988. Maternal sensitivity and patterns of infant-mother attachment. Child Dev. 59, 1097–1101.
Spreng, R.N., Mar, R.A., Kim, A.S., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J. Cogn. Neurosci. 21, 489–510.
Stamatakis, A., Kalpachidou, T., Raftogianni, A., Zografou, E., Tzanou, A., Pondiki, S., Stylianopoulou, F., 2015. Rat dams exposed repeatedly to a daily brief separation from the pups exhibit increased maternal behavior, decreased anxiety and altered levels of receptors for estrogens (ERα, ERβ), oxytocin and serotonin (5-HT1A) in their brain. Psychoneuroendocrinol. 52, 212–228.
Stanczyk, A.B., 2016. Greater Financial Supports Could Improve Household Economic Wellbeing around a Birth. Davis: University of California, Davis, Center for Policy Research, 4.
Strathearn, L., Fonagy, P., Amico, J., Montague, P.R., 2009. Adult attachment predicts maternal brain and oxytocin response to infant cues. Neuropsychopharmacology. 34, 2655–2666.
Strathearn, L., Li, J., Fonagy, P., Montague, P.R., 2008. What's in a smile? Maternal brain responses to infant facial cues. Pediatrics 122, 40–51.
Sullivan, R.M., Gratton, A., 2002. Prefrontal cortical regulation of hypothalamic–pituitary–adrenal function in the rat and implications for psychopathology: side matters. Psychoneuroendocrinology. 27, 99–114. https://doi.org/10.1016/S0306-4530(01)00038-5.

Swain, J.E., Ho, S.S., Fox, H., Garry, D., Brummelte, S., 2019. Effects of opioids on the parental brain in health and disease. Front. Neuroendocrinol. 54, 100766. https://doi.org/10.1016/j.yfrne.2019.100766.
Swain, J.E., Ho, S.S., Rosenblum, K.L., Morelen, D., Dayton, C.J., Muzik, M., 2017. Parent-child intervention decreases stress and increases maternal brain activity and connectivity during own baby-cry: An exploratory study. Dev. Psychopathol. 29, 535–553. https://doi.org/10.1017/s0954579417000165.
Swain, J.E., Kim, P., Ho, S.S., 2011. Neuroendocrinology of parental response to baby-cry. J. Neuroendocrinol. 23, 1036–1041.
Tanya Nagahawatte, N., Goldenberg, R.L., 2008. Poverty, maternal health, and adverse pregnancy outcomes. Ann. N. Y. Acad. Sci. 1136, 80–85.
Taylor, S.E., Eisenberger, N.I., Saxbe, D., Lehman, B.J., Lieberman, M.D., 2006. Neural responses to emotional stimuli are associated with childhood family stress. Biol. Psychiatry 60, 296–301. https://doi.org/10.1016/j.biopsych.2005.09.027.
Teti, D.M., Gelfand, D.M., 1991. Behavioral competence among mothers of infants in the first year: the mediational role of maternal self-efficacy. Child Dev. 62, 918–929.
Thomason, E., Volling, B.L., Flynn, H.A., McDonough, S.C., Marcus, S.M., Lopez, J.F., Vazquez, D.M., 2014. Parenting stress and depressive symptoms in postpartum mothers: Bidirectional or unidirectional effects? Infant. Behav. Dev. 37, 406–415.
Torner, L., 2016. Actions of Prolactin in the Brain: From Physiological Adaptations to Stress and Neurogenesis to Psychopathology. Front. Endocrinol. 7 https://doi.org/10.3389/fendo.2016.00025.
Torner, L., Neumann, I.D., 2002. The brain prolactin system: involvement in stress response adaptations in lactation. Stress. 5, 249–257.
Torner, L., Toschi, N., Pohlinger, A., Landgraf, R., Neumann, I.D., 2001. Anxiolytic and anti-stress effects of brain prolactin: improved efficacy of antisense targeting of the prolactin receptor by molecular modeling. J. Neurosci. 21, 3207–3214.
Tottenham, N., 2020. Early adversity and the neotenous human brain. Biol. Psychiatry 87, 350–358. https://doi.org/10.1016/j.biopsych.2019.06.018.
Tottenham, N., Sheridan, M.A., 2010. A review of adversity, the amygdala and the hippocampus: a consideration of developmental timing. Front. Hum. Neurosci. 3, 68.
Urizar, G.G., Muñoz, R.F., 2011. Impact of a prenatal cognitive-behavioral stress management intervention on salivary cortisol levels in low-income mothers and their infants. Psychoneuroendocrinology. 36, 1480–1494. https://doi.org/10.1016/j.psyneuen.2011.04.002.
Van Ijzendoorn, M.H., 1992. Intergenerational transmission of parenting: A review of studies in nonclinical populations. Dev. Rev. 12, 76–99.
Van Ijzendoorn, M.H., 1995. Adult attachment representations, parental responsiveness, and infant attachment: a meta-analysis on the predictive validity of the Adult Attachment Interview. Psychol. Bull. 117, 387.
van IJzendoorn, M.H., Juffer, F., Duyvesteyn, M.G., 1995. Breaking the intergenerational cycle of insecure attachment: A review of the effects of attachment-based interventions on maternal sensitivity and infant security. J. Child Psychol. Psychiatry. 36, 225–248.
Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. Hum. Brain Mapp. 30, 829–858.
Van Overwalle, F., Baetens, K., 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. Neuroimage. 48, 564–584.
Venuti, P., Caria, A., Esposito, G., De Pisapia, N., Bornstein, M.H., de Falco, S., 2012. Differential brain responses to cries of infants with autistic disorder and typical development: An fMRI study. Res. Dev. Disabil. 33, 2255–2264. https://doi.org/10.1016/j.ridd.2012.06.011.
Vieten, C., Astin, J., 2008. Effects of a mindfulness-based intervention during pregnancy on prenatal stress and mood: results of a pilot study. Arch Womens Ment Health. 11, 67–74.
Walker, C.-D., Bath, K.G., Joels, M., Korosi, A., Larauche, M., Lucassen, P.J., Morris, M.J., Raineki, C., Roth, T.L., Sullivan, R.M., Taché, Y., Baram, T.Z., 2017. Chronic early life stress induced by limited bedding and nesting (LBN) material in rodents: critical considerations of methodology, outcomes and translational potential. Stress. 20, 421–448. https://doi.org/10.1080/10253890.2017.1343296.
Wan, M.W., Downey, D., Strachan, H., Elliott, R., Williams, S.R., Abel, K.M., 2014. The neural basis of maternal bonding. PLoS One 9, e88436. https://doi.org/10.1371/journal.pone.0088436.
Weaver, I.C., Cervoni, N., Champagne, F.A., D'Alessio, A.C., Sharma, S., Seckl, J.R., Dymov, S., Szyf, M., Meaney, M.J., 2004. Epigenetic programming by maternal behavior. Nat. Neurosci. 7, 847–854.
Wells, N.M., Harris, J.D., 2007. Housing quality, psychological distress, and the mediating role of social withdrawal: A longitudinal study of low-income women. J Environ Psychol. 27, 69–78.
Witteman, J., Van IJzendoorn, M., Rilling, J., Bos, P., Schiller, N., Bakermans-Kranenburg, M., 2019. Towards a neural model of infant cry perception. Neurosci. Biobehav. Rev.
Wolf, I.A.-C., Gilles, M., Peus, V., Scharnholz, B., Seibert, J., Jennen-Steinmetz, C., Krumm, B., Deuschle, M., Laucht, M., 2017. Impact of prenatal stress on the dyadic behavior of mothers and their 6-month-old infants during a play situation: role of different dimensions of stress. J. Neural Transm. 124, 1251–1260.
Wonch, K.E., de Medeiros, C.B., Barrett, J.A., Dudin, A., Cunningham, W.A., Hall, G.B., Steiner, M., Fleming, A.S., 2015. Postpartum depression and brain response to infants: Differential amygdala response and connectivity. Soc. Neurosci. 1–18 https://doi.org/10.1080/17470919.2015.1131193.
Wright, D.B., Laurent, H.K., Ablow, J.C., 2016. Mothers who were neglected in childhood show differences in neural response to their Infant's Cry. Child Maltreatment. 1077559516683503.
Yu, C.-L., Chou, T.-L., 2018. A Dual Route Model of Empathy: A Neurobiological Prospective. Front. Psychol. 9 https://doi.org/10.3389/fpsyg.2018.02212, 2212–2212.
Zaki, J., Davis, J.I., Ochsner, K.N., 2012. Overlapping activity in anterior insula during interoception and emotional experience. Neuroimage. 62, 493–499. https://doi.org/10.1016/j.neuroimage.2012.05.012.
Zoubovsky, S.P., Hoseus, S., Tumukuntala, S., Schulkin, J.O., Williams, M.T., Vorhees, C.V., Muglia, L.J., 2020. Chronic psychosocial stress during pregnancy affects maternal behavior and neuroendocrine function and modulates hypothalamic CRH and nuclear steroid receptor expression. Transl Psychiatr. 10, 6. https://doi.org/10.1038/s41398-020-0704-2.