

CHAPTER 12

Neurobiology of Parenting and Implications for Emotion Regulation

Helena J. V. Rutherford

The transition to parenthood is a time of psychological change that serves to support parent and child development. While a breadth of research in animal studies of the neurobiology of maternal behavior exists (Pawluski et al., 2021), efforts to identify the neurobiology of parenthood in humans is a more recent endeavor (Mayes et al., 2012). Investigating the neurobiology of parenting has theoretical value in understanding periods of adult development but has important clinical implications when considering contexts where parents may struggle in their caregiving role, with consequences for their own and their child's well-being (Squire & Stein, 2003). Critically, a common challenge for all new parents is the capacity to regulate their own and their child's emotions, especially during infancy and early childhood. In particular, it has been hypothesized that one outcome of the neural and psychological reorganization during the transition to parenthood is to support the unique demands of parental emotion regulation (Rutherford, Wallace, et al., 2015).

In this chapter, the neurobiology of human parenting is examined and implications for emotion regulation considered. Specifically, studies documenting maternal brain structure and function are reviewed. In advancing this area of inquiry, several studies will also be described that have examined maternal neural responses to negative stimuli (infant and noninfant) following distraction and cognitive reappraisal instructions to examine the neurobiological basis of parental emotion regulation more directly. Importantly, most parental brain research focuses on mothers, representing an inherent limitation to our understanding of this critical transitional period for nonbirthing parents, including fathers. While the studies discussed here focus on the maternal brain, where fathers are included this is noted, and the importance of understanding the paternal and nonbirthing parent brain is revisited when considering the next steps for this body of work.

12.1 Maternal Brain Structure

Only a handful of studies have examined the impact of pregnancy and the postpartum period on maternal brain structure, with a specific focus on gray matter (GM) volume measured using structural magnetic resonance imaging (MRI). Specifically, these studies of GM volume indicate both growth and decline in GM during the perinatal period. In the first investigation of changing GM volume across the postpartum period, mothers completed an MRI scan at 2–4 weeks postpartum and again at 3–4 months postpartum (Kim, Leckman, Mayes, Feldman, et al., 2010). GM volume increases over time were observed in the parietal lobes, prefrontal cortex, and the midbrain (including the hypothalamus, amygdala, and substantia nigra). Critically, GM growth in the midbrain areas was associated with mothers' positive perceptions of their child, linking maternal brain structure to real-world parenting. Luders et al. (2020) also found widespread GM increases from 1–2 days post delivery to 4–6 weeks following delivery in recent mothers, including in the pre- and postcentral gyrus, middle and inferior frontal gyrus (IFG), insula, parietal and temporal lobes, and the thalamus. Including a control group of nulliparous women, Lisofsky et al. (2019) also showed maternal GM volume increases from 2 months to 4–5 months postpartum in numerous regions, including the ventromedial prefrontal cortex, middle frontal gyrus, cerebellum, and nucleus accumbens. Taken together, these studies suggest significant growth of the maternal brain during the postpartum period as indexed by GM volume.

Although the majority of structural MRI studies have focused on the maternal brain postpartum, one study has examined GM volume in nulliparous women prior to conception and then again in the postpartum period to examine the impact of pregnancy on the maternal brain. In this study, Hoekzema et al. (2017) reported decreased GM volume in multiple brain areas from pregnancy to approximately 2 months postpartum, including across the anterior and posterior midline, and the lateral prefrontal and temporal cortex. Notably, fathers and a control group of men without children were scanned following the same timeline as the nulliparous women to examine whether the experience of becoming a parent, versus the biological experience of pregnancy, would lead to structural GM changes. Importantly, no difference in GM volume over time was observed between fathers and the men without children. Hoekzema et al. (2017) concluded that it was the biological experience of pregnancy underscoring the GM volume changes observed in nulliparous women, rather than the transition to parenthood alone.

These findings by Hoekzema et al. (2017) build on prior work evidencing reduced brain volume in women scanned during pregnancy and

again in the postpartum period (Oatridge et al., 2002). While the widespread reductions in GM volume were the primary focus of the Hoekzema et al. (2017) study, GM growth within the hippocampus from preconception to the postpartum period was also reported. Although GM volume decline may have negative connotations, decreased GM volume may reflect neural reorganization of the maternal brain conferring a benefit through “fine tuning” the brain to support mother and child well-being (Pawluski et al., 2021).

In sum, the maternal brain undergoes significant structural reorganization during pregnancy and the postpartum period, evidenced by GM growth and decline. Of note, these structural brain changes in response to motherhood do not appear transitory; GM volume reductions reported by Hoekzema et al. (2017) were still apparent at 2 years postpartum, with a follow-up study evidencing the persistence of GM volume reductions 6 years later in a subset of women from the original sample (Martínez-García et al., 2021). Critically, many of the brain regions identified in structural GM studies of the maternal brain overlap with those implicated in emotion regulation (Etkin et al., 2015), suggesting the structural plasticity of the perinatal period (and beyond) may be important in our understanding of maternal emotion regulation, and parenting more generally.

12.2 Maternal Brain Function

The majority of maternal brain research has used functional MRI (fMRI) and event-related potentials (ERPs) to examine neural responses to infant stimuli (infant faces and vocalizations) as an index of maternal brain function (Maupin et al., 2015; Parsons et al., 2017; Swain, 2011). Both these neuroimaging approaches provide insight into the detection and processing of salient infant signals (or cues) within and across samples of parents and nonparents. Importantly, neural responses to infant signals may reflect both reactivity and regulatory responding in the maternal brain. For instance, when presented with infant distress signals, neurobiological markers of reactivity to infant cry may be modulated by maternal regulatory function. Thus, reactivity and regulatory responding to infant signals may be interwoven, presenting a potential limitation when interpreting maternal neural responses to infant signals to inform the neurobiology of emotion regulation and parenting.

Nevertheless, converging lines of research have identified several “parental brain networks” responsive to infant cues that include brain areas implicated in mentalization, empathy, and emotion regulation (Feldman, 2015). This latter emotion regulation network includes the orbitofrontal cortex (OFC), dorsolateral prefrontal cortex (DLPFC), middle frontal gyrus

(MFG), and the frontopolar cortex. The identification of these parental brain networks has been driven by research that presents infant face and cry stimuli, including stimuli from mother's own child. Infant faces are hypothesized to be particularly salient cues motivating caregiving, activating brain regions implicated in reward processing in parents and nonparents (Glocker et al., 2009; Kringelbach et al., 2016; Lorenz, 1943). Given the breadth of work in this area, an increasing number of meta-analyses have been conducted to refine understanding on maternal brain function. In meta-analytic fMRI maternal brain research, heightened reactivity to own as compared to unfamiliar infant faces (only positive and neutral expressions) is reported as prominent in the midbrain (substantia nigra and ventral tegmental area), amygdala, striatum, insula, and ventrolateral prefrontal cortex (VLPFC; Rigo et al., 2019; see also Paul et al., 2019). Across parents and nonparents, meta-analytic maternal (and nonparent) ERP work has evidenced increased neural responding to infant distress as compared to positive and neutral infant faces (Kuzava et al., 2020).

Although maternal brain function can be studied in isolation by examining neural patterns of responding to infant cues, to understand the functional significance of these neural responses, an increasing number of studies are incorporating measures of both maternal brain and behavior. For instance, ERP responses to infant faces in mothers have been associated with sensitive and intrusive maternal behavior observed during interaction tasks (Bernard et al., 2015; Endendijk et al., 2018; Kuzava et al., 2019). Notably, one study measured ERP responses to infant faces in the third trimester of pregnancy and again at 3–5 months postpartum, finding that changing neural responses to infant faces was associated with postpartum maternal bonding (Dudek et al., 2020).

Understanding the sources of variability in maternal processing of infant faces has also been explored, recognizing that while parental brain networks exist, each person transitions to parenthood differently, reflected in the uniqueness of their current or previous life experiences. Indeed, maternal early experiences as indexed by attachment security has also been associated with maternal neural responses to infant faces in fMRI and ERP studies (e.g. Groh & Haydon, 2018; Lowell et al., 2021; Strathearn et al., 2009). Concurrently, studies of maternal infant face processing have been informative in beginning to understand where challenges related to emotion regulation may emerge and affect caregiving. Specifically, a number of studies have examined how symptoms of emotion dysregulation may contribute to neural reactivity to infant face stimuli. Specifically, neural responses to infant faces may be modulated by depression (Bjertrup et al., 2019), anxiety (Yatziv et al., 2021), and maternal substance use (Rutherford et al., 2021). Taken together, these studies evidence that maternal brain function can be captured by neural responses to infant facial cues

and may have important implications for maternal behavior, including emotion regulation and sensitive caregiving.

Infant cries have also been employed to probe maternal brain function. Behavioral and neuroimaging data suggest parental responding to infant cries may be consistent across cultures (Bornstein et al., 2017). Notably too, several neuroimaging studies indicate that parents (mothers and fathers) respond to infant signals differently to nonparents, particularly when infants express distress (e.g. Proverbio et al., 2006; Purhonen et al., 2001; Seifritz et al., 2003). In particular, the latter studies suggest a heightened response to infant distress cues in parents as compared to nonparents. Heightened responding to infant distress may confer an adaptive advantage for the developing child in eliciting caregiving behavior. Consistent with this hypothesis, infant cries have been shown to activate midbrain dopaminergic regions implicated in reward neural circuitry, presumably motivating approach to elicit caregiving behavior in some maternal brain studies (Rilling, 2013). However, infant cries may also be dysregulating for parents. Indeed, one of the earliest challenges many parents face is regulating their own emotional response to their crying child, while also trying to help their child become more regulated (Rutherford, Wallace, et al., 2015). Although there is variability in mothers' capacity to tolerate infant distress (Rutherford, Booth, et al., 2015; Rutherford et al., 2013), inconsolable infant crying has been linked with harsh and abusive parenting during the postpartum period (Barr, 2014). Given associations between increased reactivity to infant cries and negative parenting behaviors, interventions have been designed to help parents regulate during bouts of infant crying during the early postpartum months (e.g. Bechtel et al., 2020).

Given the importance of parental responding to infant cries, a number of studies have examined neural responses to varying types of infant cry stimuli in maternal samples (Wittman et al., 2019). Converging evidence supports the notion that neural responding to infant cries is associated with caregiving behavior. Musser et al. (2012) found that maternal sensitive behavior measured at 18 months postpartum was associated with neural responses to infant cries, including in the IFG and right frontal pole. Similarly, neural responding to infant cries in the superior frontal gyrus (SFG) and amygdala measured at 2–4 weeks postpartum was associated with maternal sensitivity measured at 3–4 months postpartum (Kim et al., 2011). Activity in the right frontal insula cortex, rolandic operculum, and subcortical regions (e.g. amygdala, hippocampus) in response to mothers listening to own infant cries has also been associated with maternal mental state talk during an interaction with their child (Hipwell et al., 2015). While maternal sensitive behavior and use of mental state language are believed important antecedents for child development, Laurent and Ablow (2012) advanced this area of work by

evidencing that mothers' brain responses to own infant cry predicted their child's attachment security – evidencing for the first time a link between maternal neurobiology and child developmental outcomes.

A number of other factors have been associated with maternal brain responses to infant cries. Clinically, maternal substance use has also been associated with decreased and delayed neural responses to unfamiliar infant cries (Rutherford et al., 2021), whereas maternal depression has been associated with altered responding to own and unfamiliar infant cries (Bjertrup et al., 2019). Poverty and maternal distress have been associated with decreased responses to infant cries, including in the medial prefrontal gyrus, middle prefrontal gyrus, and superior temporal gyrus (STG; Kim et al., 2016). Building on this work, increased exposure to a variety of stressors has also been associated with decreased cry responses in the right insula/IFG and STG, activity which was also linked with maternal sensitivity (Kim et al., 2020). Finally, it is worth noting that there are preliminary data to suggest that both mode of delivery (vaginal versus cesarean section; Swain et al., 2008) and feeding (exclusive breastfeeding versus exclusive formula feeding; Kim et al., 2011) may also shape maternal brain responding to their own infant's cries.

Taken together, employing infant face and cry stimuli in experimental tasks may be particularly valuable to probe reactivity and regulation in the maternal brain and how this may be associated with caregiving behavior. Notably, some studies have also linked maternal brain structure with functional brain responses to these salient infant stimuli. Hoekzema et al. (2017) reported that the regions evidencing GM volume reductions from pregnancy to postpartum were those regions that were activated when mothers viewed images of their infants during the postpartum MRI scan. Moreover, individual differences in perceived maternal care may shape both brain structure and function: mothers reporting higher level of maternal care in their own childhood, relative to those with lower levels of maternal care, evidenced greater GM volume and increased reactivity to infant cries in overlapping areas, including the MFG, STG, and fusiform gyrus (Kim, Leckman, Mayes, Newman, et al., 2010). Therefore, it is important to consider both structural and functional brain changes during the transition to parenthood wherever possible to bridge these two methodological approaches, incorporating maternal characteristics too.

12.3 Empirical Studies of the Neurobiology of Maternal Emotion Regulation

In the research reviewed thus far, the focus has been on brain structure and functional response to infant cues in mothers. Although informative in

understanding the neurobiology of parenting, as described earlier, reactivity and regulatory responding to these infant cues may be confounded and caution is warranted with interpreting these findings within an emotion regulation framework. Critically, an emerging body of research has begun to address this issue by focusing specifically on the neurobiological basis of regulatory responding to affective stimuli in maternal samples. Firk et al. (2018) investigated whether self-distraction would modulate neural responses to infant crying in primiparous mothers 5–8 months postpartum. In this context, self-distraction refers to the emotion regulation strategy of orienting attention away from an affective experience. Mothers in this sample evidenced a decreased response to infant cries in the amygdala, as well as the parahippocampal gyrus, insula, OFC, STG/MTG, precuneus, and cerebellum, when completing a counting task while infant cries were played, relative to when they were instructed only to listen to infant cries. Critically, this downregulation of the amygdala during self-distraction was associated with observed parenting behavior, such that higher levels of maternal sensitivity and nonhostility were correlated with less reactivity to infant cries during the self-distraction task. These findings evidenced for the first-time that an emotion regulation strategy can modulate the maternal brain but also that the neural correlates of maternal emotion regulation observed in this study may have downstream implications for caregiving behavior.

Two additional studies have examined cognitive reappraisal to negative affective (noninfant) stimuli in primiparous women at approximately 4 months postpartum. Grande et al. (2021) reported that mothers with higher levels of perceived stress evidenced greater activation to negative images in the DLPFC during cognitive reappraisal (as well as decreased activity in the caudate) relative to a condition where mothers were instructed to maintain their emotional response. The authors interpreted this heightened reactivity of the DLPFC to suggest that in highly stressed mothers, emotion regulation may be more effortful or inefficient, or that these mothers may be more reactive to negative emotional stimuli more generally. Interestingly, exploratory analyses in this sample showed that the heightened DLPFC activation in response to negative stimuli during the regulation (versus maintain) condition was also associated with self-reported perceived parenting-specific stress. Although exploratory, this latter finding suggests DLPFC reactivity during emotion regulation tasks may be associated with real-world experiences of parenting.

Building on this prior work, Capistrano et al. (2022) examined whether socioeconomic disadvantage (measured by income to needs ratio) would also be associated with cognitive reappraisal in recently postpartum primiparous women viewing negative affective stimuli. Consistent with their work on perceived stress, they found that mothers with greater

socioeconomic disadvantage also evidenced decreased activity in prefrontal cortical regions, including in the SFG (including DLPFC), IFG (including VLPFC), precentral gyrus, MTG, as well as the caudate during the cognitive reappraisal condition. Consequently, heightened stress and socioeconomic disadvantage may shape the neural correlates of maternal emotion regulation by affecting prefrontal cortical function. It is also important to note that Capistrano et al. found lower behaviorally observed maternal sensitivity was associated with decreased responding in the precentral gyrus during cognitive reappraisal. Again, evidencing task-based regulatory responses may have implications for caregiving behavior beyond the MRI scanner.

12.4 Limitations and Future Directions

In this chapter, studies relevant to the neurobiology of parenting have been reviewed and their implications for emotion regulation considered. While informative, these studies should be considered in the context of their limitations and directions for future research. Indeed, it is important to note that the studies reviewed here focus on the maternal brain, with overlap as well as divergence reported in the few studies of the paternal brain and responding to infant cues (Feldman, 2015). Indeed, paternal brain changes may be driven more by the experience of caregiving following the arrival of a child (Abraham et al., 2014). Nevertheless, a clear path forward requires greater consideration of paternal reactivity and regulation toward infant signals and extending this approach to all birthing and nonbirthing parents. In addition to understanding how different parenting experiences shape the brain, a critical advance in this area is recognizing the need for larger and more diverse samples of parents with respect to race and ethnicity in parental brain research (Penner et al., 2023).

Understanding the transition to parenthood inherently requires more longitudinal studies, ideally beginning before conception with repeat assessments during pregnancy (or an equivalent timeframe) and the postpartum period. Hoekzema et al. (2017) have evidenced the value of such a longitudinal approach but more work is needed in this area. Critically, this would be true for both structural and functional neuroimaging research. In particular, there may be value to understanding changes in the maternal brain unfolding prior to birth in pregnant people, which may prompt the identification of risk and protective factors during the transition to parenthood. Indeed the challenges related to maternal emotion regulation may unfold before birth (Penner & Rutherford, 2022). For example, how maternal anxiety shapes neural processing of infant faces

postpartum is comparable to how maternal anxiety is associated with processing infant faces during pregnancy (Rutherford, Byrne, et al., 2017).

The current chapter has focused on studies of maternal structure and function. As this work continues it will be important to incorporate our understanding of the changing levels of hormones during the transition to parenthood and their implications for the neurobiology of parenting. Oxytocin has been widely implicated in parenting behavior (Feldman & Bakermans-Kranenburg, 2017), with peripheral levels of oxytocin increasing across the postpartum period in mothers and fathers (e.g. Gordon et al., 2010). A number of studies have examined how administration of oxytocin modulates neural responses to infant cues in parents and non-parents (e.g. Peltola et al., 2018; Riem et al., 2011; Rutherford, Guo, et al., 2017) as well as how variation in the oxytocin receptor gene is associated with neural responses to infant stimuli (Peltola et al., 2014). Of course, oxytocin is not the only hormone that may shape maternal brain responding during the transition to parenthood (Brunton & Russell, 2008), requiring further extension of this approach to other hormones, including estrogen and progesterone.

Although the literature regarding the neural correlates of maternal emotion regulation is in its own infancy, the initial fMRI studies described here are promising in evidencing that explicit emotion regulation strategies modulate reactivity of the maternal brain and that this reactivity is associated with different aspects of caregiving. As this work continues, it will be important to consider the nature of the affective stimuli employed during emotion regulation tasks (i.e. infant versus noninfant stimuli), as well as the generalizability of these tasks to parenting experiences outside of the experimental setting. It may be valuable to include self-report assessments of how parents use different emotion regulation strategies (e.g. Gross & John, 2003), as well as adapting such measures to parenting-specific contexts. Understanding how regulatory functioning changes throughout the perinatal period would also be valuable, in particular in identifying periods of heightened risk and vulnerability for parents. This would allow a unique opportunity for parental brain researchers to partner with clinicians to both refine therapeutic approaches related to parental emotion regulation and to optimize the timing of these interventions for parents.

12.5 Conclusion

In the current chapter, structural and functional neuroimaging data has been presented that supports the notion that the transition to parenthood may be accompanied by neural reorganization, which may have

important implications for caregiving. Meta-analytic work highlights that heightened reactivity to infant cues is particularly evident when parents view photographs of their own infant as well as when infants are expressing distress. Critically, increasing studies are evidencing important associations between maternal brain structure and function and different aspects of parenting to ensure the functional significance of this work is clear. An exciting development in this field are those studies specifically targeting maternal emotion regulation, moving beyond the combined reactivity and regulatory approach typically used. While there has been a strong foundation for studies of the neurobiological basis of the transition to parenthood, advancements are needed in relation to the extension of this work to birthing and nonbirthing parents, incorporating more longitudinal designs, and understanding the role of changing hormonal profiles to neural reorganization. Given only a paucity of research has been conducted to date in the neural correlates of maternal emotion regulation, there is significant space for the growth and development of this work, including partnerships with clinicians supporting parents during this transitional period.

References

- Abraham, E., Hendler, T., Shapira-Lichter, I., Kanat-Maymon, Y., Zagoory-Sharon, O., & Feldman, R. (2014). Father's brain is sensitive to childcare experiences. *Proceedings of the National Academy of Sciences*, 111(27), 9792–9797.
- Barr, R. G. (2014). Crying as a trigger for abusive head trauma: A key to prevention. *Pediatric Radiology*, 44(4), 559–564.
- Bechtel, K., Gaither, J. R., & Leventhal, J. M. (2020). Impact of the Take 5 Safety Plan for Crying on the occurrence of abusive head trauma in infants. *Child abuse review*, 29(3), 282–290.
- Bernard, K., Simons, R., & Dozier, M. (2015). Effects of an attachment-based intervention on Child Protective Services-referred mothers' event-related potentials to children's emotions. *Child Development*, 86(6), 1673–1684.
- Bjertrup, A. J., Friis, N. K., & Miskowiak, K. W. (2019). The maternal brain: neural responses to infants in mothers with and without mood disorder. *Neuroscience & Biobehavioral Reviews*, 107, 196–207.
- Bornstein, M. H., Putnick, D. L., Rigo, P., Esposito, G., Swain, J. E., Suwalsky, J. T., Su, X., Du, X., Zhang, K., Cote, L. R., De Pisapia, N., & Venuti, P. (2017). Neurobiology of culturally common maternal responses to infant cry. *Proceedings of the National Academy of Sciences*, 114(45), E9465–E9473.
- Brunton, P. J., & Russell, J. A. (2008). The expectant brain: adapting for motherhood. *Nature Reviews Neuroscience*, 9(1), 11–25.
- Capistrano, C. G., Grande, L. A., McRae, K., Phan, K. L., & Kim, P. (2022). Maternal socioeconomic disadvantage, neural function during volitional emotion regulation, and parenting. *Social Neuroscience*, 17(3) 276–292. doi: 10.1080/17470919.2022.2082521.

- 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 Development*, 91(1), e198–e217. doi: 10.1111/cdev.13182
- Endendijk, J. J., Spencer, H., van Baar, A. L., & Bos, P. A. (2018). Mothers' neural responses to infant faces are associated with activation of the maternal care system and observed intrusiveness with their own child. *Cognitive, Affective, & Behavioral Neuroscience*, 18(4), 609–621.
- Etkin, A., Büchel, C., & Gross, J. J. (2015). The neural bases of emotion regulation. *Nature Reviews Neuroscience*, 16(11), 693–700.
- Feldman, R. (2015). The adaptive human parental brain: Implications for children's social development. *Trends in Neurosciences*, 38(6), 387–399. <https://doi.org/10.1016/j.tins.2015.04.004>
- Feldman, R., & Bakermans-Kranenburg, M. J. (2017). Oxytocin: A parenting hormone. *Current Opinion in Psychology*, 15, 13–18.
- Firk, C., Dahmen, B., Lehmann, C., Herpertz-Dahlmann, B., & Konrad, K. (2018). Down-regulation of amygdala response to infant crying: A role for distraction in maternal emotion regulation. *Emotion*, 18(3), 412–423.
- Glocker, M., Langleben, D. D., Ruparel, K., Loughead, J. W., Gur, R. C., & Sachser, N. (2009). Baby schema in infant faces induces cuteness perception and motivation for caretaking in adults. *Ethology*, 115(3), 257–263.
- Gordon, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2010). Oxytocin and the development of parenting in humans. *Biological Psychiatry*, 68(4), 377–382. <https://doi.org/10.1016/j.biopsych.2010.02.005>
- Grande, L. A., Olsavsky, A. K., Erhart, A., Dufford, A. J., Tribble, R., Phan, K. L., & Kim, P. (2021). Postpartum stress and neural regulation of emotion among first-time mothers. *Cognitive, Affective, & Behavioral Neuroscience*, 21(5), 1066–1082.
- Groh, A. M., & Haydon, K. C. (2018). Mothers' neural and behavioral responses to their infants' distress cues: The role of secure base script knowledge. *Psychological Science*, 29(2), 242–253.
- Gross, J. J., & John, O. P. (2003). Individual differences in two emotion regulation processes: implications for affect, relationships, and well-being. *Journal of Personality and Social Psychology*, 85(2), 348–362.
- 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. *The Journal of Neuroscience*, 35(37), 12725–12732.
- Hoekzema, E., Barba-Müller, E., Pozzobon, C., Picado, M., Lucco, F., García-García, D., Soliva, J. C., Tobeña, A., Desco, M., Crone, E. A., Ballesteros, A., Carmona, S., & Vilarroya, O. (2017). Pregnancy leads to long-lasting changes in human brain structure. *Nature Neuroscience*, 20(2), 287–296. <https://doi.org/10.1038/nn.4458>
- Kim, P., Capistrano, C., & Congleton, C. (2016). Socioeconomic disadvantages and neural sensitivity to infant cry: Role of maternal distress. *Social Cognitive and Affective Neuroscience*, 11(10), 1597–1607.
- 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. *Journal of Child Psychology and Psychiatry*, 52(8), 907–915. <https://doi.org/10.1111/j.1469-7610.2011.02406.x>
- Kim, P., Leckman, J. F., Mayes, L. C., Feldman, R., Wang, X., & Swain, J. E. (2010). The plasticity of human maternal brain: Longitudinal changes in brain anatomy during the early postpartum period. *Behavioral Neuroscience*, 124(5), 695–700. <https://doi.org/10.1037/a0020884>
- Kim, P., Leckman, J. F., Mayes, L. C., Newman, M. A., Feldman, R., & Swain, J. E. (2010). Perceived quality of maternal care in childhood and structure and function of mothers' brain. *Developmental Science*, 13(4), 662–673.
- 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.
- Kringelbach, M. L., Stark, E. A., Alexander, C., Bornstein, M. H., & Stein, A. (2016). On cuteness: Unlocking the parental brain and beyond. *Trends in Cognitive Sciences*, 20(7), 545–558.
- Kuzava, S., Frost, A., Perrone, L., Kang, E., Lindhiem, O., & Bernard, K. (2020). Adult processing of child emotional expressions: A meta-analysis of ERP studies. *Developmental Psychology*, 56(6), 1170–1190.
- Kuzava, S., Nissim, G., Frost, A., Nelson, B., & Bernard, K. (2019). Latent profiles of maternal neural response to infant emotional stimuli: Associations with maternal sensitivity. *Biological Psychology*, 143, 113–120.
- Laurent, H. K., & Ablow, J. C. (2012). The missing link: Mothers' neural response to infant cry related to infant attachment behaviors. *Infant Behavior and Development*, 35(4), 761–772.
- Lisofsky, N., Gallinat, J., Lindenberger, U., & Kühn, S. (2019). Postpartal neural plasticity of the maternal brain: Early renormalization of pregnancy-related decreases? *Neurosignals*, 27, 12–24.
- Lorenz, K. (1943). Die angeborenen Formen möglicher Erfahrung [The innate forms of potential experience]. *Zeitschrift für Tierpsychologie*, 5, 233–519.
- Lowell, A. F., Dell, J., Potenza, M. N., Strathearn, L., Mayes, L. C., & Rutherford, H. J. (2021). Adult attachment is related to maternal neural response to infant cues: An ERP study. *Attachment & human development*, 1–18.
- 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.
- Martínez-García, M., Paternina-Die, M., Barba-Müller, E., Martín de Blas, D., Beumala, L., Cortizo, R., Pozzobon, C., Marcos-Vidal, L., Fernández-Pena, A., Picado, M., Belmonte-Padilla, E., Massó-Rodríguez, A., Ballesteros, A., Desco, M., Vilarroya, Ó., Hoekzema, E., & Carmona, S. (2021). Do pregnancy-induced brain changes reverse? The brain of a mother six years after parturition. *Brain sciences*, 11(2), 168.
- Maupin, A. N., Hayes, N., Mayes, L., & Rutherford, H. J. V. (2015). The application of electroencephalography to investigate the neural basis of parenting. *Parenting: Science and Practice*, 15(1), 9–23. <https://doi.org/10.1080/15295192.2015.992735>

- Mayes, L., Rutherford, H. J. V., Suchman, N., & Close, N. (2012). The neural and psychological dynamics of adults' transition to parenthood. *Zero to Three*, 33 (2), 83–84.
- Musser, E. D., Kaiser-Laurent, H., & Ablow, J. C. (2012). The neural correlates of maternal sensitivity: An fMRI study. *Developmental Cognitive Neuroscience*, 2 (4), 428–436. <https://doi.org/10.1016/j.dcn.2012.04.003>
- 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. *American Journal of Neuroradiology*, 23(1), 19–26.
- Parsons, C. E., Young, K. S., Stein, A., & Kringelbach, M. L. (2017). Intuitive parenting: understanding the neural mechanisms of parents' adaptive responses to infants. *Current Opinion in Psychology*, 15, 40–44.
- 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. *Archives of Women's Mental Health*, 22(2), 179–187.
- Pawluski, J. L., Hoekzema, E., Leuner, B., & Lonstein, J. S. (2021). Less can be more: Fine tuning the maternal brain. *Neuroscience & Biobehavioral Reviews*, 133, 104475. <https://doi.org/10.1016/j.neubiorev.2021.11.045>
- Peltola, M. J., Strathearn, L., & Puura, K. (2018). Oxytocin promotes face-sensitive neural responses to infant and adult faces in mothers. *Psychoneuroendocrinology*, 91, 261–270.
- Peltola, M. J., Yrttiaho, S., Puura, K., Proverbio, A. M., Mononen, N., Lehtimäki, T., & Leppänen, J. M. (2014). Motherhood and oxytocin receptor genetic variation are associated with selective changes in electrocortical responses to infant facial expressions. *Emotion*, 14(3), 469–477.
- Penner, F., & Rutherford, H. J. (2022). Emotion regulation during pregnancy: A call to action for increased research, screening, and intervention. *Archives of Women's Mental Health*, 25(2), 527–531.
- Penner, F., Wall, K., Guan, K., Huang, H., Richardson, L., Dunbar, A., Groh, A. M., & Rutherford, H. (2023). Racial disparities in EEG research and their implications for our understanding of the maternal brain. *Cognitive, Affective, & Behavioral Neuroscience*, 23, 1–16. <https://doi.org/10.3758/s13415-022-01040-w>
- Proverbio, A. M., Brignone, V., Matarazzo, S., Del Zotto, M., & Zani, A. (2006). Gender and parental status affect the visual cortical response to infant facial expression. *Neuropsychologia*, 44(14), 2987–2999. <https://doi.org/10.1016/j.neuropsychologia.2006.06.015>
- Purhonen, M., Kilpeläinen-Lees, R., Pääkkönen, A., Yppärilä, H., Lehtonen, J., & Karhu, J. (2001). Effects of maternity on auditory event-related potentials to human sound. *Neuroreport*, 12(13), 2975–2979. <https://doi.org/10.1097/00001756-200109170-00044>
- Riem, M. M., Bakermans-Kranenburg, M. J., Pieper, S., Tops, M., Boksem, M. A., Vermeiren, R. R., van Ijzendoorn, M. H., & Rombouts, S. A. (2011). Oxytocin modulates amygdala, insula, and inferior frontal gyrus responses to infant crying: A randomized controlled trial. *Biological Psychiatry*, 70(3), 291–297.

- Rigo, P., Kim, P., Esposito, G., Putnick, D. L., Venuti, P., & Bornstein, M. H. (2019). Specific maternal brain responses to their own child's face: An fMRI meta-analysis. *Developmental Review*, 51, 58–69.
- Rilling, J. K. (2013). The neural and hormonal bases of human parental care. *Neuropsychologia*, 51(4), 731–747.
- Rutherford, H., Booth, C. R., Luyten, P., Bridgett, D. J., & Mayes, L. C. (2015). Investigating the association between parental reflective functioning and distress tolerance in motherhood. *Infant Behavior and Development*, 40, 54–63. <https://doi.org/10.1016/j.infbeh.2015.04.005>
- Rutherford, H., Byrne, S. P., Austin, G. M., Lee, J. D., Crowley, M. J., & Mayes, L. C. (2017). Anxiety and neural responses to infant and adult faces during pregnancy. *Biological Psychology*, 125, 115–120. <https://doi.org/10.1016/j.biopsycho.2017.03.002>
- Rutherford, H., Goldberg, B., Luyten, P., Bridgett, D. J., & Mayes, L. C. (2013). Parental reflective functioning is associated with tolerance of infant distress but not general distress: Evidence for a specific relationship using a simulated baby paradigm. *Infant Behavior and Development*, 36(4), 635–641. <https://doi.org/10.1016/j.infbeh.2013.06.008>
- Rutherford, H., Guo, X. M., Graber, K. M., Hayes, N. J., Pelphrey, K. A., & Mayes, L. C. (2017). Intranasal oxytocin and the neural correlates of infant face processing in non-parent women. *Biological Psychology*, 129, 45–48. <https://doi.org/10.1016/j.biopsycho.2017.08.002>
- Rutherford, H., Kim, S., Yip, S. W., Potenza, M. N., Mayes, L. C., & Strathearn, L. (2021). Parenting and addictions: Current insights from human neuroscience. *Current addiction reports*, 8(3), 380–388.
- Rutherford, H., Wallace, N. S., Laurent, H. K., & Mayes, L. C. (2015). Emotion regulation in parenthood. *Developmental Review*, 36, 1–14. <https://doi.org/10.1016/j.dr.2014.12.008>
- Seifritz, E., Esposito, F., Neuhoff, J. G., Luthi, A., Mustovic, H., Dammann, G., von Bardeleben, U., Radue, E. W., Cirillo, S., Tedeschi, G., & Di Salle, F. (2003). Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents. *Biological Psychiatry*, 54(12), 1367–1375.
- Squire, S., & Stein, A. (2003). Functional MRI and parental responsiveness: a new avenue into parental psychopathology and early parent–child interactions? *The British Journal of Psychiatry*, 183(6), 481–483. <https://doi.org/10.1192/bjp.183.6.481>
- Strathearn, L., Fonagy, P., Amico, J., & Montague, P. R. (2009). Adult attachment predicts maternal brain and oxytocin response to infant cues. *Neuropsychopharmacology*, 34(13), 2655–2666. <https://doi.org/10.1038/npp.2009.103>
- Swain, J. E. (2011). The human parental brain: In vivo neuroimaging. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, 35(5), 1242–1254. <https://doi.org/10.1016/j.pnpbp.2010.10.017>
- Swain, J. E., Tasgin, E., Mayes, L. C., Feldman, R., Todd Constable, R., & Leckman, J. F. (2008). Maternal brain response to own baby-cry is affected

- by cesarean section delivery. *Journal of Child Psychology and Psychiatry*, 49(10), 1042–1052. <https://doi.org/10.1111/j.1469-7610.2008.01963.x>
- Wittman, J., Van IJzendoorn, M., Rilling, J., Bos, P., Schiller, N., & Bakermans-Kranenburg, M. (2019). Towards a neural model of infant cry perception. *Neuroscience & Biobehavioral Reviews*, 99, 23–32.
- Yatziv, T., Vancor, E. A., Bunderson, M., & Rutherford, H. J. (2021). Maternal perinatal anxiety and neural responding to infant affective signals: Insights, challenges, and a road map for neuroimaging research. *Neuroscience & Biobehavioral Reviews*, 131, 387–399.