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Perceptions of Parental Care and Overprotection in Childhood: Influences on the Neurobiological Adaptation to Motherhood

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Abstract

Recalled memories of caregiving in childhood are especially salient during the postpartum period and inform mothers' conceptualization of her new parenting role. Positive perceptions of care received from one's parents are related to improved maternal-infant bonding and positive parenting behaviors, whereas negative perceptions of care convey risk for maladaptive parenting. Few studies have investigated neural and biological mechanisms contributing to observed associations between childhood care and the adaptation to motherhood. The following studies address this gap by examining how perceptions of childhood parental care and overprotection are related to maternal behavior, oxytocin levels, and neural response. Methods: Perceived childhood maternal and paternal care and overprotection were measured using the Parental Bonding Instrument (PBI) for 54 first-time mothers. Participants' salivary oxytocin and direct observations of sensitive and intrusive parenting behaviors were assessed during mother-infant play. Lastly, participants completed fMRI scanning, wherein neural activation was measured while listening to her own and control infant cry. Paper one examined maternal care and overprotection during childhood, whereas paper two focused on childhood care and overprotection received from fathers. Results: Both papers revealed independent and interactive associations of perceptions of childhood care, overprotection, and average oxytocin in relation to maternal neural response. Of note, paper one demonstrated that higher childhood maternal care and higher oxytocin interactively related to enhanced anterior cingulate activation to own infant cry. Paper two showed that oxytocin moderated the effects of paternal overprotection in the supramarginal gyrus; exploratory analyses revealed that neural response was associated with sensitive and intrusive behaviors. Conclusion: Findings demonstrate that recollections of childhood care and overprotection relate to maternal neural response, with downstream impacts for parenting behaviors. In addition, childhood caregiving and oxytocin interact in ways that contribute to vulnerability or resilience during the postpartum period.

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higher childhood maternal care and higher oxytocin interactively related to enhanced anterior cingulate activation to own infant cry. Paper two showed that oxytocin moderated the effects of paternal overprotection in the supramarginal gyrus; exploratory analyses revealed that neural response was associated with sensitive and intrusive behaviors. **Conclusion:** Findings demonstrate that recollections of childhood care and overprotection relate to maternal neural response, with downstream impacts for parenting behaviors. In addition, childhood caregiving and oxytocin interact in ways that contribute to vulnerability or resilience during the postpartum period.

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Chapter One: Introduction

"God blessed me with two unbelievable parents, and I am just like both of them."

-Magic Johnson

"How can it be, after all this concentrated effort and separation, how can it be that I still resemble, so very closely, my own detestable mother?"

-Gabrielle Hamilton

The ways in which we were parented have important implications for who we become as parents. The enclosed project examines how perceptions of childhood caregiving impact adaptation to parenthood. Based on growing evidence that childhood caregiving experiences have a long-lasting influence on neuroendocrine systems, we conducted a novel research design examining neural, hormonal, and behavioral parenting outcomes among new mothers. The role of perceived childhood parenting, oxytocin, and neural response will be explored in detail within the following two papers. Thus, this introduction will be used to provide an overview of the research project and to share a high-level conceptualization/roadmap for the two papers. As a note, all relevant topics discussed in this introduction and conclusion will be added to the enclosed papers prior to future submission to a journal.

Project Selection and Strengths of the Study Design

A pre-existing dataset was selected to answer the research question: *How do childhood caregiving experiences influence the adaptation to motherhood (via brain, body, and behavior)?* The selected research project, the Infant Development, Environment, and Attachment (IDEA) Project, included two research visits, a Home Visit and an fMRI Visit. A timeline of the two visits is described in **Figures 1 and 2**, for your reference. The IDEA Project was uniquely suited to answering our research question for a number of reasons, which are detailed below.

First, this project recruited first-time mothers during the postpartum period, such that we could directly tap into adaptation to becoming a parent. The postpartum period is a time of dramatic psychological and physiological changes, especially for new parents who are adjusting to an entirely new role (George, 2005). This is also a time of enhanced vulnerability to mood disorders and bonding disruptions (Abdollahi et al., 2016; Gjerdingen & Center, 2003). Additionally, by studying first-time mothers, we know that observed neural, hormonal, and parenting differences are not attributable to differences in previous parenting experience.

Second, the IDEA Project selectively recruited mothers living in low- and middle-income contexts. This is important in that low- and middle-income populations are relatively less studied in psychological research (Bornstein et al., 2013; Jang & Vorderstrasse, 2019). From an equity perspective, it is important to study maternal adaptation across socio-economic and risk contexts. Without this, research and intervention work cannot effectively capture or leverage maternal adaptation and

resilience processes. From a psychometric perspective, it was expected that mothers in the IDEA Project would experience a range of postpartum stressors. This could in turn be related to varied expressions of parenting adaptation (e.g., a range of parenting behaviors and neural and hormonal correlates).

Importantly, this dataset included a retrospective measure of perceived childhood caregiving, the Parental Bonding Instrument (PBI). This measure assesses perceptions of both maternal and paternal care and overprotection during the first 16 years of life. In addition, the PBI is related to differential adaptation to motherhood (e.g., differences in postpartum mood, mother-infant bonding), as well as continuity in parenting styles across generations (Fukui et al., 2021; Grant et al., 2012; Hall et al., 2015; Kitamura et al., 2009; Miller et al., 1997; Ohara et al., 2018). It is worth noting that in an ideal scenario, we would have a prospective measure of observed childhood caregiving quality, via a longitudinal study. However, due to limitations related to time and funds, this was not feasible. The PBI is a solid alternative, with strong psychometric qualities and demonstrated associations with postpartum outcomes (Grant et al., 2012; Murphy et al., 2010).

Although it was not possible to obtain observational assessments of childhood caregiving, the IDEA Project did directly assess current maternal behavior. Observational assessments of parenting are important to directly capture differences in caregiver behavior (Biringen et al., 2014; Cooke et al., 2022). Maternal behaviors during mother-infant free play were observationally coded using the Emotional Availability Scales (Biringen, 2008). The current study focused on assessments of maternal sensitivity and

intrusiveness because 1) they are important indices of maternal behavior and child development outcomes (Bigelow et al., 2010; Egeland et al., 1993; Warren & Simmens, 2005), and 2) they have been previously associated with PBI care and overprotection (Barrig Jo, 2008; M. A. Brown, 2019; Burrous et al., 2009; Jacobvitz et al., 1991).

Perhaps the greatest strength of the IDEA Project is that it assesses multiple markers of mothers' endocrine and neural function. The reason for studying mothers' brain and biology is because they help to elucidate the mechanisms contributing to associations between childhood care experiences and postpartum outcomes. We chose to examine the hormone oxytocin, because oxytocin plays an important role in mother-infant bonding and has been shown to vary based on childhood caregiving experiences (including PBI) (Feldman et al., 2007, 2011, 2012; Gordon et al., 2008). Please see **Figure 1** for a timeline of maternal salivary oxytocin sampling within the context of the Home Visit. The hypothesized interactions between oxytocin and perceptions of childhood caregiving are described in detail in the enclosed papers. Visual depictions of hypothesized interactions are provided in **Figures 3 and 4** for future reference.

In addition to hormonal sampling, mothers also completed a number of tasks during fMRI scanning (see **Figure 2**). We selected a neuroimaging task involving infant-relevant stimuli, such that mothers' neural response might relate to her parenting adaptation and behaviors. Specifically, we selected the infant cry task (Swain et al., 2008). Please see **Figure 5** for a visual depiction of the infant cry fMRI paradigm. This task was selected for a few reasons. First, the neurohormone oxytocin is central in modulating mothers' neural and behavioral response to infant cry (Swain et al., 2011),

such that we expected an interaction between maternal oxytocin level and neural response. Second, exposure to infant cry can elicit a variety of parental responses. While it can increase parental approach and caregiving behavior (Bornstein et al., 2017), infant cry can also be experienced as highly aversive and anxiety-provoking (Kurth et al., 2011; Lee et al., 2007; Swain et al., 2011). For this reason, response to infant cry is shown to relate to both positive and negative aspects of parenting (e.g., sensitive and intrusive parenting) (Kim et al., 2011; Musser et al., 2012). A neural model of the circuits involved in infant cry is presented in **Figure 6** (Swain et al., 2011; Witteman et al., 2019). This model is by no means comprehensive and by nature is somewhat of an oversimplification, as many brain regions are involved with multiple functions. However, it can be helpful to understand the general neural networks related to infant cry and their function. Disruptions to particular circuits within this neural model (e.g., disruption to the emotional empathy network or disruption to the subcortical reward network) can help us to better understand *how* perceptions of childhood care experiences alter maternal response to infant cry, and relatedly her parenting behaviors.

Limitations of the Study Design

In addition to strengths, we also want to acknowledge the potential limitations of this study design, including research questions that this project is less equipped to answer.

First, the recruitment methods and assessment tools used do not incorporate an inclusive definition of parenthood. All participants in the IDEA Project were gestational and biological mothers to their infant. Thus, this study cannot capture the experiences of

fathers and the many ways that individuals can come into a caregiving role (e.g., parents who welcomed a child via adoption, surrogacy, a blended family, and so on). Additionally, the Parental Bonding Instrument (PBI) separately assesses care received from mothers and fathers during childhood. Gendered language regarding parenthood may exclude non-binary individuals who provide caregiving. The PBI did not inquire about caregiving received from same-sex parents, step-parents, grandparents, extended family members, or other caregivers. In the current project, participants were instructed to fill out the questionnaire for any maternal or paternal figure. Still, five participants declined to fill out the paternal section of the PBI as they reported not having a father figure during childhood. Due to the small number, it was not feasible to examine this subset of participants separately. It is important that future studies examine parenting adaptation among individuals with diverse gender identities and varied families of origin, to more accurately represent the experience of current families. This project is limited in its ability to speak to the diversity of parenting experiences due to the study sample, methods of assessment, and the current state of the literature. We want to recognize these limitations and work towards creating a more inclusive definition of parenthood in future research.

Second, the current study drew from a much larger dataset, including many different questionnaires and tasks which were unrelated to the current research question. It is possible that manipulations related to other research topics influenced the current study. Most relevant is that mothers received instruction in cognitive reappraisal prior to fMRI scanning due to the inclusion of the emotion regulation fMRI task as a part of the

same fMRI session. The infant cry task was performed before the emotion regulation task. However, it is possible that mothers might have used cognitive reappraisal to regulate their emotional response to infant cry, since they were recently trained in this strategy.

Third, the current project includes a wide range of postpartum months, such that this study is limited to answer questions that are related to specific postpartum months. On average, mothers completed the home visit at 3 months postpartum (ranging from the first postpartum month to 7 months) and the fMRI visit at 4 months postpartum (ranging from the first postpartum month to 10 months). The first year postpartum can be a challenging time for many first-time mothers, with elevated rates of maternal depressed mood and parenting stress exhibited across the first year (Goodman, 2004; Oddi et al., 2013; Patel et al., 2012); thus, it makes sense to include mothers across this range. However, it is important to note that the maternal brain shows pronounced changes during the postpartum period, which could impact findings. For this reason, postpartum months are included as a covariate in all neural models.

Lastly, due to the significant costs related to neuroimaging, the current study had a modest sample size (N= 54). The present study is not the most robust test of behavioral parenting associations (e.g., the correlation between PBI and parenting behaviors) because of reduced statistical power. However, this project is ideally situated to capture the role of neurobiological mechanisms contributing to parenting adaptation.

The Two Papers

The two enclosed papers investigate perceived childhood maternal and paternal caregiving separately. The importance of fathers on child development outcomes has been historically under-studied, despite research suggesting that fathers may have a unique or even greater impact on areas of offspring psychological development (Bretherton, 2010; Lamb, 2004; Rohner & Veneziano, 2001; Videon, 2005). We selected to examine maternal and paternal caregiving separately in order to fill this research gap and to illuminate both similarities and differences across parenting experiences.

Figures

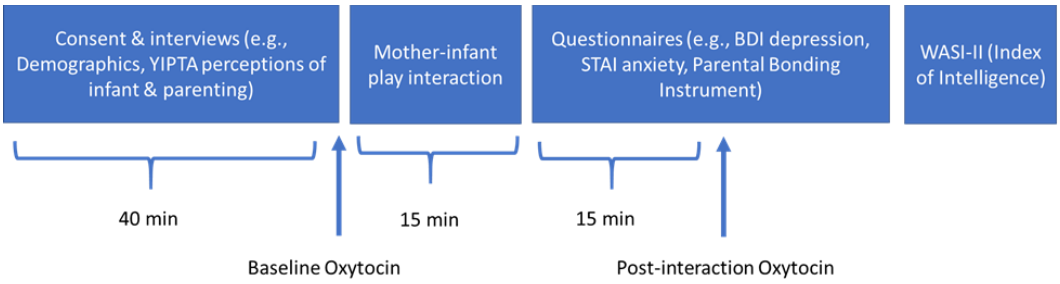

Figure 1. IDEA Project Home Visit Timeline

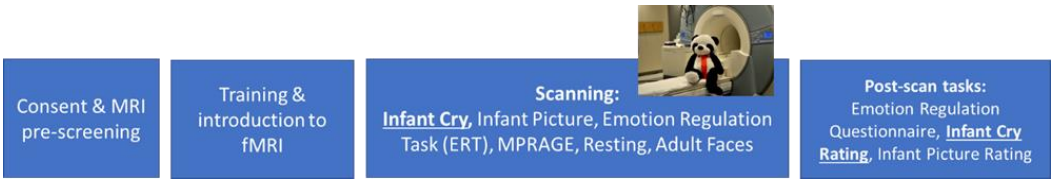

Figure 2. IDEA Project fMRI Visit Timeline

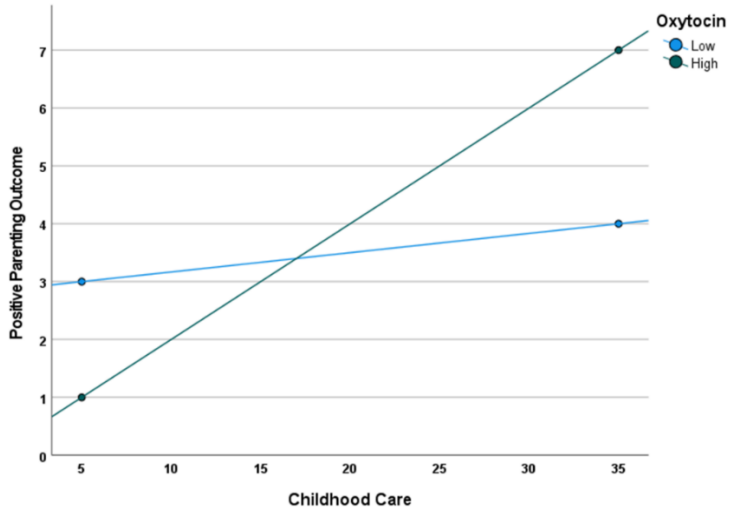

Figure 3. Visual depiction of the hypothesized relation between perceived childhood parental care and maternal salivary oxytocin level in predicting positive parenting outcomes (i.e., maternal sensitivity, non-intrusiveness). *Note.* Oxytocin was analyzed as a continuous variable, but for illustrative purposes is depicted here as low and high levels of oxytocin.

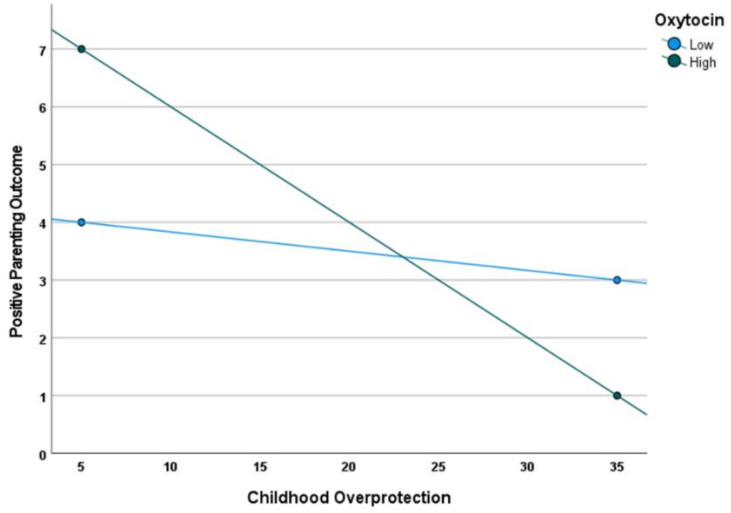

Figure 4. Visual depiction of the hypothesized relation between perceived childhood parental overprotection and maternal salivary oxytocin level in predicting positive parenting outcomes (i.e., maternal sensitivity, non-intrusiveness). Note. Oxytocin was analyzed as a continuous variable, but for illustrative purposes is depicted here as low and high levels of oxytocin.

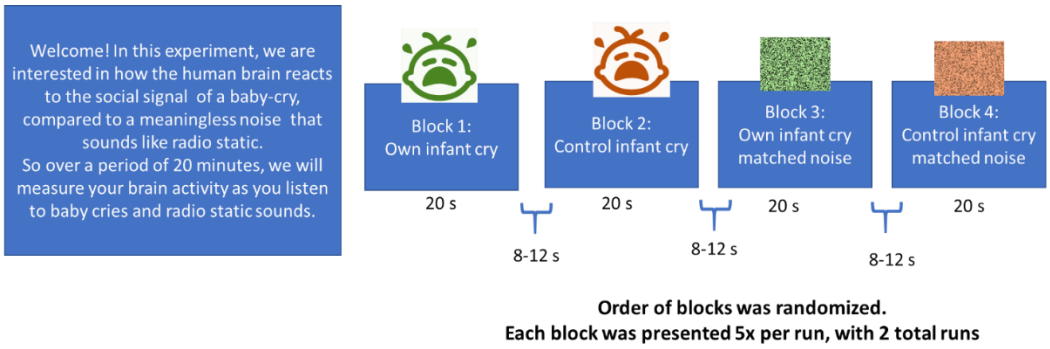

Figure 5. Infant Cry Task Paradigm

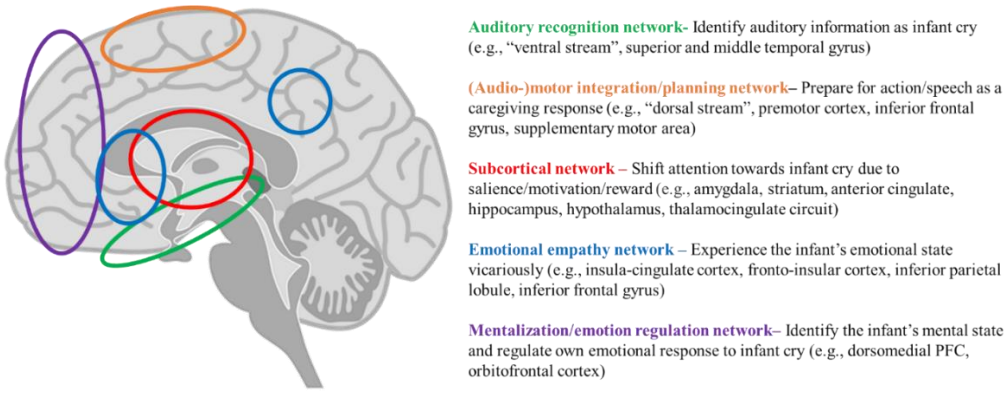

Figure 6. Neural Circuits Involved in Infant Cry

Note. This is a schematic representation for descriptive purposes; circles do not accurately reflect the location of each brain region.

Chapter Two: Paper One

Neural Adaptation to Motherhood: Moderating Effects of Oxytocin and Perceptions of Childhood Maternal Care and Overprotection

The postpartum period is a time of transformation and reorganization, defined by long-lasting neural, hormonal, and psychosocial changes for new mothers. This is a time when many first-time mothers reflect on their childhood relationship with their own mother and begin to conceptualize who they want to be as a parent (Handelzalts et al., 2018; Narayan et al., 2020). Individuals who report that their childhood maternal care was affectionless or controlling exhibit increased risk for postpartum anxiety and depressive symptoms, as well as greater bonding difficulties with their own infant (Fukui et al., 2021; Grant et al., 2012; Mayes & Leckman, 2007; McMahon et al., 2005; Ohara et al., 2018). Further, individual's reports of their childhood maternal care and overprotection are related to their own sensitive behaviors and parenting styles with their infant (Barrig Jo, 2008; Brown, 2019; Burrous et al., 2009; Kitamura et al., 2009; Miller et al., 1997).

Despite research suggesting the importance of perceived maternal care for the transition to parenthood, relatively less is known about the neurobiological mechanisms underlying this relationship. Growing research suggests that childhood caregiving

experiences have long-lasting impacts on neural and oxytocin systems (Kim, Leckman, Mayes, Newman, et al., 2010; Riem et al., 2012, 2016; Strathearn et al., 2009; Unternaehrer et al., 2015). Further, these systems undergo rapid changes during the postpartum period and are important for facilitating sensitive caregiving (Elmadih et al., 2014; Feldman, Gordon, Schneiderman, et al., 2010; Kim, Leckman, Mayes, Feldman, et al., 2010; Lomanowska et al., 2015). Few studies have examined the role of multiple biological systems in explaining how childhood maternal caregiving impacts adaptation to motherhood. The current study investigates how maternal brain response to infant cry is interactively predicted by perceived childhood maternal caregiving (care and overprotection) and salivary oxytocin levels. Further, we explore how differences in neural and oxytocin systems relate to parenting behaviors and perceptions within a socioeconomically diverse sample of first-time mothers.

Childhood Maternal Care and Overprotection

Mental representations of early experiences with caregivers have long-lasting implications for adult psychological and physical health (Enns et al., 2002; Kullberg et al., 2020; Mallers et al., 2010; Overbeek et al., 2007; Parker & Barnett, 1988; Russek & Schwartz, 1996). Early caregiving relationships convey enduring vulnerability or protection to later life stressors, particularly during vulnerable developmental stages such as the postpartum period (Ainsworth & Bowlby, 1991; Slade et al., 2012). Memories of early caregiving are especially salient during the transition to motherhood (Narayan et al., 2018; Priel & Besser, 2000). This is when many adults draw on their childhood experiences with their mother to begin to conceptualize their own maternal self-identity

(Handelzalts et al., 2018). The postpartum period can be especially challenging for individuals who recall mothering that was cold or unaffectionate, who may question their capability to provide nurturance to their own child (Della Vedova et al., 2011; Siddiqui et al., 2000). A validated and widely-used measure of perceived parenting quality during childhood is the Parental Bonding Instrument (PBI; Parker, 1990), which assesses caring and affectionate parenting (Care domain), as well as overcontrolling, intrusive parenting that limits the child's autonomy (Overprotection domain). Individuals who recalled their mothers as providing low affectionate care or high overprotection are at heightened risk for postpartum depression and anxiety (Boyce et al., 1991; Grant et al., 2012; Mayes & Leckman, 2007; McMahon et al., 2005). Affectionless and overprotective childhood maternal care are further associated with greater self-reported mother-infant bonding difficulties (Choi et al., 2010; Fukui et al., 2021; Hall et al., 2015; Ohara et al., 2018).

In addition to heightened vulnerability for disrupted postpartum mood and mother-infant bonding, perceived childhood mothering appears to have important implications for current parenting behaviors. Observational assessments of parenting behaviors demonstrate that higher childhood care is related to increased maternal sensitivity when her child is 2 years old (Barrig Jo, 2008; Burrous et al., 2009). By contrast, childhood maternal overprotection is related to increased intrusiveness at 9 months and decreased engagement at 2 years (Jacobvitz et al., 1991; Madden et al., 2015). Combined scores of higher childhood maternal care and lower overprotection are also related to increased sensitivity at 7 months (Brown, 2019). Self-reports of parenting style mirror these findings. Childhood perceived maternal care is associated with mothers' own self-

reported care of their school-age child (Kitamura et al., 2009). Mothers who reported experiencing low maternal care and high maternal overprotection during their childhood had daughters who were likely to also report experiencing low childhood maternal care and high overprotection (Miller et al., 1997). Taken together, findings suggest that perceptions of childhood maternal caregiving convey risk or resilience for the adaptation to motherhood.

Parenting Behaviors

Research is needed to understand how perceived childhood maternal caregiving, and accompanying neural and hormonal differences, contribute to parenting behaviors. Maternal sensitivity and intrusiveness are two important indices of maternal behavior, which are also related to perceived childhood care and overprotection (Barrig, 2008; Brown, 2019; Burrous et al., 2009; Jacobvitz et al., 1991). Highly sensitive mothers are warm, responsive, and emotionally connected with their child (Biringen, 2008). Non-intrusiveness captures the extent to which the mother follows her child's lead and is emotionally present to her child without being over-directive, overprotective, or overstimulating (Biringen, 2008). Maternal sensitivity and non-intrusiveness are both important contributors to child attachment security and cognitive and emotional development (Bigelow et al., 2010; Egeland et al., 1993; Warren & Simmens, 2005).

Maternal Oxytocin

Of particular interest to the current study is how childhood caregiving experiences interact with the neuroendocrine system to inform maternal behavior. The neuropeptide oxytocin emerges as a likely candidate as it is highly implicated in maternal-infant

bonding, and may function differently depending on early life experience. Oxytocin plays a key role in social bonding and functions to decrease stress and promote social approach and affiliation (Tops et al., 2007). Further, oxytocin is involved in parturition, lactation, and the activation of maternal behaviors in humans and other animals (Bales et al., 2007; Cox et al., 2015; Feldman, Gordon, Schneiderman, et al., 2010; Feldman, Gordon, & Zagoory-Sharon, 2010; Jobst et al., 2016; Kendrick et al., 1987). Mothers typically experience pronounced elevations in oxytocin during late pregnancy and childbirth, which are associated with heightened responsiveness to infants (Lomanowska et al., 2015; Uvnäs-Moberg et al., 2019). However, there is considerable individual variability in oxytocin trajectory during the perinatal period (Levine et al., 2007; Prevost et al., 2014). Following delivery, some mothers show stable, increasing, or decreasing levels at 1 to 6 months postpartum (Cevik & Alan, 2021; Feldman et al., 2007; Jobst et al., 2016; Levine et al., 2007). Oxytocin functions dually to promote affiliation and reduce stress, which can make interpretation of endogenous oxytocin levels complex and highly dependent on context. In situations of high stress (especially social stress), oxytocin is released due to its anxiolytic effects (Feldman et al., 2011; Olff et al., 2013). Some studies emphasize the protective effects of high endogenous oxytocin, whereas others view this is as marker of stress (Weisman et al., 2013). In addition to contextual factors, there are significant inter-individual differences in endogenous oxytocin, with positive and negative caregiving experiences predicting lasting differences in basal oxytocin level.

The majority of existing literature suggests that higher endogenous oxytocin promotes maternal-infant bonding and sensitive parenting. Moreover, there is evidence for the

intergenerational transmission and regulation of oxytocin, such that high oxytocin levels (and relatedly, positive caregiving) are maintained across generations (Feldman et al., 2013; Feldman, Gordon, & Zagoory-Sharon, 2010). Maternal plasma and salivary oxytocin levels are related to aspects of sensitive parenting, such as increased affectionate touch and positive affect (Feldman et al., 2007, 2011, 2012; Feldman, Gordon, Schneiderman, et al., 2010; Gordon et al., 2010b). Additionally, initial research suggests that higher maternal oxytocin is related to fewer intrusive behaviors (i.e., fewer overly directive and controlling behaviors) during infant play (Samuel et al., 2015). This is in line with a body of work suggesting that oxytocin supports understanding of others' emotions and mental states (Domes et al., 2007; Lischke et al., 2012). Caregiving experiences profoundly shape the development of the oxytocin system during early life (Alves et al., 2015). In rodent models, patterns of maternal behavior (e.g., frequency of licking and grooming) are transmitted across generations via epigenetic regulation of the oxytocin receptor gene (Champagne, 2008; Champagne et al., 2001). In humans, prospective studies suggest that positive caregiving and elevated maternal oxytocin levels are related to increased child oxytocin levels (Feldman et al., 2013; Feldman, Gordon, & Zagoory-Sharon, 2010). Retrospective studies also find higher basal plasma oxytocin levels among individuals reporting high perceived childhood care (Feldman et al., 2011, 2012; Gordon et al., 2008) and with secure adult attachment (Tops et al., 2007).

It is important to acknowledge that some studies of maternal oxytocin have yielded divergent findings. This could be attributable to oxytocin's dual role as an anxiolytic. Elmadih and colleagues (2014, 2016) found that high sensitive mothers demonstrated

lower oxytocin levels at baseline and following a mother-infant play interaction, compared to low sensitive mothers. Similarly, Markova and Siposova (2019) demonstrated that high maternal oxytocin was associated with poorer maternal sensitivity. This could be because low sensitive mothers find parenting more stressful; higher oxytocin may then be released to regulate this stress response (Elmadih et al., 2016; Marazziti et al., 2006; Markova & Siposova, 2019). Relatedly, greater interactive stress during mother-infant play (i.e., times when the infant is negatively engaged and mother is attempting to re-engage infant) is associated with elevated maternal urinary oxytocin (Feldman et al., 2011). Rather than an indicator of affectionate care and bonding, elevated oxytocin in contexts of stress can be related to parenting stress and relationship anxiety (Feldman et al., 2011; Tabak et al., 2011; Taylor et al., 2006; Weisman et al., 2013). The relation between childhood caregiving experiences and oxytocin also appears more nuanced in high-stress contexts. Research on peripheral oxytocin levels among adults with a history of child abuse and neglect has been conflicting, with reports of both higher and lower oxytocin levels (Bhandari et al., 2014; Heim et al., 2009; Müller et al., 2019; Pierrehumbert et al., 2010). Associations between childhood maternal overprotection and adult oxytocin levels also appear complex (Boccia et al., 2021; Elmadih et al., 2014). One study found that childhood maternal overprotection was related to lower adult urinary oxytocin levels (Boccia et al., 2021). In another study, childhood maternal overprotection was related to higher baseline and post-interaction plasma oxytocin levels, but only among mothers with low sensitivity (Elmadih et al., 2014). While there is strong evidence for oxytocin's role in parenting,

findings should be interpreted carefully particularly in the context of maternal stress and negative childhood experiences.

An additional reason for the discrepant findings is that oxytocin may function differently among adults depending on their childhood care experiences. Julian and colleagues (2018) found that higher salivary oxytocin was associated with more positive parenting of children 2-4 years old among mothers with low adverse child experiences (ACEs), but fewer positive parenting behaviors among mothers with high ACEs. Research examining the intranasal administration of oxytocin similarly demonstrates that exogenous oxytocin functions differently among adults with negative caregiving experiences (e.g., experiences of maternal love withdrawal, harsh parental discipline). Some studies suggests that oxytocin administration is only beneficial (e.g., for reducing anxiety, improving emotion recognition) in adults with negative childhood experiences (Riem et al., 2014, 2020; Schwaiger et al., 2019). By contrast, other studies find that the positive effects of oxytocin administration are limited to adults *without* negative childhood experiences (Bakermans-Kranenburg & van IJzendoorn, 2013; Van Ijzendoorn et al., 2011), and may even have opposite, adverse effects in anxiously attached adults (Bartz et al., 2010). Oxytocin is best considered within an interactionist model that considers both contextual and individual factors (Bartz et al., 2011). The current study assesses not only the association between childhood maternal caregiving and oxytocin level, but also how oxytocin may relate to parenting outcomes differently for mothers who received low vs. high quality care.

Maternal Neural Response to Infant Cry

In conjunction with the endocrine system, altered neural response is a likely mechanism through which perceptions of childhood caregiving may relate to maternal behaviors and adaptation. During the postpartum period, mothers exhibit heightened perceptual sensitivity and enhanced reward processing to infant cues (Barba-Müller et al., 2019; Kim, Leckman, Mayes, Feldman, et al., 2010). The current study examines maternal neural response to a very important signal of infant distress: infant cry. Infant cry sounds capture parental attention and motivate approach and the initiation of caregiving behaviors (Bornstein et al., 2017). At the same time, prolonged exposure to infant cry is highly aversive; infant cry can heighten maternal stress and risk for child maltreatment (Kurth et al., 2011; Lee et al., 2007; Swain et al., 2011). Across cultures, infant cry stimulates maternal brain activity in subcortical regions important for reward and motivation (striatum, amygdala, hippocampus, hypothalamus, midbrain) and cortical regions important for social cognition and empathy (superior, middle, and inferior frontal cortices, orbitofrontal cortex, superior temporal cortex, insula, fusiform gyrus, anterior cingulate) (Bornstein et al., 2017; Lorberbaum et al., 2002; Swain, 2011; Swain et al., 2011). At a closer look, areas activated by infant cry may serve specific functions to facilitate caregiving, such enhancing processing of auditory information (e.g., superior temporal regions), preparing mothers for action and speech (e.g., supplementary motor area), and regulating mothers' initial negative emotional response to infant cry (e.g., superior frontal regions) (Bornstein et al., 2017; Musser et al., 2012). Mothers also show differential response to their own infant's cry, compared to an unknown control cry. In

particular, mothers show enhanced responses in cortical areas involved in empathy and mentalization (i.e., understanding of other's mental states) when listening to their own infant, including the right frontoinsular cortex, inferior parietal lobule, and inferior frontal gyrus/precentral gyrus (Hipwell et al., 2015; Swain et al., 2017).

Importantly, maternal neural response to infant cry is related to individual differences in sensitivity and intrusiveness. Enhanced activation to own infant cry (compared to control cry) in areas such as the superior and inferior frontal gyrus and frontal pole is related to increased maternal sensitivity, perhaps reflecting enhanced maternal emotion regulation and understanding of her infants' emotional state (Kim et al., 2011; Musser et al., 2012). By contrast, hyperactivation in the anterior insula and temporal pole to own infant cry is associated with intrusive maternal behaviors at 18 months postpartum (Musser et al., 2012). These areas are important for emotional empathy and affiliative behaviors. It is possible that intrusive mothers may exhibit heightened reactivity and empathic pain response to their child's distress signals, contributing to the expression of overly intrusive maternal behaviors (Musser et al., 2012). Amygdala response to own infant cry has been related to increased maternal sensitivity (Kim et al., 2011). By contrast, amygdala hyperactivation to infant cry generally (own and control cry combined) is related to decreased maternal sensitivity (Firk et al., 2018). Perhaps enhanced amygdala response to own infant cry may reflect heightened salience and motivation towards own infant, whereas enhanced response to infant cry generally may be a marker of stress. Alternatively, there may be optimal level of amygdala activation that most mothers exhibit in response to infant cry, whereas amygdala hyperactivation

may suggest emotional overwhelm. Taken together, findings suggest that the infant cry task taps into important neural correlates of parenting. Further, response to infant cry is associated with differential early caregiving experience and oxytocin response.

Initial research suggests that maternal neural response is altered by early caregiving experience, particularly care received from mothers. Most relevant to the current study, Kim and colleagues (2010) found that mothers with high perceived childhood maternal care exhibited greater activation in the middle frontal gyrus, superior temporal gyrus, and fusiform gyrus when listening to unfamiliar infant cry stimuli at 2-4 weeks postpartum. Greater neural activation of these regions may be important for understanding infants' emotional states and facilitating appropriate maternal responses. By contrast, mothers who reported low childhood maternal care showed increased left hippocampus activation when listening to infant cry, perhaps indicating greater stress reactivity to infant distress signals. Within adult populations, higher perceived childhood maternal care has also been associated with greater activation in the right prefrontal cortex during exposure to distressing cry stimuli (although not specific to infant cry), perhaps suggesting increased readiness to act (Cataldo et al., 2020). Interestingly, childhood maternal care and oxytocin-related genetic variation interactively predicted neural response, such that individuals with higher genetic susceptibility to environment (i.e., G/G homozygous individuals) had greater prefrontal response (Cataldo et al., 2020). This suggests that both childhood maternal care and oxytocin may be important for predicting neural response to cry.

To our knowledge, no prior studies have investigated whether childhood maternal overprotection relates to brain response among mothers. Childhood maternal overprotection has been associated with disrupted adult brain structure and function in areas important for the detection and regulation of threat cues. Young adults who reported high childhood maternal overprotection showed increased amygdala reactivity to signs of interpersonal threat, as well as reduced structural integrity of the uncinate fasciculus, a white matter tract connecting the amygdala to regulatory regions of the medial PFC (Farber et al., 2019). Perceived childhood maternal overprotection is also associated with reduced volume in the dorsolateral PFC, which is further related to elevated trait anxiety and depressive symptoms. This is consistent with research suggesting that children of overcontrolling parents are at higher risk for anxiety (Ballash et al., 2006; Borelli et al., 2015). Childhood maternal care that is overprotective in nature may limit the development of regulatory strategies to cope with distress later in life.

In addition to perceptions of childhood maternal care and overprotection, researchers have investigated adult attachment representations, which can be aligned with positive early caregiving experiences. Specifically, perceptions of maternal care are negatively associated with attachment anxiety and attachment avoidance, while maternal overprotection is positively associated with attachment anxiety and avoidance (Craig et al., 2013; Lopez et al., 2000). Women with insecure attachment representations showed heightened amygdala activation while listening to an unfamiliar infant cry compared to women with secure representations; insecure individuals also reported increased feelings of irritation and used excessive force on a handgrip-force task during infant crying (Riem,

Bakermans-Kranenburg, IJzendoorn, Out, & Rombouts, 2012). Secure mothers also showed greater activation in oxytocin-associated and dopaminergic reward processing regions, such as the hypothalamus/pituitary region and ventral striatum, when viewing her own infant's crying and smiling faces at 11 months postpartum (Strathearn, Fonagy, Amico, & Montague, 2009). In sum, early caregiving experiences appear to alter maternal brain circuitry, and may support or disrupt adaptive maternal behavior during the postpartum period.

In addition to childhood caregiving experiences, the neurohormone oxytocin also plays an important role in coordinating neural and behavioral changes in response to infant cry. Upon hearing infant cry, oxytocin rises relatively quickly with hypothalamus brain activity, facilitates milk let-down for nursing, and promotes parenting behaviors (Swain et al., 2011). Oxytocin is synthesized in the paraventricular and supraoptic nuclei of hypothalamus, is released by the posterior pituitary, and projects to areas of the brain such as the amygdala, hippocampus, striatum, suprachiasmatic nucleus, and brainstem (Boccia et al., 2013; Loup et al., 1991; Meyer-Lindenberg et al., 2011). Higher maternal basal plasma oxytocin level is associated with enhanced activation in regions involved in limbic and motivational circuits (i.e., nucleus accumbens, amygdala, ventral anterior cingulate) and social cognition (i.e., superior and middle frontal cortices, insula, superior and middle temporal cortices, inferior parietal lobule) in response to viewing own vs. unknown infant videos at 4-6 months postpartum (Atzil et al., 2012). Greater maternal plasma oxytocin increase following a mother-child interaction is associated with enhanced hypothalamus/pituitary and ventral striatum activation in response to own

neutral infant faces (Strathearn et al., 2009). Further, both oxytocin and neural response were higher among mothers with secure (compared to insecure) attachment (Strathearn et al., 2009). A few studies have examined breastfeeding status (compared to formula-feeding) and vaginal delivery (compared to Caesarian delivery) as a proxy for high maternal oxytocin level during the early postpartum period (i.e., 2-4 weeks postpartum) (Kim et al., 2011; Swain et al., 2008). These studies suggest that higher oxytocin may be related to elevated activation to own infant cry (compared to control cry) in subcortical circuits (e.g., hypothalamus, amygdala, midbrain, striatum, caudate, anterior cingulate) and social cognition/mentalization circuits (e.g., medial prefrontal cortex, orbitofrontal cortex/insula, lateral temporal cortex, fusiform gyrus) (Kim et al., 2011; Swain et al., 2008). Interestingly, the majority of prior studies demonstrate that oxytocin level is related to differences specifically in the contrast of own infant cry vs. control cry. Conceptually this makes sense as maternal oxytocin level is more directly relevant to own infant, rather than infant stimuli generally. Overall, studies suggest that high endogenous oxytocin may motivate maternal care by activating motivation, social cognition, and care-related circuits.

Mechanistically, research on intranasal administration of oxytocin (i.e., exogenous oxytocin) suggests that oxytocin may promote adaptive response to infant cry by attenuating fear and distress. Intranasal oxytocin decreases right amygdala activation and increases activation in the insula and inferior frontal gyrus when listening to infant cries among nulliparous women (Riem et al., 2011). Decreased amygdala activation may promote more responsive caregiving by decreasing aversive and anxious feelings

associated with infant crying (Riem et al., 2011). Further, the insula and inferior frontal gyrus are areas involved in empathy and emotional understanding and may help to facilitate sensitive maternal caregiving (Gallese et al., 2004; Riem et al., 2011). Intranasal administration of oxytocin appears to decrease amygdala hyperactivation specifically for insecurely-attached women, which also relates to decreased excessive handgrip force when listening to infant cry among non-parents (Riem et al., 2016). Taken together, findings suggest that maternal neural response to infant cry may be dually influenced by oxytocin level and childhood caregiving experience.

Current Study and Hypotheses

The current study employed a functional neuroimaging (fMRI) approach to test the relation between perceived childhood maternal care, maternal overprotection, and oxytocin on neural response during exposure to relevant infant stimuli (i.e., infant cry). Additionally, we explored how differences in maternal neural response and salivary oxytocin were related to direct observations of caregiving behaviors (i.e., sensitivity and non-intrusiveness). Hypotheses were as follows:

1. Childhood Care

Higher childhood maternal care will be associated with greater activations in the ventral striatum, hypothalamus and pituitary, insula, middle and inferior frontal gyrus, superior temporal gyrus, and fusiform gyrus when listening to own infant cry compared to control cry. Lower childhood maternal care will be associated with hyperactivation of the amygdala and hippocampus when listening to own infant cry vs. control cry. Higher maternal care and associated neural activation will be associated with greater oxytocin

response following a mother-infant play interaction, which will be further associated with increased maternal sensitivity during mother-infant play.

2. Childhood Overprotection

Higher childhood maternal overprotection will be associated with amygdala hyperactivation when listening to own infant cry vs. control cry. Higher maternal overprotection and related neural activation will be associated with lower oxytocin response following a mother-infant play interaction, which will be further associated with decreased maternal non-intrusiveness during mother-infant play.

3. Oxytocin

Higher oxytocin increase following a mother-infant play interaction will be associated with enhanced activation in the ventral striatum, hypothalamus/pituitary, anterior cingulate, insula, and middle and superior frontal gyrus when listening to own infant cry vs. control cry. Higher oxytocin response and associated neural activation will be related to increased maternal sensitivity and non-intrusiveness.

3a. Higher childhood maternal care will be related to increased oxytocin response.

3b. Higher childhood maternal overprotection will be related to decreased oxytocin response.

4. Oxytocin Alternative Hypothesis

4a. If oxytocin is not associated with childhood maternal care, it is hypothesized that there will be a significant interaction between care and oxytocin response. Higher care and higher oxytocin will be interactively related to enhanced neural activation in social cognition and reward regions (e.g., middle, superior, and inferior frontal gyrus, striatum,

anterior cingulate) during own infant cry vs. control cry. Exploratory analyses will suggest that enhanced neural activation will be related to increased sensitivity and non-intrusiveness.

4b. If oxytocin is not associated with childhood maternal overprotection, it is hypothesized that there will be a significant interaction between overprotection and oxytocin response. Lower overprotection and higher oxytocin will be interactively related to enhanced neural activation in social cognition and reward regions (e.g., middle, superior, and inferior frontal gyrus, striatum, anterior cingulate) during own infant cry vs. control cry. Exploratory analyses will suggest that enhanced neural activation will be related to increased sensitivity and non-intrusiveness.

Materials and Methods

Participants

Participants were English-speaking, first-time mothers and their biological infants, at an average of 3.6 months postpartum. All participants were recruited within the first 7 months postpartum. Mothers were recruited via fliers and brochures distributed throughout the Denver Metro area, with a focus on recruiting a socioeconomically diverse sample. Fliers were posted at OB/GYN and midwifery clinics, Women, Infants, and Children (WIC) centers, and Prenatal Plus programs (a program for pregnant members of Colorado's Medicaid Program). Mothers were excluded due to history or current psychiatric illness other than depression and anxiety, as well as current psychoactive medication use other than antidepressants. This was due to literature suggesting pronounced brain differences related to psychiatric disorders and psychoactive

medication use, such as schizophrenia and the use of antipsychotics (Arnone et al., 2009; Ho, Andreasen, Ziebell, Pierson, & Magnotta, 2011). Mothers were also be excluded if they experienced significant delivery and postnatal complications, such as infant illnesses requiring more than a one-night stay in the neonatal intensive care unit (NICU). Further, mothers were excluded from the neuroimaging portion of the study due to MRI safety issues, such as magnetic metal in the mother's body, current pregnancy, and claustrophobia. Participants with excessive motion (above 15% of TRs removed; see fMRI Preprocessing Section) were also excluded from the neuroimaging analysis.

54 participants were included in the present study. Prior to analysis, one participant was excluded due to a technical error during scanning (i.e., use of incorrect stimuli) and two participants were excluded due to excessive motion (above 15% TRs removed; please see fMRI Preprocessing Section). Two participants were missing oxytocin data, due to not producing a sufficient saliva sample for both the baseline and post-interaction samples. One participant was removed as their baseline and post-interaction values were greater than 3 standard deviations above the mean (please see Oxytocin section for detailed information). An overlapping sample of fMRI data from the current study has been included in previous publications (Grande et al., 2021; Kim et al., 2016; Kim et al., 2020; Olsavsky et al., 2021). However, the current research question has not been examined; previous publications did not examine the role of oxytocin or the Parental Bonding Instrument (PBI).

Research Procedures

The Infant Development, Environment, and Attachment (IDEA) Project study protocol was approved by the University of Denver Institutional Review Board. Mothers were contacted via phone to assess their eligibility for the study. Mothers completed two sessions: a home visit and an fMRI visit. At each phase of the study, mothers provided written informed consent in accordance with Institutional Review Board guidelines. The research team visited mothers in their homes to conduct interviews, questionnaires, and the mother-infant interaction. Next, mothers visited the Intermountain Neuroimaging Center at the University of Colorado – Boulder to complete the fMRI portion of the study. Mothers received financial compensation for all visits; child care and transportation assistance were also provided as needed.

Measures

Sociodemographic Covariates

Maternal age, postpartum months, education, race and ethnicity, handedness, relationship status, income-to-needs ratio in the past year, history of depression, anxiety or other psychiatric disorder, current psychiatric medication use, infant sex, and breastfeeding status were assessed via maternal interview at the home visit. Income-to-needs ratio was calculated by dividing total household income in the past year by the poverty threshold at the time of assessment, specified by the U.S. Census Bureau. An index of maternal intelligence was assessed at the home visit using the Wechsler Abbreviated Scale of Intelligence-II (WASI-II). Maternal current depressive and anxiety symptoms were assessed via questionnaire using the Beck Depression Inventory (BDI;

Beck, Ward, Mendelson, Mock, & Erbaugh, 1961) and State-Trait Personality Inventory (STAI; Spielberger, 1983), respectively.

Parental Bonding Instrument

The Parental Bonding Instrument (PBI) is a retrospective, self-report measure assessing adults' caregiving experiences during the first 16 years of life (Parker et al., 1979). Although retrospective in nature, the PBI is considered to capture important aspects of the childhood experience and demonstrates long-term stability over a 20-year-period (Murphy et al., 2010; Wilhelm et al., 2005). The PBI has demonstrated criterion validity, including high correlations with related measures such as The Parental Attitude Research Instrument, Parenting Style Inventory, and Emotional Warmth, Rejection and Protection scale (Arrindell et al., 1998; Kapçi & Küçüker, 2006). PBI ratings are correlated among siblings (Parker, 1989) and associated with ratings by other family members (Kitamura & Suzuki, 1993), suggesting that the PBI may provide a somewhat accurate assessment of caregiving, rather than solely perceived characteristics. The PBI has been utilized previously among pregnant and postpartum samples (Della Vedova et al., 2011; Gómez-Beneyto et al., 1993; Sato et al., 2021). PBI items assess the perceived caregiving received from both mother and father, and yield scores of maternal and paternal care and overprotection during childhood. Maternal care and overprotection were the focus of the current study.

Parental affectionate care describes aspects of emotional closeness, warmth, and understanding, as opposed to emotional coldness, neglect, and indifference. An example of an item is: '(Mother) Could make me feel better when I was upset'. Parental control or

overprotection describes excessive contact, intrusion, and prevention of independence, as opposed to encouragement of child autonomy. An example of an item is: '(Mother) Felt I could not look after myself unless she was around'. Items are rated on a 4-point Likert scale, describing *very unlike* (0), *moderately unlike* (1), *moderately like* (2), and *very like* (3). Care scores can range from 0 to 36 and overprotection scores can range from 0 to 39.

The current study assessed the variables maternal care and maternal overprotection. Please see **Table 1** for detailed descriptive information. Perceived maternal care and overprotection were not significantly correlated in the current study (r = -.13, p > .10). According to defined PBI classification cut-offs (Parker et al., 1979), 29 participants (53.7%) perceived their mothers as caring whereas 25 participants (46.3%) did not. 32 participants (59.3%) perceived their mothers as overprotective whereas 22 participants (40.7%) did not. Although perceived care received from the father was not the focus of the current study, it can be noted that perceived maternal care was not significantly associated with perceived paternal care (r = .01, p > .10), but maternal overprotection was associated with paternal overprotection (r = .42, p = .003). Maternal care had excellent internal consistency in the current study with a Cronbach's α coefficient of .92. Maternal overprotection had acceptable internal consistency in the current study with a Cronbach's α coefficient of .79.

Parenting Behavior

Maternal parenting behaviors were assessed via a 15-minute mother-infant play interaction conducted during the home visit. Infants were 3.5 months old on average at the time of the play interaction. Mothers were asked to interact naturally with their infant

without the use of toys. Maternal behavior was videotaped and observationally coded based on the Emotional Availability Scales, 4th Edition (Biringen, 2008; Biringen et al., 2014). Researchers were trained and certified by Dr. Biringen, creator of the Emotional Availability scales. The Emotional Availability Scales provides assessments of maternal behavior on four dimensions: sensitivity, structuring, non-intrusiveness, and non-hostility; each score ranges from 1 to 7 with higher scores reflecting more optimal maternal behaviors. Maternal sensitivity and intrusiveness were of particular interest to the current study. Maternal sensitivity scores capture the extent to which mothers are emotionally attuned to her infant and can respond appropriately and flexibly to her infant's needs. During the mother-child interaction, they demonstrate authentic and congruent positive affect and pleasure when playing with their child (e.g., warm smiles and giggles, interested eye contact). In the current sample, maternal sensitivity scores ranged from 3.5 (reflecting inconsistent or apparent sensitivity) to 7.0 (highly sensitive), with a mean of 5.38 (*SD* = 1.17). Scores of 5.5 and 6 reflect "bland sensitivity", including mothers who demonstrated less optimal parenting within a few domains or who exhibited neutral affect but an otherwise good style of relating. Maternal intrusiveness scores (reverse-coded non-intrusiveness) capture the extent to which mothers provide excessive stimulation, over-protection, and over-direction, such that she denies the infant's autonomy during play. In the current sample, maternal non-intrusiveness scores ranged from 3.0 (somewhat intrusive) to 7.0 (non-intrusive but emotionally present/available), with a mean score of 5.59 (*SD* = 1.23). Scores of 5.5 and 6 reflect generally non-intrusive behavior, with sometimes benign forms of intrusiveness (such as overdone reminders or

safety tips). Maternal sensitivity and non-intrusiveness were significantly correlated in the current sample ($r = .56$, $p < .001$). Two researchers coded the videos, with 24% overlap. The average intraclass correlation (ICC) was 0.91. Researchers coded if the infant was sleeping and if the infant was crying for the majority of the mother-child interaction, to examine as potential covariates.

Oxytocin

Baseline saliva samples were collected 40 minutes after arriving at the home and before the start of the mother-infant interaction, ranging between 4:39pm and 5:16pm for study participants. Post-interaction samples were collected 15 minutes after the conclusion of the mother-infant interaction, ranging from 5:20 to 6:08pm. The timing of samples was set based on prior studies assessing salivary oxytocin in the context of a mother-infant play paradigm (Feldman, Gordon, & Zagoory-Sharon, 2010; Julian et al., 2018). Additionally, all home visits started in the afternoon to avoid potential interference with diurnal patterns of oxytocin (typically peaking in the morning and declining across the day) (Julian et al., 2018). Oxytocin was collected via Salivette (Sarstedt, Rommelsdorft, Germany) and chilled for 3-4 hours until being spun down by centrifuge at 4°C at 1500 x *g* for 15 minutes. Samples were stored in a -80°C freezer. Oxytocin levels were determined via a commercial oxytocin ELISA kit (Assay Design, MI, USA) which has been used in prior studies (Feldman, Gordon, Schneiderman, et al., 2010; Gordon et al., 2008). Oxytocin analyses were performed by Dr. Ruth Feldman's research laboratory; all analyses were performed in duplicate. Oxytocin concentrations were calculated using Matlab-7 according to relevant standard curves.

Prior to analysis, one participant's oxytocin baseline and post-interaction oxytocin values were removed as they were more than 3 standard deviations above the mean. This is consistent with prior studies of oxytocin and due to the concern that such values are not valid (Feldman et al., 2013; Fujiwara et al., 2019; Gordon et al., 2010c). One participant did not produce adequate saliva for the post-interaction sample in order to undergo oxytocin analysis. For this participant, their baseline oxytocin sample was inputted for the average oxytocin score. Breastfeeding status was assessed in order to control for the effects of breastfeeding on oxytocin level (Grewen et al., 2010; Uvnäs-Moberg et al., 2020). The time of oxytocin sampling and the time since the participant last ate were also assessed as potential covariates.

fMRI Measure

Infant Cry Task. We assessed maternal neural response to hearing her own and an unknown control cry using the infant cry fMRI paradigm (Swain et al., 2008). During fMRI scanning, mothers listened to cry and control sounds via headphones. Mothers were asked to allow themselves to respond naturally to each sound. The task had two functional runs, with 20-second stimulus blocks, followed by a 10-second inter-stimulus interval on average (ranging 8-12 s). Block designs, such as the infant cry paradigm, benefit from increased robustness and statistical power (Brockway, 2000; Friston et al., 1999). Each run contained four blocks, including: 1) own infant cry, 2) control cry, 3) own infant cry matched noise, and 4) control cry matched noise. Each block was presented 5 times and the order of blocks was randomized; in total, each condition was presented 10 times during the task.

Own infant cry samples were recorded at the home visit following natural instances of infant crying (e.g., crying due to hunger or mild discomfort). The control cry was the same for all participants in the study, and was collected from an infant not in the current study. Own infant cry and control cry sounds were matched for volume. Additionally, any background noise in the cry samples was removed using sound editing software (Cool Edit Pro Version 2.0, Syntrillium Software, Phoenix, AZ). Control matched noises consisted of white noise synthesized from a spectral average of the cry; this was matched to the gross temporal envelope of own infant and control cry sounds. After fMRI scanning, mothers completed a computer task in which she listened again to own infant cry, control cry, own infant cry matched noise, and control cry matched noise and rated how each sound made her feel on a variety of dimensions (i.e., pleasing, soothing, urgent, piecing, comforting, aversive, and distressing).

fMRI Acquisition. Scanning was conducted using two different scanners due to a scheduled scanner update; scanners were Siemens Trio and Siemens Prisma. Both were 3.0 T Siemens magnet scanners using a standard 32-channel head coil, acquiring 540 T2*-weighted echo-planar-imaging (EPI) volumes. The parameters of functional data were matched across the scanners (TR = 2300ms; TE = 27 ms; flip angle = 73; field of view = 192 mm; matrix size, 64 × 64; 36 axial slices; voxels = 3 mm^3). In addition to functional data, high-resolution anatomical T1-weighted images were acquired using 3D magnetization-prepared rapid gradient-echo (MPRAGE) protocol and matched across scanners. For the Siemens Trio, high resolution T1 - weighted magnetization prepared rapid gradient -echo (MPRAGE) images were acquired with the following parameters:

192 sagittal slices, TR = 2530 ms, TE = 1.64 ms, flip angle = 7°, FOV = 256 mm 2 and voxel size 1 x 1 x 1 mm. For the Siemens Prisma, T1 sequence parameters were 224 sagittal slices, TR = 2400 ms, TE = 2.07 ms, flip angle = 8°, FOV = 256 mm 2 and voxel size 0.8 x 0.8 x 0.8 mm.

fMRI Preprocessing. Preprocessing and statistical analysis were conducted in Analysis of Functional Neuroimages software (AFNI) (R. W. Cox, 1996). The first four pre-steady-state volumes (two dummy TRs and two additional TRs) for each run were removed. This was due to scanner gradients becoming fully stabilized and brain tissues reaching necessary levels of excitation during this time. Preprocessing steps involved slice timing correction, motion correction, affine alignment, and normalization to the Talairach template. Since fMRI scanning acquires slices at different time intervals, slice timing correction temporally interpolates slices such that the resulting data is as close as possible to if the brain image was acquired at a single time point. Then, motion correction or realignment corrected for head motion during scanning by aligning data to a reference time volume (in this study, the last volume of the last run). Head motion typically involves small movements; very large movements are often best dealt with by removing the given image entirely. Images with motion greater than 0.5 mm in any direction were censored. After motion correction, the functional, echo-planar image (EPI) was aligned with the structural image via coregistration. Each participant's brain was then normalized, or translated to a common shape and size, to map onto the Talairach template (Talairach & Tournoux, 1988). Lastly, spatial smoothing was applied using 6 mm full width at half maximum blur estimates and intensity scaling. Smoothing, or "blurring" of

the image, increases the signal-to-noise ratio by reducing spatial differences between subjects.

A general linear model (GLM) was used to analyze BOLD signal changes in response to the four task conditions (own infant cry, control cry, matched noise for own infant cry, and matched noise for control cry). Linear regression modeling was performed per voxel with the following regressors: four condition regressors and six motion parameter regressors. First-level, subject-specific data were normalized, transformed into standard space, and then submitted for second-level, mixed-effects whole-brain analyses. Participants with excessive motion (N=2; above 15% of TRs removed) were excluded from the analysis. Motion cut-off was framewise displacement in any direction exceeding 0.5 mm.

Analysis Plan

Covariate Selection

The following sociodemographic variables were evaluated for associations $p < .05$ with variables of interest (i.e., maternal care, maternal overprotection, oxytocin, sensitivity, non-intrusiveness): maternal age, education, race and ethnicity, handedness, postpartum months, infant sex, breastfeeding status, income-to-needs ratio in the past year, relationship status, an index of maternal intelligence, maternal psychiatric medication use, maternal self-reported history of depression, anxiety, or other psychiatric disorder, and maternal current depressive and anxiety symptoms. Additionally, the time of oxytocin sampling and the time since the participant last ate was evaluated for associations $p < .05$ with oxytocin. Infant crying for the majority of the mother-child

interaction and infant sleeping for the majority of the mother-child interaction was also evaluated for associations $p < .05$ with oxytocin, sensitivity, and non-intrusiveness.

Associations Between Variables of Interest

The associations of perceived childhood maternal caregiving (i.e., care and overprotection) and oxytocin level with parenting behaviors (sensitivity and non-intrusiveness) were examined using bivariate Pearson correlation in IBM SPSS Statistics (Version 27). Additionally, associations of perceived childhood maternal caregiving (care and overprotection) with oxytocin level were examined. Correlations were corrected for multiple comparisons via the Holm-Bonferroni method, which demonstrates enhanced statistical power compared to the standard Bonferroni correction (Abdi, 2010).

Interactions Between Variables of Interest

To investigate whether oxytocin moderated the effects of maternal care and maternal overprotection on parenting behaviors (i.e., maternal sensitivity and non-intrusiveness) via a simple moderation analysis (i.e., model 1) in PROCESS in SPSS (Hayes, 2013). Sociodemographic covariates were examined; covariates associated $p < .05$ with the dependent variable were included in post-hoc analyses.

Whole-Brain fMRI Analysis

Whole-brain linear mixed-effects models were conducted with 3dLME in AFNI (Cox, 1996). A whole brain mask was created based on 90% EPI coverage. In order to correct for multiple comparisons, whole-brain cluster extent thresholding calculations were performed with the 3dClustSim spatial autocorrelation function (ACF). A cluster extent threshold of $k \geq 32$ with a height threshold of $p < .001$ was used, equivalent to a

whole-brain corrected false positive probability of $p < .05$. Whole-brain analyses examined the effects of: 1) Childhood Maternal Care, 2) Childhood Maternal Overprotection, and 3) Oxytocin. In order to examine possible interactions, two additional whole-brain analyses examined the effects of: 1) Childhood Maternal Care and Oxytocin, and 2) Childhood Maternal Overprotection and Oxytocin. Within subject factors were the four task conditions, which were grouped across Sound (Cry vs. Noise) and Identity (Own vs. Control). Interaction effects and main effects in the whole-brain analysis were examined.

Covariates included were scanner type, postpartum months, and income-to-needs ratio. Postpartum months at the time of the fMRI scan was included as a covariate in all fMRI models because the current sample had considerable variability in postpartum age (M = 4.53 months, SD = 2.00, range: 0 – 10). Post-hoc analyses included additional variables associated $p < .05$ with the variables of interest in the whole brain model (e.g., maternal education, breastfeeding status, and Hispanic ethnicity). In order to decompose two-way interactions (e.g., Oxytocin x Sound), the between-subject variable was correlated with the brain activation difference score for infant cry sounds (both own and control infant cry sounds) vs. matching white noise sounds. In order to decompose three-way and four-way interactions (e.g., Childhood Care x Oxytocin x Sound x Identity), repeated measures ANOVAs were conducted with within-subjects variables as (1) own infant cry vs. control cry, (2) own infant cry vs. matched own cry white noise, and (3) control cry vs. matched control cry white noise. The association of between-subject variables and brain activation difference scores were also evaluated.

Exploratory Analyses – Cry Ratings and Parenting. We examined exploratory associations between neural activation extracted from the results of 3dLME whole-brain analyses in suprathreshold clusters with maternal cry ratings, sensitivity, and non-intrusiveness using bivariate Pearson correlations and repeated measures ANCOVA in SPSS. These analyses were exploratory in nature and thus should be interpreted with caution and investigated further in future research.

A Priori Regions-of-Interest Analysis

A priori regions-of-interest (ROI) analysis was performed in the amygdala using an anatomical mask. A ROI analysis was utilized due to the amygdala's small volume and difficulties detecting amygdala activation in whole-brain models. Further, strong existing literature demonstrates that the amygdala contains oxytocin receptors and is differentially activated by infant cry and other infant-relevant stimuli, with important implications for attachment, parenting, and oxytocin systems (Atzil et al., 2011; Boccia et al., 2013; Riem, Bakermans-Kranenburg, et al., 2012; Riem et al., 2011, 2016). ROIs were defined via the AAL probabilistic atlas of regions provided by AFNI. Neural activation was extracted from the left and right amygdala ROI and averaged across values. Repeated measures ANOVAs were conducted for the left and right amygdala. Brain response across conditions (Sound, Identity) was the within-subjects variable. Continuous between-subjects variables were 1) Childhood Maternal Care, 2) Childhood Maternal Overprotection, 3) Oxytocin, 4a) Childhood Maternal Care and Oxytocin, and 4b) Childhood Maternal Overprotection and Oxytocin. Covariates included were scanner type, postpartum months, and income-to-needs ratio. Post-hoc analyses included

additional variables associated $p < .05$ with the between-subjects variables (e.g., maternal education, breastfeeding status, and Hispanic ethnicity). In order to decompose three-way and four-way interactions, repeated measures ANOVAs were conducted with within-subjects variables as (1) own infant cry vs. control cry, (2) own infant cry vs. matched own cry white noise, and (3) control cry vs. matched control cry white noise. The association of between-subject variables and brain activation difference scores were also evaluated.

Exploratory Analyses – Cry Ratings and Parenting. We examined exploratory associations between neural activation extracted from the amygdala ROI analysis with maternal cry ratings, sensitivity, and non-intrusiveness using bivariate Pearson correlations and repeated measures ANCOVA in SPSS.

Results

Sample Characteristics

Mothers were 25 years old on average ($M = 25.88$, $SD = 5.35$) and over half of the participants had 14 or fewer years of education. Mothers primarily identified as Hispanic/Latinx (45.2%), followed by non-Hispanic White (41.1%). The sample was socioeconomically diverse; 43.8% of families were low-income (income-to-needs ratio ≤ 2). See **Table 1** for detailed participant demographic information.

Salivary Oxytocin

Baseline and post-interaction oxytocin values were highly correlated ($r = .52$, $p < .001$). A paired samples t-test revealed that there was not a significant change between the baseline and post-interaction oxytocin values ($t = 1.59$, $p = .119$). Due to the high

correlation between baseline and post-interaction measures of oxytocin, oxytocin levels were averaged together for subsequent analyses. The approach of averaging oxytocin levels across time-points has been used previously when samples were highly correlated (Feldman et al., 2013; Gordon et al., 2010c).

Sociodemographic Covariates

Sociodemographic associations with variables of interest were examined. Please see **Appendix A** for correlations between sociodemographic covariates and variables of interest. Perceived childhood care was not associated with any sociodemographic variables tested. Higher perceived childhood overprotection was associated with lower participant education (r = -.42, p = .001) and lower income-to-needs ratio (r = -.29, p = .032). Childhood overprotection was higher among Hispanic/Latinx participants (M = 20.05, SD = 7.06) compared to non-Hispanic participants (M =12.75, SD = 6.01), t = -4.10, p < .001. Childhood overprotection was also lower among non-Hispanic White participants (M = 11.86, SD = 5.83) compared to the rest of the sample (M = 19.07, SD = 7.06), t = 3.91, p < .001. Higher average oxytocin level was associated with higher income-to-needs ratio (r = .31, p = .022). Average oxytocin levels were also higher among participants who were breastfeeding exclusively (M = 44.15, SD = 14.70), compared to those who were not (M = 35.78, SD = 14.64), t = -2.04, p = .046.

With regards to parenting outcomes, higher sensitivity was associated with higher participant age (r = .27, p = .049), education (r = .38, p = .005) and IQ (r = .43, p = .001). Higher non-intrusiveness was associated with higher participant IQ (r = .33, p = .014).

Non-intrusiveness was also lower among Hispanic/Latinx participants (M = 5.19, SD = 1.24) compared to non-Hispanic participants (M = 5.96, SD = 1.11), t = 2.41, p = .020.

Associations Between Variables of Interest

The associations between variables of interest were examined using Holm-Bonferroni correction. There were no significant associations between perceived childhood maternal caregiving (i.e., care and overprotection) and oxytocin level with parenting behaviors (sensitivity and non-intrusiveness). Additionally, there were no significant associations between perceived childhood maternal caregiving (care and overprotection) and oxytocin level.

Interactions Between Variables of Interest

Average oxytocin level did not moderate the effects of childhood care or overprotection on parenting behaviors (i.e., sensitivity, non-intrusiveness).

Whole-Brain fMRI Analysis

Childhood Maternal Care

No significant findings.

Childhood Maternal Overprotection

Group-level whole-brain analysis revealed an interaction of Childhood Overprotection x Sound. Covariates included were scanner type, postpartum months, and maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when maternal education and Hispanic ethnicity were included as additional covariates in the whole brain model.

A significant two-way interaction of **Childhood Overprotection x Sound** (Cry, White noise) was identified in the right medial frontal gyrus and right superior frontal gyrus (**Table 2**). Higher overprotection was associated with less activation in both clusters in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed that greater activation in the right medial frontal gyrus during infant cry vs. noise was associated with finding the cry (across both own and control infant) less aversive compared to noise (r = -.28, p = .042). Greater activation in the right superior frontal gyrus during infant cry vs. noise was associated with finding the cry less comforting compared to noise (r = -.28, p = .042).

Oxytocin

Group-level whole-brain analysis revealed an interaction of Oxytocin x Sound. Covariates included were scanner type, postpartum months, and maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when breastfeeding status was included as an additional covariate in the whole brain model.

A significant two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus and right inferior frontal gyrus (**Table 3**). Higher oxytocin was associated with less activation in both clusters in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed no significant associations.

Childhood Maternal Care x Oxytocin

Group-level whole-brain analysis revealed interactions of Childhood Care x Oxytocin x Sound x Identity, Oxytocin x Sound x Identity, and Oxytocin x Sound. Covariates included were scanner type, postpartum months, and maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when breastfeeding status was added as a covariate to the whole brain model.

A four-way interaction of **Childhood Care x Oxytocin x Sound x Identity** was identified in the right anterior cingulate (**Table 4**). To decompose findings, repeated measures ANOVAs revealed significant contrasts for own infant cry vs. control cry, (F = 13.672, $p < .001$), own infant cry vs. matched noise (F = 16.217, $p < .001$), and control cry vs. matched noise (F = 6.001, p =.018). Additional post-hoc analyses divided the sample into low oxytocin and high oxytocin groups around the mean, in order to better understand findings. In the high oxytocin group, higher care was associated with greater activation to own infant cry vs. control cry (r = .45, p = .020), greater activation to own cry vs. matched noise (r = .47, p = .017), and reduced activation to control cry vs. matched noise (r = -.49, p = .012). There were no significant associations in the low oxytocin group. Exploratory analyses showed that greater activation in the right anterior cingulate during own infant cry vs. noise was associated with higher approach ratings for own infant cry (r = .34, p = .014).

A three-way interaction of **Oxytocin x Sound x Identity** was identified in the left cuneus (including the left precuneus) (**Table 4**). To decompose findings, repeated measures ANOVAs revealed significant contrasts for own infant cry vs. control cry, (F =

13.404, $p < .001$), own cry vs. matched noise ($F = 7.868$, $p = .007$), and control cry vs. matched noise ($F = 6.595$, $p = .013$). Higher oxytocin was associated with reduced left cuneus activation in response to own infant cry vs. control cry, reduced activation for own cry vs. matched noise, and increased activation for control cry vs. matched noise. Exploratory analyses demonstrated that greater activation in the left cuneus during own infant cry vs. noise was associated with higher sensitivity ($r = .30$, $p = .029$) and higher non-intrusiveness ($r = .29$, $p = .031$). Greater activation in the left cuneus during own infant cry vs. control cry was trending with higher sensitivity ($r = .27$, $p = .052$). Greater activation in the left cuneus during own infant cry vs. noise was associated with higher approach ratings for own infant cry ($r = .29$, $p = .038$). Greater activation in the left cuneus during control cry vs. noise was associated with reduced aversive ratings for control cry vs. noise ($r = -.33$, $p = .014$).

A two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right inferior frontal gyrus and right superior temporal gyrus (**Table 4**). Please see **Appendix B** for additional analyses.

Childhood Maternal Overprotection x Oxytocin

Group-level whole-brain analysis revealed interactions of Childhood Overprotection x Sound and Oxytocin x Sound. Covariates included were scanner type, postpartum months, and maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when maternal education, Hispanic ethnicity, and breastfeeding status were added as covariates to the whole brain model.

A two-way interaction of **Childhood Overprotection x Sound** (Cry, White noise) was identified in the right medial frontal gyrus (including right superior frontal gyrus) (**Table 5**). Please see **Appendix C** for additional analyses.

A two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus **(Table 5)**. Please see **Appendix C** for additional analyses.

A Priori Regions-of-Interest Analysis

Neural activation was extracted from the left and right amygdala ROIs and averaged across values. Repeated measures ANOVAs were conducted for the left and right amygdala. Within-subjects variables were brain response across conditions (Sound, Identity) and continuous, between-subjects variables tested were: 1) Childhood Maternal Care 2) Childhood Maternal Overprotection 3) Oxytocin 4a) Childhood Maternal Care and Oxytocin, and 4b) Childhood Maternal Overprotection and Oxytocin. Covariates included were scanner type, postpartum months, and income-to-needs ratio.

Childhood Maternal Care

No significant findings.

Childhood Maternal Overprotection

No significant findings.

Oxytocin

No significant findings.

Childhood Maternal Care x Oxytocin

No significant findings.

Childhood Maternal Overprotection x Oxytocin

No significant findings.

Discussion

The current study demonstrates that perceptions of childhood maternal caregiving and salivary oxytocin are, both independently and interactively, related to differences in new mother's neural response to infant cry. Independently, perceived overprotective maternal caregiving was related to dampened medial frontal and superior frontal response during infant cry. High maternal oxytocin level also emerged as a potential marker of stress in the current sample. High salivary oxytocin was related to dampened neural activation in regions important for emotion regulation and saliency, including frontal, temporal, and cuneus regions. Exploratory analyses suggest that suppressed activation in the cuneus (including the precuneus) in response to own infant cry was further associated with negative reactions to infant cry (i.e., low approach ratings) and decreased observed maternal sensitivity and non-intrusiveness. Interestingly, perceptions of childhood maternal care (specifically viewing mothers as warm and affectionate) interacted with oxytocin to predict more adaptive brain response. Among mothers with high levels of oxytocin, higher perceived childhood maternal care was related to increased anterior cingulate activation in response to own infant cry. This may suggest a unique, protective role of recollections of maternal care for postpartum mothers with high endogenous oxytocin. Taken together, findings suggest that recollections of childhood caregiving experiences and the neuropeptide oxytocin have combined influences on the neural adaptation to motherhood.

Childhood Maternal Care and Overprotection

Although there were no direct associations between perceptions of childhood maternal caregiving and observed parenting behaviors in the current study, childhood recollections did relate uniquely to maternal brain response. Perceptions of childhood maternal caregiving as overprotective and controlling were related to dampened neural activation to infant cry (both own infant and control cry sounds) compared to noise in the medial and superior frontal gyrus. Findings build on previous work suggesting that childhood overprotection is related to altered structure and function of the prefrontal cortex (PFC) (e.g., decreased gray matter volume, altered amygdala-medial PFC structural connectivity; Farber et al., 2019; Narita et al., 2010). The medial and superior PFC are typically activated in response to own infant cry sounds and associated with sensitive maternal behaviors (Kim et al., 2011; Laurent & Ablow, 2012; Swain, 2011; Swain et al., 2008, 2011; Witteman et al., 2019). The medial PFC supports the reappraisal of emotional responses (e.g., interpreting infant cry as less negative) and cognitive empathy (e.g., "theory of mind" with regards to the infant's mental state) (Moses-Kolko et al., 2010; Witteman et al., 2019). Further, hypoactivation of the medial PFC is observed among individuals with postpartum depression (Moses-Kolko et al., 2010). Hypoactivation among mothers with overprotective childhood caregiving may reflect poorer mentalization or emotion regulation in response to infant cry. Consistent with this, the current study found that dampened activation in the medial PFC was related to rating infant cry sounds as more aversive compared to noise. Conceptually, it makes sense that overprotective caregiving during childhood may be related to dampened activation in

mentalization circuits later in life. One of the hallmarks of overprotective parenting are restrictions on the child's autonomy; in other words, the child's interests or desires are not readily factored into decision-making. Individuals who grow up seeing this style of parenting modeled may be less likely to naturally engage in perspective-taking when responding to infant distress signals.

Maternal Oxytocin

Contrary to expectations, higher maternal oxytocin was associated with attenuated neural activation in areas typically stimulated by infant cry (Kim et al., 2011; Laurent & Ablow, 2012a; Swain et al., 2011; Swain, 2011). Higher maternal oxytocin was related to blunted activation in the right inferior frontal gyrus and superior temporal gyrus in response to infant cry sounds. Higher oxytocin was also related to dampened left cuneus activation (including the left precuneus) to own infant cry (compared to control cry and compared to matched noise). Findings contrast with prior research showing elevated frontal and temporal response to infant-relevant stimuli among mothers with higher plasma oxytocin (Atzil et al., 2012), and among women following intranasal oxytocin administration (Riem et al., 2011; Voorthuis et al., 2014). Although initially paradoxical, this observed dampening effect of oxytocin may be due to the known anxiolytic role of oxytocin in situations of social stress. Intranasal oxytocin administration has been observed to reduce frontal, temporal, and precuneus activation in response to negative social stimuli (e.g., angry faces) (Kanat et al., 2015; Ma, Ran, et al., 2020; Petrovic et al., 2008). Of particular relevance to the current study, higher maternal plasma oxytocin following a mother-infant interaction has been associated with *reduced* activation in the

superior temporal gyrus when viewing videos of own vs. unknown infant (Elmadih et al., 2016). Suppression in these areas may reflect maternal attempts to decrease arousal and avoidance associated with negative social stimuli.

Although the majority of prior studies relate increased oxytocin to positive parenting (Feldman et al., 2007; Feldman, Gordon, Schneiderman, et al., 2010; Gordon et al., 2010b), there is a burgeoning research base tying elevated oxytocin to heightened parenting stress and decreased sensitivity (Elmadih et al., 2014; Feldman et al., 2011). Broadly, elevated basal oxytocin is an index of interpersonal stress among women, such as relationship distress and attachment anxiety (Tabak et al., 2011; Taylor et al., 2006; Weisman et al., 2013). High basal oxytocin has also been related to increased intrusiveness in interpersonal relationships, such as attention-seeking behaviors and having difficulty spending time alone (Turner et al., 1999). Importantly, elevated maternal urinary oxytocin is associated with increased interactive stress during a mother-infant interaction and heightened parenting stress (Feldman et al., 2011). A separate line of research also suggests that dampened maternal brain activation to infant stimuli reflects postpartum stress and low mood (Laurent & Ablow, 2012a; Moses-Kolko et al., 2010; Pawluski et al., 2017), including in partially overlapping samples (Kim et al., 2016, 2020). Taken together, higher oxytocin levels may reflect mothers' stress in the parenting role, which is further associated with attenuated brain activation in response to infant cry.

Within the current study, attenuated neural response among mothers with high oxytocin appeared to have downstream impacts for observed parenting behaviors. Specifically, dampened cuneus response (including the precuneus) to own infant cry was

related to decreased maternal sensitivity and increased intrusiveness, as well as lower approach ratings for own infant cry. The precuneus and cuneus play an important role in parental mentalizing and social cognition (Atzil et al., 2014; Feldman, 2015; Völlm et al., 2006). Greater precuneus and cuneus response has been associated with positive caregiving and greater perceived warmth towards infant (Morgan et al., 2017; Wan et al., 2014); further, parenting interventions appear to increase neural response in the precuneus for own vs. control infant cry sounds (Swain et al., 2017). Decreased engagement of this area important for theory of mind could contribute to less sensitive and more intrusive maternal behaviors. Interestingly, mothers with higher salivary oxytocin appeared to up-regulate cuneus/precuneus responses to control infant cry, but down-regulate for their own infant cry, suggesting disrupted saliency processing. Although this pattern of neural responding was related to finding control cry less aversive, it was also associated with less adaptive maternal responses to own infant cry and poorer parenting behaviors.

Childhood Maternal Care and Oxytocin Interaction

There was a significant interaction between perceptions of childhood maternal care and oxytocin, such that higher maternal childhood care paired with higher oxytocin was associated with greater activation in the right anterior cingulate cortex (ACC) during own infant cry (compared to control cry and to matched noise), but reduced activation during control cry (compared to matched control noise). Further, exploratory analyses revealed that greater ACC activation during own infant cry (compared to matched noise) was associated with higher approach ratings for own infant cry. The ACC is known to be

important for emotional response, empathy, and social reward (Elmadih et al., 2016; Völlm et al., 2006). Mothers typically show heightened ACC response to own vs. unknown child stimuli, reflecting enhanced salience and emotive processing for own infant (Barrett et al., 2012; Bartels & Zeki, 2004; Elmadih et al., 2016; Leibenluft et al., 2004; Noriuchi et al., 2008); by contrast, mothers with depression history show blunted ACC response (Laurent & Ablow, 2013). Although the current study did not find observed parenting differences related to ACC activation, prior work suggests that greater ACC response is associated with observed positive parenting (Michalska et al., 2014), mother-infant synchrony during play (Atzil et al., 2014), and self-reported caregiving motivation (Bos et al., 2018).

The current findings complement existing research suggesting that both caregiving experiences and oxytocin are related to ACC activation to infant stimuli. Women with a secure attachment style exhibit greater ACC activation when empathizing with infant faces, whereas women with dismissing attachment deactivate in the ACC (Lenzi et al., 2013). Adults with perceived dysfunctional parenting in childhood also exhibit decreased default mode connectivity, specifically between the temporoparietal conjunction and ACC, after the activation of attachment memories (Adenzato et al., 2019). Drawing from a separate line of research, we know that oxytocin receptors are expressed in the ACC; oxytocin in the ACC promotes prosocial behavior and behavioral synchrony in animal models (Jiang & Platt, 2018; Yamagishi et al., 2020). Intranasal oxytocin administration enhances connectivity to the ACC (Riem et al., 2011; Riem, van IJzendoorn, et al., 2012) and stimulates response to own child pictures in the ACC (Li et

al., 2017). Taken together, the ACC appears to respond differentially to assessments of childhood caregiving and attachment, and to be stimulated by the hormone oxytocin. The question then remains, why would high perceived childhood maternal care relate to ACC activation specifically among mothers with high oxytocin?

Interestingly, with the exception of the ACC, high maternal oxytocin was related to dampened neural activation in the current study, including a number of areas known to be important for caregiving. This fits with a line of research suggesting that high maternal oxytocin is a marker of interpersonal distress, including stress in the mother-child relationship (Elmadih et al., 2014; Feldman et al., 2011; Tabak et al., 2011; Taylor et al., 2006). From this lens, it is possible that positive perceptions of childhood care may have a protective influence on maternal neural adaptation specifically within contexts of stress. Enhanced ACC activation during infant cry may reflect a compensatory response to increase motivation and empathy for infant cry; similarly, enhanced maternal oxytocin could reflect efforts to promote social affiliation and bonding under stress. Relatedly, heightened ACC activation to infant cry has been observed among individuals with high state attachment anxiety, suggesting enhanced attention and empathy for infant crying (Ma, Hu, et al., 2020). The current moderating relationship fits well with the interactionist model of oxytocin (Bartz et al., 2011), and research showing that oxytocin administration may have beneficial effects only for individuals with a history of childhood adversity (Riem et al., 2014, 2020; Schwaiger et al., 2019).

Limitations and Future Directions

The following limitations should be noted. First, the Parental Bonding Instrument (PBI) is a retrospective measure of childhood parenting experiences. The PBI assesses perceptions of parenting quality; it is not an objective or observational measure of parenting behaviors and is also independent from assessments of adult attachment (Manassis et al., 1999; Roisman et al., 2007). It is possible that mothers' recollections of their childhood maternal caregiving may differ from observational accounts. This does not negate the importance of subjective accounts of parenting. Rather, memories of childhood caregiving may have a unique and powerful influence on maternal adaptation that extends beyond observed caregiving behaviors (Fukui et al., 2021; Grant et al., 2012; Narayan et al., 2019). The current study evaluated potential confounding maternal and infant variables that could contribute to associations between reported childhood maternal caregiving and observed neural findings. Despite this, it is possible that potential third variables affected mothers' ratings. As an example, it is possible that participants' relationship quality with their mother in adulthood influenced their recollections of relationship quality in childhood.

Second, the current sample represents a healthy community sample with limited range in childhood caregiving experiences and parenting behaviors. This may have been why there were no observed associations between perceived childhood maternal caregiving and related parenting behaviors in the current sample. Perceptions of childhood maternal care were somewhat negatively skewed, with few mothers reporting very low maternal care in childhood. Similarly, few mothers exhibited very poor

parenting during the mother-infant interaction. The lowest performing mothers exhibited inconsistent or apparent sensitivity (i.e., sensitivity score of 3.50) or somewhat intrusive behaviors (i.e., non-intrusiveness score of 3.00). Further, few mothers reported clinically significant postpartum mood symptoms. With regards to depressive symptoms, 16 participants (29.6%) reported mild depressive symptoms and one participant (1.9%) indicated moderate depressive symptoms, Further, 16 mothers (29.6%) reported clinically significant trait anxiety. Research is needed to extend findings to diverse mother and infant populations, including mothers with adverse childhood experiences (e.g., childhood maltreatment) and mothers at risk for postpartum mood and parenting difficulties.

Third, the mother-infant interaction paradigm in the current study did not elicit a significant change in maternal salivary oxytocin level. Given individual stability in maternal oxytocin levels, it can be challenging to capture maternal oxytocin response change to naturalistic play interactions (Altemus et al., 2001; Elmadih et al., 2016; Gordon et al., 2010c; Levine et al., 2007). Prior studies that did document maternal oxytocin change assessed oxytocin across four time points (Kim, Fonagy, Koos, et al., 2014; Strathearn et al., 2009) and implemented mother-infant separation or "no-touch" periods prior to the play interaction (Feldman, Gordon, Schneiderman, et al., 2010; Kim, Fonagy, Koos, et al., 2014; Strathearn et al., 2009). It is recommended that future studies implement these methodological changes to better capture oxytocin responsivity.

Although the nonsignificant oxytocin change in the current study was not unusual, it does make the interpretation of oxytocin results more difficult. Factors that could have

contributed to basal oxytocin are varied, including individual factors (e.g., maternal anxiety), interpersonal factors (e.g., maternal social sensitivity and motivation), and situational factors (e.g., mothers perceiving the research home visit as being evaluative/stressful) (Bartz et al., 2011; Koven & Max, 2014). We discussed a body of literature suggesting that high maternal oxytocin is a marker of interpersonal and parenting stress. However, it is important to acknowledge that high oxytocin could reflect a variety of risk or resilience factors, which requires further investigation.

Fourth, it is not possible to infer causality of findings as measures were assessed concurrently. Dampened neural response could be a cause or a consequence of perceived childhood caregiving and oxytocin. Additionally, it is important to note that maternal oxytocin was assessed within the context of the mother-child interaction, not during exposure to the fMRI infant cry paradigm. Given the stability of intra-individual oxytocin levels, it is likely that maternal endogenous oxytocin level could relate to her brain response at a separate time point. However, the present study cannot speak directly to the relation between brain findings and concurrent oxytocin release during infant cry. Future research is needed to explore how oxytocin response differs across caregiving settings and relates to neural differences. Further, longitudinal research is needed to draw prospective associations between childhood caregiving experiences and subsequent neural, hormonal, and parenting differences.

The current study is one of the first to examine both neural and hormonal underpinnings of childhood caregiving experiences during the transition to motherhood. Findings suggest that poor perceptions of childhood maternal caregiving and high

maternal oxytocin may be important markers of risk for the neural adaptation to motherhood, reflected by dampened response to infant cry. The postpartum period is a time of rapid reorganization and vulnerability to psychopathology, particularly for mothers who recall their own mothers as overprotective or unaffectionate (Della Vedova et al., 2011; Siddiqui et al., 2000). Public health and home-visiting interventions are essential for supporting new mothers with negative caregiving experiences, as well as altering intergenerational patterns of parenting (Lieberman et al., 2020; Narayan et al., 2021; Sadler et al., 2013; Slade et al., 2020). In addition to exploring risk factors, the current study provides evidence for interactive, protective influences during the postpartum period. Specifically, perceptions of childhood maternal care as warm and affectionate appeared to interact with high maternal oxytocin to enhance ACC response to infant cry, a region important for maternal motivation and empathy. This speaks to the complexity of oxytocin in conveying both risk and resilience, depending on context and individual differences in caregiving history. Continued investigation is needed both to understand the neural and hormonal adaptations to parenthood, and to promote pathways to resilience among vulnerable mothers and infants.

Tables and Figures

Table 1. Sample Characteristics

Maternal Characteristics	N(%)	Mean ± SD	Range
Age at home visit (years)	--	25.62±5.41	18-37
Age at fMRI Scan (years)	--	25.70±5.40	18-37
Ethnicity			
Hispanic/Latinx	26 (48.1)		
Race			
White/Caucasian	27 (50.0)		
Black/African American	2 (3.7)		
Asian	1 (1.9)		
Multiracial	4 (7.4)		
Other/Unspecified [a]	20 (37.0)		
Income-to-needs ratio (last 12 months)	--	2.58±1.50	0.43-6.24
Years of education	--	14.04±2.36	9-20
Handedness (right) [b]	46 (85.2)	--	--
Relationship status (Married/engaged/common law marriage/long-term relationship)	44 (81.5)	--	--
Index of maternal intelligence (FSIQ on the WASI-II)	--	98.15 ±11.86	73-125
Breastfeeding exclusively (Yes)	21 (38.9)	--	--
Time between home visit and fMRI visit (months)	--	1.04±1.06	0.07-6.25
State anxiety symptoms (STAI-State)	--	31.66±7.52	20-54
Trait anxiety symptoms (STAI-Trait)	--	35.65±10.28	20-60
Depressive symptoms (BDI)	--	7.22±5.12	0-22
Self-reported history of psychiatric disorder (Yes) [c]	20 (37.0)	--	--

Current anxiety or depression medication use (Yes)	4 (7.4)	--	--
Perceived Maternal Care	--	26.46±8.54	4-36
Perceived Maternal Overprotection	--	16.26±7.45	2-31
Sensitivity	--	5.38±1.17	3.5-7.0
Non-intrusiveness	--	5.59±1.23	3.0-7.0
Baseline oxytocin	--	40.87±17.66	7.03-91.23
Post-interaction oxytocin	--	37.39±17.08	9.26-86.03
Average oxytocin	--	39.03±15.09	8.15-69.81

Infant Characteristics	**N(%)**	**Mean ± SD**	**Range**
Sex (female)	33 (61.1)	--	--
Gestational age at birth (weeks)	--	39.34±1.53	36-42
Age at home visit (months)	--	3.52±1.68	0.72-7.00
Age at fMRI Visit (months)	--	4.56±2.04	0.89-10.65

[a] Of the 20 participants who identified their race as "Other", 10 participants self-identified their race as "Hispanic/Latinx", 5 participants as "Mexican/Mexican-American", 1 participant as "West Indian", 1 participant as "American", and 3 participants did not self-identify.

[b] 2 participants missing handedness data

[c] Self-reported history of Anxiety (N=5), Depression (N=4), Depression and Anxiety (N=7), Postpartum Depression (N=1), Anorexia (N=1), PTSD (N=1), OCD and Anxiety (N=1)

Table 2. Significant Brain Areas from Whole Brain Analysis: Childhood Maternal Overprotection x Condition (Sound, Identity)

Regions	BA	Side	x	y	z	Cluster size	F
Maternal Overprotection x Sound							
Medial Frontal Gyrus	8	R	5	32	38	67	25.19
Superior Frontal Gyrus	10	R	23	47	5	34	18.24

Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

Table 3. Significant Brain Areas from Whole Brain Analysis: Oxytocin x Condition (Sound, Identity)

Regions	BA	Side	x	y	z	Cluster size	F
Oxytocin x Sound							
Superior Temporal Gyrus	21	R	59	-22	2	57	35.38
Inferior Frontal Gyrus	45	R	47	20	2	52	27.54

Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

Table 4. Significant Brain Areas from Whole Brain Analysis: Childhood Maternal Care x Oxytocin x Condition (Sound, Identity)

Regions	BA	Side	x	y	z	Cluster size	F
Maternal Care x Oxytocin x Sound x Identity							
Anterior Cingulate	32	R	17	41	5	48	16.51
Oxytocin x Sound x Identity							
Cuneus	18	L	-10	-79	17	39	16.67
Oxytocin x Sound							
Inferior Frontal Gyrus	45	R	47	20	2	37	26.41
Superior Temporal Gyrus	21	R	59	-22	2	34	30.60

Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

Table 5. Significant Brain Areas from Whole Brain Analysis: Childhood Maternal Overprotection x Oxytocin x Condition (Sound, Identity)

Regions	BA	Side	x	y	z	Cluster size	F
Maternal Overprotection x Sound							
Medial Frontal Gyrus	9	R	8	32	35	38	21.55
Oxytocin x Sound							
Superior Temporal Gyrus	21	R	59	-22	2	143	31.74

Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

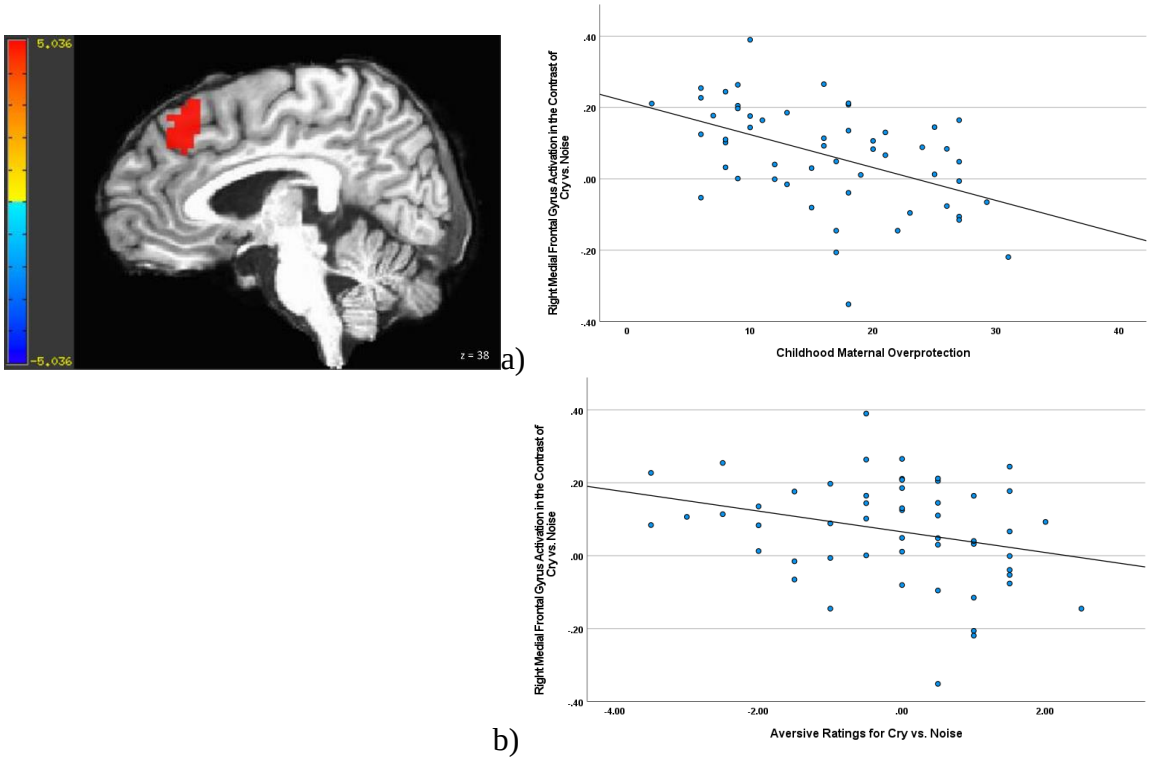

Figure 1. Right medial frontal gyrus activation (x, y, z = 5, 32, 38, k = 67, $p < .05$ corrected) showing a Childhood Maternal Overprotection x Sound interaction. a) Higher childhood maternal overprotection was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. b) Greater activation in the right medial frontal gyrus during infant cry vs. noise was associated with finding the cry (both own and control infant) less aversive compared to noise (r = -.28, p = .042).

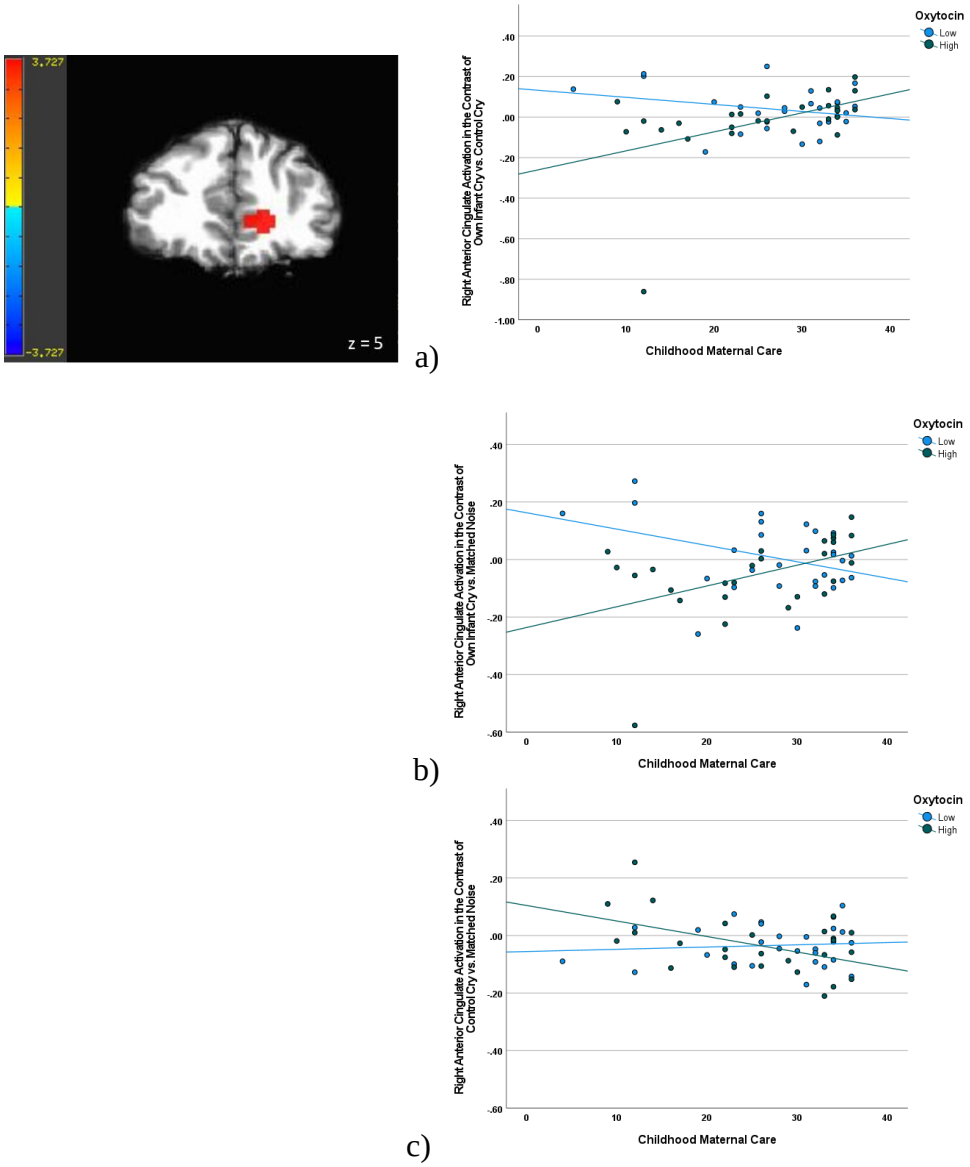

Figure 2. Right anterior cingulate activation (x, y, z = 17, 41, 5, k = 48, $p < .05$ corrected) showing a Childhood Maternal Care x Oxytocin x Sound x Identity interaction. Oxytocin was analyzed continuously; however, for ease of interpretation, post-hoc analyses examined findings by divided into low oxytocin and high oxytocin groups around the mean. Among participants with high oxytocin, higher care was associated with a) greater activation to own infant cry vs. control cry, b) greater activation to own cry vs. matched noise, and c) reduced activation to control cry vs. matched noise.

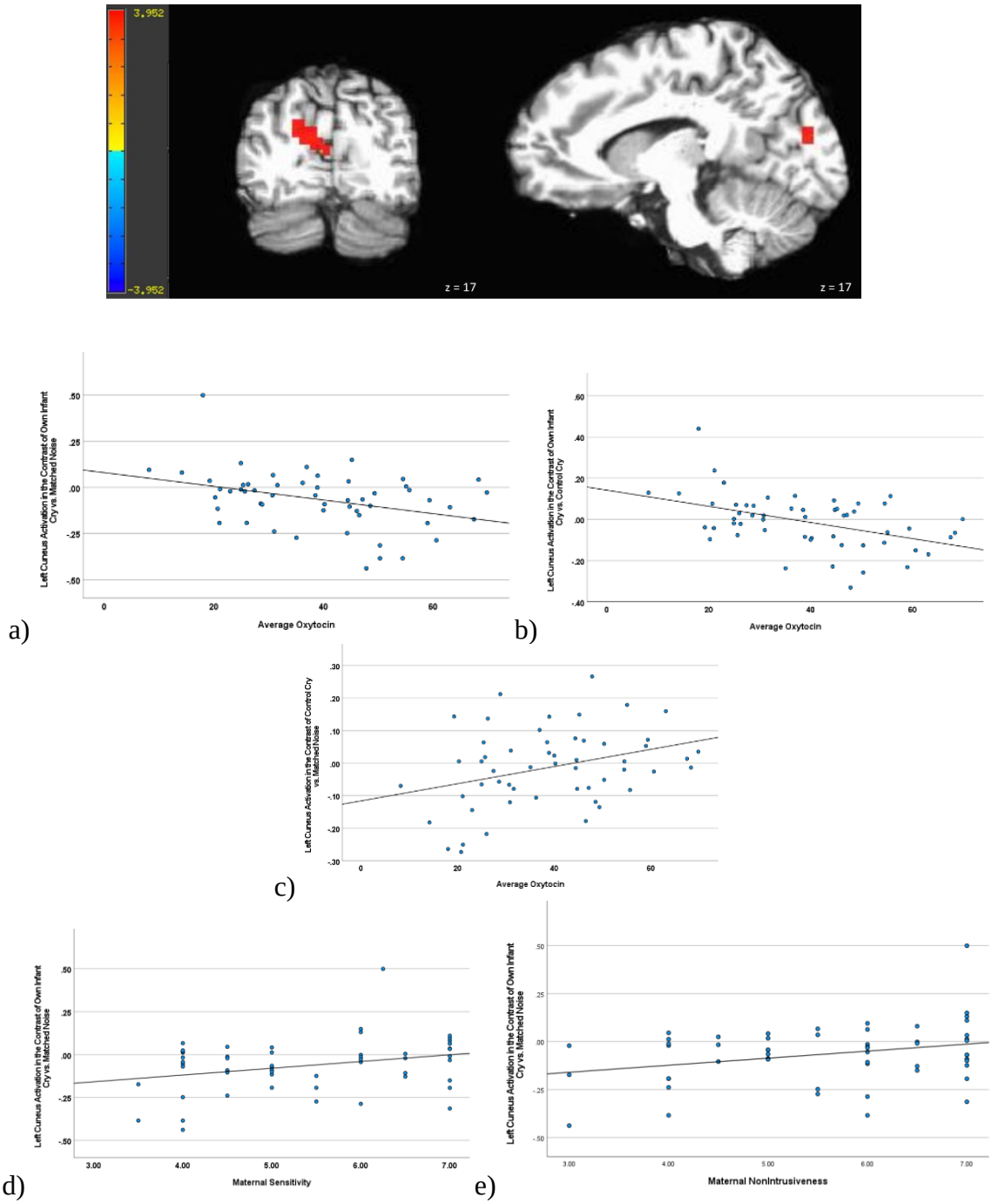

Figure 3. Left cuneus activation (x, y, z = -10, -79, 17, k = 39, $p < .05$, corrected) showing an Oxytocin x Sound x Identity interaction. Higher maternal oxytocin was associated with a) reduced activation in response to infant cry vs. control cry, b) reduced activation for own cry vs. matched noise, and c) increased activation for control cry vs. matched noise. Exploratory analyses revealed higher activation in response to own infant cry vs. matched noise was associated with d) higher maternal sensitivity ($r = .30$, $p = .029$) and e) non-intrusiveness ($r = .29$, $p = .031$).

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Appendix A.

Demographics Correlation Table

	Childhood Maternal Care	Childhood Maternal Overprotection	Average Oxytocin	Sensitivity	Non-intrusiveness
Maternal Characteristics					
Age at home visit (years)	0.137	-0.256	0.064	.270*	0.144
Age at fMRI scan (years)	0.134	-0.258	0.067	.269*	0.145
Hispanic ethnicity	-0.101	.494**	0.139	-0.185	-.317*
Non-Hispanic White	0.140	-.476**	-0.109	0.095	0.236
Income-to-needs ratio (last 12 months)	0.073	-.292*	.311*	0.153	0.012
Years of education	0.212	-.422**	0.085	.380**	0.198
Handedness (right)	0.213	-0.181	-0.039	0.086	-0.044
Relationship status (Married/long-term relationship)	0.030	0.060	-0.064	-0.017	-0.092
Index of maternal intelligence (FSIQ on the WASI-II)	0.214	-0.246	0.038	.432**	.338*
Breastfeeding exclusively (Yes)	0.051	-0.161	.273*	0.053	0.173

Time between home visit and fMRI visit (months)	-0.210	-0.070	0.210	-0.106	0.026
State anxiety symptoms (STAI-State)	-0.153	0.038	-0.148	0.036	-0.011
Trait anxiety symptoms (STAI-Trait)	-0.085	0.063	-0.130	0.061	0.225
Depressive symptoms (BDI)	-0.041	-0.117	-0.058	0.124	0.214
Self-reported history of psychiatric disorder (Yes)	-0.142	-0.005	-0.182	0.224	0.162
Current anxiety or depression medication use (Yes)	0.010	-0.039	-0.078	-0.061	0.037
Time between eating and oxytocin sampling	0.148	-0.073	-0.123	0.007	0.016
Infant Characteristics					
Infant sex (female)	0.066	-0.040	-0.032	0.103	0.076
Gestational age at birth (weeks)	0.151	-0.081	0.144	0.175	0.197
Child age at home visit (months)	0.058	0.143	-0.036	-0.015	-0.189
Child age at fMRI visit (months)	-0.061	0.081	0.079	-0.067	-0.142

$^{*}p < .05$. $^{**}p < .01$.

Appendix B.

Childhood Maternal Care x Oxytocin Model: Additional Analyses

A two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right inferior frontal gyrus and right superior temporal gyrus (**Table 4**). Higher oxytocin was associated with lower inferior frontal gyrus activation in response to infant cry sounds (both own and control infant) compared to matching white noise sounds. Higher oxytocin was associated with lower superior temporal gyrus activation in response to infant cry sounds (both own and control infant) compared to matching white noise sounds. Exploratory analyses revealed no significant associations with right inferior frontal gyrus and right superior temporal gyrus activation.

Appendix C.

Childhood Maternal Overprotection x Oxytocin: Additional Analyses

A two-way interaction of **Childhood Overprotection x Sound** (Cry, White noise) was identified in the right medial frontal gyrus (including right superior frontal gyrus) (**Table 5**). Higher overprotection was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed greater activation in the right medial frontal gyrus during infant cry vs. noise was associated with finding the cry (both own and control infant) less aversive compared to noise (r = -.29, p = .037).

A two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus **(Table 5)**. Higher oxytocin was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed nonsignificant associations with right superior temporal gyrus activation.

Chapter Three: Paper Two

Recollections of Father's Care and Overprotection in Childhood: Influences on Neural Response and Parenting Behaviors Among New Mothers

Fathers have a unique and important influence on child development, with long-lasting effects for adult emotional wellbeing (Flouri & Buchanan, 2004; Rohner & Veneziano, 2001; Sarkadi et al., 2008). Early caregiving experiences with fathers can provide protection or vulnerability for later psychological distress, and lay the groundwork for future relationships and parenting experiences (Ainsworth & Bowlby, 1991; Grant et al., 2012). Yet, research on the transition to parenthood has largely focused on the influence of childhood experiences with mothers rather than fathers. Studies often highlight intergenerational continuity in parenting styles from mother-to-daughter, rather than father-to-daughter, despite research suggesting that paternal care is equally or sometimes more influential than maternal care (Lamb, 2004; Videon, 2005). Even less is known about the implications of childhood paternal care for new mothers' neural and hormonal development, and how these may differ from the effects of childhood maternal care. Investigating these underlying neural and hormonal correlates can help to provide insight into the mechanisms contributing to intergenerational patterns of risk in parenting. Greater understanding can also inform early identification and intervention efforts to support positive postpartum adaptation and parenting. The current

study evaluates how perceived childhood paternal care and overprotection are related to first-time mothers' parenting behaviors, oxytocin levels, and brain response to infant cry.

The Importance of Fathers

The importance of fathers on child development outcomes has been historically under-studied. As cultural norms and values around fatherhood have changed, research investigating the impacts of paternal care have grown in number and sophistication (e.g., studying constructs beyond the presence or absence of a father figure) (Cabrera, Tamis-LeMonda, Bradley, Hofferth, & Lamb, 2000; Lamb, 2004). Research demonstrates that the influence of caregiving by fathers on offspring psychological adjustment is equal to or in some cases greater than the influence of care by mothers (Bretherton, 2010; Lamb, 2004; Rohner & Veneziano, 2001; Videon, 2005). The unique role of fathers may be due to differences in how mothers and fathers interact with their children (Möller et al., 2013). Although fathers may spend less time with their children overall compared to mothers, they spend more time playing with children (Lawson & Mace, 2009; Lewis & Lamb, 2003). Fathers are overall less sensitive and supportive compared to mothers (Lewis & Lamb, 2003). Yet, fathers engage in more "rough and tumble" play than mothers, which is thought to stimulate child risk-taking, exploration, and build confidence (Paquette, 2004). High quality paternal physical play with his child at age 4 is associated with fewer child emotional problems and fewer problems with peers (Fletcher et al., 2013). Some researchers have conceptualized fathers as the "primary playmate", helping to activate and arouse children (Paquette, 2004). This is in contrast to typical

conceptualizations of high-quality maternal care, which can involve emphasis on soothing the child during times of distress.

Perceptions of childhood paternal care as affectionate (vs. cold) or overprotective (vs. autonomy-granting) can be assessed retrospectively via the Parental Bonding Instrument (PBI; Parker, 1990). Research suggests that fathers are typically reported to be less caring and less overprotective than mothers on average (Wilhelm et al., 2005). Lower levels of paternal overcontrolling behavior could fit with the theory of fathers fulfilling an "activation relationship" (Paquette, 2004). High paternal overprotection is related to increased child anxiety (Rork & Morris, 2009). Children whose parents playfully encourage them to take risks or to go out of their comfort zone (e.g., through teasing, competition) exhibit less anxiety; moreover, this association is stronger for fathers than mothers (for review see Möller et al., 2016). Both low perceived paternal care and high perceived paternal overprotection are unique predictors of adult depression, social anxiety, drug abuse, chronic pain and reduced overall quality of life (Anhalt & Morris, 2008; Anno et al., 2015; Kullberg et al., 2020; Overbeek et al., 2007; Rikhye et al., 2008).

Recalled memories of caregiving in childhood are especially salient during the perinatal period and may have implications for the transition to motherhood (Narayan et al., 2018). Perceptions of poor quality fathering are related to increased perinatal depression, anxiety, and worries about parenting, specifically for individuals reporting low paternal care and/or high paternal overprotection (Boyce et al., 1991; Choi et al., 2010; Fukui et al., 2021; Grant et al., 2012). By contrast, mothers who report both high

paternal care and low paternal overprotection experience lower levels of parenting stress (Willinger et al., 2005). Studies that have combined maternal and paternal parenting scores find that higher care and lower overprotection are related to increased maternal sensitivity, mother-infant bonding, and infant attachment security (Barrig Jo, 2008; Hall et al., 2015; Ohara et al., 2018). However, it is unclear the extent to which paternal caregiving may predict parenting behaviors independently or uniquely from maternal care. This is in part due to limited research in this area; many studies examine sex-specific continuity in parenting (e.g., continuity from father-to-son or mother-to-daughter; Brown et al., 2017; Jessee & Adamsons, 2018; Miller et al., 1997; Otani et al., 2009). When examined separately, some studies find effects of maternal, but not paternal care for observed parenting behaviors (Madden et al., 2015). Other studies demonstrate similar perceptions of parenting between fathers and their adult offspring (e.g., continuity in harsh, authoritarian, or permissive parenting) (Campbell & Gilmore, 2007; Simons et al., 1991). Perceived childhood paternal care (assessed via the PBI) was associated with mothers' self-reported affectionate parenting, whereas paternal overprotection was associated with her self-reported overprotective parenting (Kitamura et al., 2009). Given limited observational research on the specific effects of fathering on daughters' parenting behaviors, it is currently unclear how robust the effects of fathering may be among new mothers.

Neural Response as a Potential Mechanism

Early caregiving experiences have a profound influence on offspring brain development and neural regulation in adulthood (Kim, Leckman, Mayes, Newman, et al.,

2010; Riem et al., 2012, 2016; Strathearn et al., 2009; Unternaehrer et al., 2015). Moreover, individual differences in brain response among new mothers are related to important indicators of maternal mood, infant bonding, and parenting outcomes (Kim, Leckman, Mayes, Feldman, et al., 2010; Laurent & Ablow, 2012b; Musser et al., 2012). However, to our knowledge, no studies have investigated whether childhood paternal caregiving impacts maternal brain function to infant cues. The current study examines neural response to infant cry, an important signal of infant distress and motivator for caregiving. Infant cry sounds typically activate maternal brain response in areas important for social cognition and empathy (middle, superior, and inferior frontal gyrus, superior temporal gyrus, fusiform gyrus, anterior cingulate) and reward/motivation (striatum, amygdala, hippocampus) (Kim et al., 2011; Laurent & Ablow, 2012; Swain, Kim, & Ho, 2011; Swain, 2011; Swain et al., 2008). In turn, greater activation to own infant cry in areas such as the superior and inferior frontal gyrus reflect enhanced maternal sensitivity, and may support maternal emotional regulation and mentalization (Kim et al., 2011; Musser et al., 2012). By contrast, hyperactivation in areas important for empathy, such as the insula, are related to intrusive maternal behaviors, and may reflect heightened empathic distress to infant's distress (Musser et al., 2012).

Prior research suggests that higher perceived childhood *maternal* care activates overlapping prefrontal and temporal regions (e.g., greater activation in middle frontal gyrus, superior temporal gyrus, and fusiform gyrus) in response to infant cry among new mothers (Kim, Leckman, Mayes, Newman, et al., 2010). By contrast, mothers reporting low childhood maternal care show increased left hippocampus activation when listening

to infant cries, perhaps indicating greater stress reactivity to infant distress signals (Kim, Leckman, Mayes, Newman, et al., 2010). In a study focused on young adults, perceptions of childhood paternal caregiving were related to differential prefrontal response, and moderated by genetic factors (Cataldo et al., 2020). For individuals with specific oxytocin receptor gene polymorphisms, higher childhood parental care was related to greater brain activation in the right middle frontal gyrus when listening to distress vocalizations; higher childhood paternal overprotection was also related to greater activation in the left middle frontal gyrus and part of the dorsolateral prefrontal cortex (PFC). This may suggest potentially lateralized effects of paternal care and overprotection. In another study, childhood maternal overprotection, but not paternal overprotection, was related to heightened amygdala response to signs of interpersonal threat (i.e., angry faces) (Farber et al., 2019).

Despite few functional neuroimaging studies, preliminary structural research suggests volumetric differences based on childhood paternal care. Among a sample of young adults, higher childhood paternal care was associated with increased gray matter volume in the left dorsolateral prefrontal cortex (PFC), the right ventromedial PFC, and the right orbitolateral PFC. Further, ROI analysis of the dorsolateral PFC revealed that low paternal care and high paternal overprotection were associated with reduced gray matter volume (Narita et al., 2010). Decreased gray matter volume in the left DLPFC was in turn associated with higher trait anxiety and depressive symptoms; poor paternal care was also associated with higher depressive symptoms. Findings suggest that low paternal care and excessive paternal overprotection during childhood may induce morphological

changes of the DLPFC, which could predispose adults to mood disorders. These results, combined with previously reported associations between childhood paternal care and perinatal mood symptoms (Boyce et al., 1991; Choi et al., 2010; Fukui et al., 2021; Grant et al., 2012), could suggest potentially overlapping neural circuits. Lack of childhood paternal care could dampen limbic and prefrontal cortical activation to infant stimuli similarly to depressed or anxious mothers (e.g., blunted striatal, anterior cingulate, and medial superior frontal activation; Barrett et al., 2012; Laurent & Ablow, 2012; Moses-Kolko et al., 2014; Pawluski et al., 2017). However, further research is needed to understand if and how paternal care during childhood alters maternal motivation and emotion regulation networks.

Oxytocin as a Potential Mechanism

The oxytocin system is another plausible mechanism by which paternal childhood care could have long-lasting effects on offspring. The neuropeptide oxytocin plays a key role in social bonding and has been implicated in the activation of nurturance in both mothers and fathers (Feldman, Gordon, Schneiderman, et al., 2010; Gordon et al., 2010a, 2010b; Weisman et al., 2012). Oxytocin also coordinates neural changes in response to infant cry to facilitate parenting (Meyer-Lindenberg et al., 2011; Swain et al., 2011). High plasma oxytocin is related to enhanced activation in social cognition (i.e., superior and middle frontal cortices, insula, superior and middle temporal cortices, inferior parietal lobule) and limbic/motivational circuits (e.g., nucleus accumbens, amygdala, ventral anterior cingulate) in response to infant stimuli (Atzil et al., 2012).

Paternal oxytocin levels are highly correlated with infant oxytocin, suggesting the intergenerational transmission and regulation of oxytocin (Feldman, Gordon, & Zagoory-Sharon, 2010). Experimentally increasing fathers' oxytocin levels (via intranasal administration of oxytocin) has been shown to increase fathers' social engagement behaviors and infant salivary oxytocin levels (Weisman et al., 2012). Increased parental oxytocin response following infant contact are related to higher stimulatory contact in fathers, and greater affectionate touch and responsive engagement in mothers (Feldman, Gordon, Schneiderman, et al., 2010; Kim et al., 2014). Oxytocin does not always increase following infant contact, however, with some studies demonstrating stable individual oxytocin levels (Altemus et al., 2001; Elmadih et al., 2016; Gordon et al., 2010c; Levine et al., 2007). Most studies find that mothers and fathers with higher baseline oxytocin levels demonstrate more affectionate contact and positive engagement with their infant (Apter-Levi et al., 2014; Feldman et al., 2007, 2011; Feldman, Gordon, Schneiderman, et al., 2010; Gordon et al., 2010b; Scatliffe et al., 2019). There are some exceptions, however, with a few studies finding that highly sensitive mothers have lower oxytocin levels at baseline and following a mother-infant play interaction (Elmadih et al., 2016; Markova & Siposova, 2019). This is because oxytocin functions in multiple roles; in addition to promoting social bonding and parental motivation, it also has anxiolytic and stress-reducing properties in contexts of high social stress (Elmadih et al., 2016; Markova & Siposova, 2019; Tops et al., 2007).

Early attachment relationships are central for modulating oxytocinergic systems, and show lasting effects into adulthood. Childhood care and attachment are related to

adult oxytocin levels (Feldman, Gordon, & Zagoory-Sharon, 2010; Pierrehumbert et al., 2012; Strathearn et al., 2009; Tops et al., 2007), although few studies have separated out the effects of paternal childhood care. Gordon and colleagues (2008) found that higher levels of perceived childhood paternal care were related to higher plasma oxytocin levels in young adults. However, Boccia and colleagues (2021) failed to replicate this association using urine oxytocin levels. They found no associations with perceived childhood paternal care and overprotection; by contrast, childhood maternal overprotection was related to lower oxytocin levels. Among a sample of mothers and fathers, higher plasma oxytocin level was associated with higher perceived care in childhood, using an average of maternal and paternal care (Feldman et al., 2011). Mothers with a secure attachment style, although not specific to the father-child relationship, show higher peripheral oxytocin response after infant free play (Strathearn et al., 2009). Higher peripheral oxytocin response was further associated with increased activation of the hypothalamus/pituitary region and the right ventral striatum when viewing neutral own-infant faces (Strathearn et al., 2009). Generally, high childhood care appears to be associated with increased levels of oxytocin, although study specifically on paternal care is needed.

The research on oxytocin is much less conclusive when studying individuals with a history of negative childhood experiences. Individuals who experienced childhood maltreatment, neglect, or adverse child experiences broadly (which may or may not be related to the parenting relationship) can show both decreased or increased oxytocin levels (Bhandari et al., 2014; Eapen et al., 2014; Heim et al., 2009; Müller et al., 2019;

Pierrehumbert et al., 2010). This is because oxytocin's function is highly dependent on context, with oxytocin levels potentially acting as a marker of stress in high-risk contexts (Weisman et al., 2013). For example, Julian and colleagues (2018) found that higher salivary oxytocin was related to increased positive parenting among mothers with low adverse child experiences (ACEs), but decreased positive parenting behaviors among mothers with high ACEs. Some research suggests that oxytocin administration is particularly beneficial for adults with negative caregiving experiences (Riem et al., 2014, 2020; Schwaiger et al., 2019), whereas others find that the effects of oxytocin are hindered in these individuals (Bakermans-Kranenburg & van IJzendoorn, 2013; Bartz et al., 2010; Van Ijzendoorn et al., 2011). Further investigation is needed to understand how oxytocin is associated with and may moderate the effects of perceived childhood paternal caregiving, and contribute to caregiving in the next generation.

The Current Study

Few studies have examined the role of multiple biological systems and their interactions in contributing to the adaptation to parenthood. An interactionist model is best suited to parse out the individual and interactive contributions of childhood care and neural and hormonal factors. In addition, investigation has been limited into the role of fathers in contributing to maternal behavior and neurobiology in the next generation. The current study investigates how childhood paternal care and overprotection influence maternal brain response to hearing her own infant cry, as well as maternal oxytocin during an infant play interaction. We explore how these differences in neural and oxytocin response relate to maternal caregiving within a socioeconomically diverse

sample of first-time mothers. Multiple measures of parenting adaptation are assessed, including direct observations of maternal behavior (i.e., sensitivity and non-intrusiveness).Maternal sensitivity and non-intrusiveness were selected as these observational assessments of parenting are important predictors of child development and attachment (Bigelow et al., 2010; Egeland et al., 1993; Warren & Simmens, 2005) and related to perceptions of childhood care and overprotection (Barrig Jo, 2008; Brown, 2019; Burrous et al., 2009; Jacobvitz et al., 1991).

Hypotheses are as follows:

1. **Childhood Paternal Care**

Higher childhood paternal care will be associated with greater activations in the ventral striatum, hypothalamus and pituitary, insula, middle and inferior frontal gyrus, superior temporal gyrus, and fusiform gyrus when listening to own infant cry compared to control cry. Lower childhood paternal care will be associated with hyperactivation of the amygdala and hippocampus when listening to own infant cry vs. control cry. Higher paternal care and associated neural activation will be associated with greater oxytocin response following a mother-infant play interaction, which will be further associated with increased maternal sensitivity during mother-infant play.

2. **Childhood Paternal Overprotection**

Higher childhood paternal overprotection will be associated with amygdala hyperactivation when listening to own infant cry vs. control cry. Higher paternal overprotection and related neural activation will be associated with lower oxytocin

response following a mother-infant play interaction, which will be further associated with decreased maternal non-intrusiveness during mother-infant play.

3. Oxytocin

Higher oxytocin increase following a mother-infant play interaction will be associated with enhanced activation in the ventral striatum, hypothalamus/pituitary, anterior cingulate, insula, and middle and superior frontal gyrus when listening to own infant cry vs. control cry. Higher oxytocin response and associated neural activation will be related to increased maternal sensitivity and non-intrusiveness.

3a. Higher childhood paternal care will be related to increased oxytocin response.

3b. Higher childhood paternal overprotection will be related to decreased oxytocin response.

4. Oxytocin Alternative Hypothesis

4a. If oxytocin is not associated with childhood paternal care, it is hypothesized that there will be a significant interaction between childhood paternal care and oxytocin response. Higher care and higher oxytocin will be interactively related to enhanced neural activation in social cognition and reward regions (e.g., middle, superior, and inferior frontal gyrus, striatum, anterior cingulate) during own infant cry vs. control cry. Exploratory analyses will suggest that enhanced neural activation will be related to increased sensitivity and non-intrusiveness.

4b. If oxytocin is not associated with childhood paternal overprotection, it is hypothesized that there will be a significant interaction between childhood paternal overprotection and oxytocin response. Lower overprotection and higher oxytocin will be

interactively related to enhanced neural activation in social cognition and reward regions (e.g., middle, superior, and inferior frontal gyrus, striatum, anterior cingulate) during own infant cry vs. control cry. Exploratory analyses will suggest that enhanced neural activation will be related to increased sensitivity and non-intrusiveness.

Materials and Methods

Participants

Participants were English-speaking, first-time mothers and their biological infants. All mothers were recruited during the first 7 months postpartum, and infants were 3.5 months old on average (*SD* = 1.72). The original study focused on recruiting low or middle-income mothers. To support recruitment of a socioeconomically diverse sample, brochures and fliers were provided to Women, Infants, and Children (WIC) centers, OB/GYN and midwifery clinics, and Colorado State Prenatal Plus programs throughout the Denver Metro area. Participants were excluded due to history/current self-reported psychiatric/neurological illness, except for reports of depression and anxiety. Participants reporting current psychoactive drug use were also excluded, except for participants reporting use of antidepressants. This choice was made due to literature suggesting that psychiatric disorders (e.g., schizophrenia) and psychoactive medication use (e.g., antipsychotics) are related to pronounced brain differences (Arnone et al., 2009; Ho, Andreasen, Ziebell, Pierson, & Magnotta, 2011). Participants were also be excluded for birthing complications or infant medical illnesses that involved more than a one-night stay in the neonatal intensive care unit (NICU). Further, participants were excluded from the neuroimaging portion of the study due to concerns related to MRI, such as magnetic

metal in the body, claustrophobia, or current pregnancy. Participants with excessive motion (above 15% of TRs removed; see fMRI Preprocessing Section) were also excluded from the neuroimaging analysis.

Forty-nine participants were included in the current study. Prior to analysis, two participants were excluded due to excessive motion (above 15% TRs removed; motion cut-off was framewise displacement in any direction exceeding 0.5 mm) and one was excluded due to a technical error during scanning (i.e., use of incorrect stimuli). Two participants were excluded due to missing both baseline and post-interaction oxytocin data (these participants did not produce sufficient saliva samples in order to undergo oxytocin analysis). One participant was removed as their baseline and post-interaction values were greater than 3 standard deviations above the mean (please see Oxytocin section below for detailed information). Lastly, five participants were excluded from the current study because they reported not having a father figure during their childhood, and thus did not complete the Paternal subscales of the Parental Bonding Instrument (PBI). An overlapping sample of fMRI data from the current study has been included in previous publications (Grande et al., 2021; Kim et al., 2016; Kim et al., 2020; Olsavsky et al., 2021); however, previous publications did not examine the role of oxytocin or the Parental Bonding Instrument (PBI).

Research Procedures

The Infant Development, Environment, and Attachment (IDEA) Project study protocol was approved by the university Institutional Review Board. Researchers contacted participants via phone to assess eligibility for the study. If eligible, participants

completed two sessions: a home visit and an fMRI visit. At each phase of the study, mothers provided written informed consent in accordance with Institutional Review Board guidelines. During the home visit, participants completed interviews, questionnaires, and the mother-infant interaction. Next, participants visited the Intermountain Neuroimaging Center at the University of Colorado – Boulder to complete the fMRI portion of the study. The average time interval between the two phases was approximately one month. Participants were provided $100 compensation for participation in the home visit and $100 for participation in the fMRI visit; compensation amounts were based on an hourly rate of $25. Child care and transportation assistance were also provided if needed. The compensation amount was selected based on multiple past projects with low-income populations; this amount was thought to respect participants' time and effort, but was not overly high to have the risk of being coercive.

Measures

Sociodemographic Covariates

Postpartum months, maternal age, handedness, education, race and ethnicity, relationship status, income-to-needs ratio in the past year, history of depression, anxiety or other psychiatric disorder, current psychiatric medication use, breastfeeding status, and infant sex were assessed via maternal interview at the home visit. Income-to-needs ratio (INR) was calculated by dividing total household income in the past year by the poverty threshold at the time of assessment, specified by the U.S. Census Bureau. An index of maternal intelligence was assessed at the home visit using the Wechsler Abbreviated Scale of Intelligence-II (WASI-II). Current depressive and anxiety symptoms were

measured via the Beck Depression Inventory (BDI; Beck, Ward, Mendelson, Mock, & Erbaugh, 1961) and State-Trait Personality Inventory (STAI; Spielberger, 1983), respectively.

Parental Bonding Instrument

The Parental Bonding Instrument (PBI) is a retrospective, self-report measure assessing the perceptions of caregiving experiences during the first 16 years of life (Parker et al., 1979). The PBI captures important aspects of the quality of caregiving experiences and demonstrates reliability, validity, and long-term stability, although being retrospective in nature (Wilhelm et al., 2005). Some studies find that PBI scores are susceptible to mood bias (Gillham et al., 2007); thus, inclusion of depression and anxiety symptoms as covariates were carefully considered. The PBI assesses the perceived care and overprotection received from both mother and father during childhood. Paternal care and overprotection were the focus of the current study. Perceived care describes aspects of emotional closeness, warmth, and understanding, as opposed to emotional coldness, indifference, or neglect. Examples of items are: '(Father) Spoke to me in a warm and friendly voice' and 'Appeared to understand my problems and worries'. Perceived control or overprotection describes excessive intrusion, contact, and prevention of independence, as opposed to encouragement of child autonomy. Examples of items are: '(Father) Did not want me to grow up' and 'Tried to control everything I did'. Items are rated on a 4-point Likert scale, describing *very unlike* (0), *moderately unlike* (1), *moderately like* (2), and *very like* (3). Perceived care scores can range from 0 to 36 and overprotection scores can range from 0 to 39.

The present study assessed the main effects and the interaction of paternal care and paternal overprotection; please see **Table 1** for detailed descriptive information. Perceived paternal care and overprotection were negatively trending in the current study (r = -.24, p = .094). According to PBI classification cut-offs (Parker et al., 1979), 24 participants (49%) perceived their fathers as caring whereas 25 participants (51%) did not. 31 participants (63.3%) perceived their fathers as overprotective whereas 18 participants (36.7%) did not. Although perceived maternal care was not the focus of the present study, it should be noted that perceived paternal care was not significantly associated with perceived maternal care (r = .03, p > .10), but paternal overprotection was associated with maternal overprotection (r = .38, p = .002). In the current study, paternal care had excellent internal consistency with a Cronbach's α coefficient of .94. Paternal overprotection had good internal consistency with a Cronbach's α coefficient of .85.

Parenting Behavior

Maternal parenting behavior was assessed during a 15-minute mother-infant free-play interaction. The mother-infant interaction was conducted during the home visit, when the infant was 3.5 months old on average. Mothers were instructed to interact naturally with their infant without using toys. Maternal and infant behavior was videotaped and observationally coded using the Emotional Availability Scales, 4th Edition (EA Scales; Biringen, 2008). Researchers were trained and certified by Dr. Biringen, creator of the EA Scales. The EA Scales provides global assessments of caregiver behavior on four dimensions: sensitivity, structuring, non-intrusiveness, and non-hostility. Each score

ranges from 1 to 7, with higher scores reflecting more optimal parenting. The sensitivity and intrusiveness scales were examined in the current study.

Sensitivity measures the parents' attunement and responsiveness to their infants' signals, as well as the warmth, authenticity, and appropriateness of the parents' affect. In the current study, maternal sensitivity ranged from 3.5 to 7.0 (M = 5.41, SD = 1.17). A mother who scored 7.0 is highly sensitive; she exhibits genuine interest and pleasure when interacting with her infant (e.g., warm smiles, playful and affectionate touch) and expresses affirming and accepting statements towards her child. Her behavior is also flexible; she responds quickly and appropriately to distress signals and handles conflict smoothly. By contrast, a participant who scored 3.5 exhibits inconsistent or apparent sensitivity. This could reflect inconsistencies between maternal behavior and affect, such as behaving attentively but exhibiting bland, forced sweet, or exaggerated excitable affect. Alternatively, a score of 3.5 could be awarded if the parent is warm, but there are sustained periods of unresponsiveness from the infant without the parent perceiving the child's state and pursuing alternative actions. A mother who scored 5.5 exhibits bland sensitivity. This captures some aspects of parenting which were less optimal, such as poorer negotiation of conflict or neutral affect, but an otherwise good style of relating.

Non-intrusiveness measures the extent to which the parent can be emotionally available to their infant without being overprotective or over-directive. Intrusive parental behavior is conceptualized as behaviors that undermine the child's autonomy; thus, ratings also take into consideration the infant's emotional state and how they respond to maternal behaviors. In the present study, maternal non-intrusiveness scores ranged from

3.0 to 7.0 (M = 5.61, SD = 1.24). A mother who scored 7.0 is non-intrusive and emotionally present. She allows the infant a great deal of opportunity to explore and follows the infant's lead during interactions. A mother who scored 3.0 is somewhat intrusive. She interferes during play, such as abruptly changing the activity rather than following the infant's interest. Interruptions can be verbal or physical, such as redirecting or moving the infant. A participant who scored 5.5 is generally non-intrusive, but sometimes exhibits benign forms of intrusiveness. This can capture mothers who are well-intentioned but overly-cautious, such that they provide excessive safety tips and redirections of play.

Maternal sensitivity and non-intrusiveness were significantly correlated in the current sample (r = .54, p < .001). Two researchers coded the videos, with 24% overlap. The average intraclass correlation (ICC) was 0.91. Researchers coded if the infant was sleeping and if the infant was crying for the majority of the mother-child interaction, to examine as potential covariates.

Oxytocin

Two salivary oxytocin samples were collected during the home visit. Baseline saliva samples were collected 40 minutes after the start of the home visit but before the start of the mother-infant interaction, ranging between 4:39pm and 5:16pm. Post-interaction saliva samples were collected 15 minutes after the conclusion of the mother-infant interaction, ranging from 5:20 to 6:08pm. Oxytocin was collected via Salivette (Sarstedt, Rommelsdorft, Germany), chilled for 3-4 hours, spun down by centrifuge at 4°C at 1500 x g for 15 minutes, and then stored in a -80°C freezer. Oxytocin levels were determined

via a commercial oxytocin ELISA kit (Assay Design, MI, USA) which has been used in prior studies (Feldman, Gordon, Schneiderman, et al., 2010; Gordon et al., 2008). All oxytocin analyses were performed in duplicate by Dr. Ruth Feldman's research laboratory. Oxytocin concentrations were calculated using Matlab-7 according to relevant standard curves.

Prior to starting analysis, one participant's data was removed as their baseline and post-interaction values were greater than 3 standard deviations above the mean. This was based on prior studies of oxytocin and due to the concern that such values are not valid (Feldman et al., 2013; Fujiwara et al., 2019; Gordon et al., 2010c). One participant did not produce sufficient saliva for the post-interaction sample. As an average oxytocin value could not be computed for this participant, their baseline sample oxytocin value was inputted instead. With regards to covariates, breastfeeding status was assessed in order to control for the influence of breastfeeding on participants' oxytocin level (Grewen et al., 2010; Uvnäs-Moberg et al., 2020). The time of oxytocin sampling and the time since the participant last ate were also assessed as potential covariates (Julian et al., 2018).

fMRI Measure

Infant Cry Task. Participants' neural response to hearing their own and an unknown control cry was assessed using the infant cry fMRI paradigm (Swain et al., 2008). During the fMRI scan, participants listened to cry and control sounds via headphones. Participants were instructed to respond naturally to each sound. The infant cry task has two functional runs, with 20-second stimulus blocks, followed by a 10-second inter-

stimulus interval on average (ranging 8-12 seconds). Block design tasks, such as the infant cry paradigm, demonstrate increased robustness and statistical power (Brockway, 2000; Friston et al., 1999). Each run contains four blocks, including: 1) own infant cry, 2) control cry, 3) own infant cry matched noise, and 4) control cry matched noise. Each block was presented 5 times and the order of blocks was randomized. In total, each condition was presented 10 times during the infant cry task.

Recordings of own infant cry were collected during the home visit following spontaneous, natural instances of infant crying, such as the infant crying due to hunger or mild discomfort. The control cry was collected from an infant not in the current study; the same control cry sound was used for all participants in the study. Own infant cry and control cry sounds were matched for volume, and sound editing software was used to remove any background noise (Cool Edit Pro Version 2.0, Syntrillium Software, Phoenix, AZ). The control matched noises contained white noise synthesized from a spectral average of the cry and were matched to the gross temporal envelope of own infant and control cry sounds. Following the fMRI scan, participants completed a computer task in which they to own infant cry, control cry, own infant cry matched noise, and control cry matched noise again. Participants rated how each sound made them feel on a number of dimensions (e.g., aversive, distressing, pleasing, approach, soothing, urgent, piecing, comforting, healthy).

fMRI Acquisition. fMRI scanning was conducted using two different scanners (i.e., Siemens Trio and Siemens Prisma) because of a scheduled scanner update. Both scanners were 3.0 T Siemens magnet scanners using a standard 32-channel head coil, acquiring

540 T2*-weighted echo-planar-imaging (EPI) volumes. The parameters of functional data were matched across the scanners (TR = 2300ms; TE = 27 ms; flip angle = 73; field of view = 192 mm; matrix size, 64 × 64; 36 axial slices; voxels = 3 mm^3). High-resolution anatomical T1-weighted images were acquired using 3D magnetization-prepared rapid gradient-echo (MPRAGE) protocol and also matched across scanners. For the Siemens Trio scanner, high resolution T1 - weighted magnetization prepared rapid gradient -echo (MPRAGE) images were acquired with the following parameters: 192 sagittal slices, TR = 2530 ms, TE = 1.64 ms, flip angle = 7°, FOV = 256 mm 2 and voxel size 1 x 1 x 1 mm. For the Siemens Prisma scanner, T1 sequence parameters were 224 sagittal slices, TR = 2400 ms, TE = 2.07 ms, flip angle = 8°, FOV = 256 mm 2 and voxel size 0.8 x 0.8 x 0.8 mm.

fMRI Preprocessing. Preprocessing and statistical analysis were conducted in Analysis of Functional Neuroimages software (AFNI; Cox, 1996). The first four pre-steady-state volumes (two dummy TRs and two additional TRs) for each run were removed. Preprocessing steps included slice timing correction, motion correction, affine alignment, and normalization to the Talairach template. fMRI scanning acquires slices at different time intervals; thus, slice timing correction temporally interpolates slices such that the resulting data is as close as possible to if the brain image was acquired at a single time point. Motion correction or realignment corrects for head motion during scanning by aligning data to a reference time volume (in this study, the last volume of the last run). Images with motion greater than 0.5 mm in any direction were censored. After motion correction, the functional, echo-planar image (EPI) was aligned with the structural image

via coregistration. Each participant's brain was then normalized to map onto the Talairach template (Talairach & Tournoux, 1988). Lastly, spatial smoothing was applied using 6 mm full width at half maximum blur estimates and intensity scaling.

A general linear model (GLM) was used to analyze BOLD signal changes in response to the four task conditions (own infant cry, control cry, matched noise for own infant cry, and matched noise for control cry). Linear regression modeling was performed per voxel with the following regressors: four condition regressors and six motion parameter regressors. First-level, subject-specific data were normalized, transformed into standard space, and then submitted for second-level, mixed-effects whole-brain analyses. Participants with excessive motion (N=1; above 15% of TRs removed) were excluded from the analysis.

Analysis Plan

Covariate Selection

Sociodemographic variables were evaluated for associations $p < .05$ with variables of interest (i.e., paternal care, paternal overprotection, oxytocin, sensitivity, non-intrusiveness): postpartum months, maternal age, handedness, education, race and ethnicity, income-to-needs ratio in the past year, relationship status, an index of maternal intelligence, infant sex, maternal psychiatric medication use, maternal self-reported history of depression, anxiety, or other psychiatric disorder, and maternal current depressive and anxiety symptoms. In addition, breastfeeding status, the time of oxytocin sampling, and the time since the participant last ate was evaluated for associations $p < .05$

with average oxytocin level. Bivariate Pearson correlations were used for continuous variables; independent samples t-tests were used for categorical variables.

Associations Between Variables of Interest

The correlations of perceived childhood paternal caregiving (i.e., care and overprotection) and oxytocin level with parenting behaviors (sensitivity and non-intrusiveness) were examined using bivariate Pearson correlation in IBM SPSS Statistics (Version 27). In addition, associations of perceived childhood paternal caregiving (care and overprotection) with oxytocin level were examined. Correlations were corrected for multiple comparisons via the Holm-Bonferroni method, which demonstrates enhanced statistical power compared to the standard Bonferroni correction (Abdi, 2010).

Interactions Between Variables of Interest

To investigate the interaction between paternal care and oxytocin in relation to parenting behaviors (maternal sensitivity and non-intrusiveness), a simple moderation analysis (model 1) was performed using PROCESS in SPSS (Hayes, 2013). Additionally, analyses examined whether oxytocin moderated the effects of paternal overprotection on parenting behaviors via simple moderation (model 1) in PROCESS. Sociodemographic covariates were examined; covariates associated $p < .05$ with the dependent variable were included in post-hoc analyses.

Whole-Brain fMRI Analysis

A whole-brain linear mixed-effects model was conducted using 3dLME in AFNI (Cox, 1996). A whole brain mask was created based on 90% EPI coverage. Whole-brain cluster extent thresholding calculations were performed with the 3dClustSim spatial

autocorrelation function (ACF) in order to correct for multiple comparisons. A cluster extent threshold of $k \geq 32$ with a height threshold of $p < .001$ was utilized, equivalent to a whole-brain corrected false positive probability of $p < .05$. Whole-brain analyses examined the effects of 1) Paternal Care, 2) Paternal Overprotection, and 3) Oxytocin. In addition, we ran two whole-brain models examining the effects of 1) Paternal Care and Oxytocin, and 2) Paternal Overprotection and Oxytocin. Within subject factors were the conditions of Sound (Cry vs. Noise) and Identity (Own vs. Control Infant). We examined both main effects and interaction effects in the whole-brain analysis.

Covariates included in the whole brain models were scanner type, postpartum months, and income-to-needs ratio (INR). Postpartum months at the time of the fMRI scan was included as a covariate in all fMRI models. This was because the current sample had considerable variability in postpartum age at the time of the fMRI visit ($M = 4.61$ months, $SD = 2.08$, range: 0 – 10). Post-hoc analyses included additional variables associated $p < .05$ with the variables of interest in the whole brain model, such as maternal state anxiety, self-reported history of psychiatric disorder, and breastfeeding status.

In order to decompose interactions by the Sound condition, the between-subject variable was correlated with the brain activation difference score for infant cry sounds (both own and control infant cry sounds) vs. matching white noise sounds. In order to decompose interactions for Sound by Identity, repeated measures ANOVAs were conducted with within-subjects variables as (1) own infant cry vs. control cry, (2) own infant cry vs. matched own cry white noise, and (3) control cry vs. matched control cry

white noise. The association of between-subject variables and brain activation difference scores were also investigated.

Exploratory Analyses – Cry Ratings and Parenting. Exploratory associations between neural activation (extracted from the results of 3dLME whole-brain analyses in suprathreshold clusters) and cry ratings, sensitivity, and non-intrusiveness were evaluated using bivariate Pearson correlations and repeated measures ANCOVA in SPSS. Given the observed association between childhood paternal care and mood measures in the current study, we also examined exploratory associations between neural activation and state anxiety and depressive symptoms using bivariate Pearson correlations and repeated measures ANCOVA. These analyses are exploratory in nature and thus should be interpreted cautiously and examined further in future research.

A Priori Regions-of-Interest Analysis

An a priori regions-of-interest (ROI) analysis was performed in the amygdala using an anatomical mask. A ROI analysis was chosen due to the amygdala's small volume and difficulties detecting amygdala activation in whole-brain models. Prior research demonstrates that the amygdala is differentially activated by infant cry, contains oxytocin receptors, and is implicated in parenting and attachment systems (Atzil et al., 2011; Boccia et al., 2013; Riem, Bakermans-Kranenburg, et al., 2012; Riem et al., 2011, 2016). ROIs were defined using the AAL probabilistic atlas of regions provided in AFNI.

Two repeated measures ANOVAs were conducted for the left and right amygdala, respectively. Neural activation was extracted from the left and right amygdala ROI and averaged across values. Brain response across conditions (Sound, Identity) was the

within-subjects variable. Continuous between-subjects variables were 1) Paternal Care, 2) Paternal Overprotection, 3) Oxytocin, 4a) Paternal Care and Oxytocin, and 4b) Paternal Overprotection and Oxytocin. Covariates included were scanner type, postpartum months, and income-to-needs ratio. Post-hoc analyses included additional variables associated $p < .05$ with the variables of interest in the whole brain model (e.g., maternal state anxiety, self-reported history of psychiatric disorder, breastfeeding status). In order to decompose three-way and four-way interactions, repeated measures ANOVAs were conducted. Within-subjects variables were: 1) own infant cry vs. control cry, 2) own infant cry vs. matched own cry white noise, and 3) control cry vs. matched control cry white noise. Correlations between brain activation difference scores and between-subject variables were also assessed.

Exploratory Analyses – Cry Ratings and Parenting. Exploratory associations between neural activation (extracted from the amygdala ROI analysis) and maternal cry ratings, sensitivity, and non-intrusiveness were evaluated using bivariate Pearson correlations and repeated measures ANCOVA in SPSS. Given the observed association between childhood parental care and mood measures in the current study, we also examined exploratory associations between neural activation and state anxiety and depressive symptoms using bivariate Pearson correlations and repeated measures ANCOVA.

Results

Sample Characteristics

Participants were 26 years old on average ($M = 25.99$, $SD = 5.55$) and over half of the participants had 14 or fewer years of education. Participants primarily identified as

Hispanic/Latinx (46.9%), followed by non-Hispanic White (40.8%). The sample was socioeconomically diverse; 40.8% of families were low-income (income-to-needs ratio ≤ 2). Seventeen participants (34.7%) self-reported a history of psychiatric disorder (e.g., anxiety, depression). See **Table 1** for detailed participant demographic information.

Salivary Oxytocin

Baseline and post-interaction oxytocin values were highly correlated ($r = .51$, $p < .001$). A paired samples t-test showed that there was a non-significant change between the baseline and post-interaction oxytocin samples ($t = 1.71$, $p = .094$). Due to the high correlation between baseline and post-interaction measures, oxytocin level values were averaged for subsequent analyses. The approach of averaging oxytocin levels across time-points has been used in prior studies when samples were highly correlated (Feldman et al., 2013; Gordon et al., 2010c).

Sociodemographic Correlations

Sociodemographic associations with variables of interest were explored. Please see **Appendix A** for correlations between sociodemographic variables and variables of interest. Higher perceived paternal care was associated with decreased maternal state anxiety ($r = -.30$, $p = .036$) and trend-level decreased depressive symptoms ($r = -.27$, $p = .059$). Perceived paternal care was also lower among participants with a self-reported history of psychiatric disorder ($M = 16.95$, $SD = 10.90$) compared to those without ($M = 25.41$, $SD = 9.45$), $t = 2.83$, $p = .007$. Higher perceived paternal overprotection was associated with reduced income-to-needs ratio in the past year ($r = -.37$, $p = .009$). Higher oxytocin was associated with higher income-to-needs ratio ($r = .28$, $p = .048$). Oxytocin

was higher among participants who were breastfeeding exclusively (M = 44.12, SD = 15.08) compared to those who were not (M = 35.31, SD = 14.26), t = -2.08, p = .043.

With regards to parenting behaviors, higher maternal sensitivity was associated with higher maternal age (r = .29, p = .046), higher education (r = .36, p = .011) and higher IQ (r = .43, p = .002). Sensitivity was also higher among participants with a self-reported history of psychiatric disorder (M = 5.88, SD = 0.96), compared to those without (M = 5.16, SD = 1.20), t = -2.15, p = .037. Higher maternal non-intrusiveness was also associated with higher IQ (r = .33, p = .002). Non-intrusiveness was lower among Hispanic participants (M = 5.24, SD = 1.28) compared to non-Hispanic participants (M = 5.94, SD = 1.13), t = 2.04, p = .047.

Correlations between Variables of Interest

The associations between variables of interest were examined using Holm-Bonferroni correction. No significant associations were observed for perceived childhood paternal caregiving (i.e., care and overprotection) and oxytocin level with parenting behaviors (sensitivity and non-intrusiveness). Additionally, no significant associations were observed for perceived childhood paternal caregiving (care and overprotection) and oxytocin level.

Interactions between Variables of Interest

Paternal Care x Oxytocin

There was not a significant interaction between paternal care and oxytocin in relation to parenting behaviors (i.e., maternal sensitivity, non-intrusiveness).

Paternal Overprotection x Oxytocin

There was not a significant interaction between paternal care and oxytocin in relation to parenting behaviors (i.e., maternal sensitivity, non-intrusiveness).

Whole-Brain fMRI Analysis

Paternal Care

Group-level whole-brain analysis revealed an interaction of Paternal Care x Sound. Covariates included were scanner type, postpartum months, and maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when maternal state anxiety, history of psychiatric disorder, and depressive symptoms were included as additional covariates in the whole brain model.

A significant two-way interaction of **Paternal Care x Sound** (Cry, White noise) was identified in the left precentral gyrus, right postcentral gyrus, right insula, right precentral gyrus, left precuneus, and left superior temporal gyrus (**Table 2**). Higher paternal care was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds in all clusters. Exploratory analyses revealed that greater activation in the right insula (r = .34, p = .016) and left superior temporal gyrus (r = .32, p = .026) during infant cry vs. noise were associated with increased non-intrusiveness. With regard to infant cry ratings, exploratory analyses showed that greater activation in the right postcentral gyrus during cry vs. noise was associated with rating infant cry as less aversive compared to noise (r = -.34, p = .017). Greater activation in the left precuneus during cry vs. noise was associated with rating infant cry as more pleasing compared to noise (r = .30, p = .039). Exploratory analyses

also revealed that greater activation in the left precentral gyrus (r = .32, p = .025), right postcentral gyrus (r = .51, p < .001), right precentral gyrus (r = .40, p = .004), and left precuneus (r = .32, p = .024) were related to higher maternal depressive symptoms. Greater activation in the right postcentral gyrus (r = .33, p = .022), left precuneus (r = .36, p = .011), and left superior temporal gyrus (r = .30, p = .039) were related to higher state anxiety.

Paternal Overprotection

No significant findings.

Oxytocin

Group-level whole-brain analysis revealed an interaction of Oxytocin x Sound. Covariates included were scanner type, postpartum months, and maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when breastfeeding status was included as an additional covariate in the whole brain model.

A significant two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus, right precentral gyrus, and right inferior frontal gyrus (**Table 3**). For all clusters, higher oxytocin was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed no significant associations.

Paternal Care x Oxytocin

Group-level whole-brain analysis revealed an interaction of Paternal Care x Sound and Oxytocin x Sound. Covariates included were scanner type, postpartum months, and

maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when maternal state anxiety, breastfeeding status, history of psychiatric disorder, and depressive symptoms were included as additional covariates in the whole brain model.

A significant two-way interaction of **Paternal Care x Sound** (Cry, White noise) was identified in the left precentral gyrus (including left insula), right postcentral gyrus (including right transverse temporal gyrus), right insula (including right inferior parietal lobule), left precuneus, left superior temporal gyrus, and right precentral gyrus (**Table 4**). Please see **Appendix B** for additional analyses.

A significant two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus (including right middle temporal gyrus), right inferior frontal gyrus, and right precentral gyrus (**Table 4**). Please see **Appendix B** for additional analyses.

Paternal Overprotection x Oxytocin

Group-level whole-brain analysis revealed an interaction of Paternal Overprotection x Oxytocin x Sound, Paternal Overprotection x Sound, and Oxytocin x Sound. Covariates included were scanner type, postpartum months, and maternal income-to-needs ratio. Post-hoc analysis revealed that findings remained significant when breastfeeding status was included as an additional covariate in the whole brain model.

A significant three-way interaction of **Paternal Overprotection x Oxytocin x Sound** (Cry, White noise) was identified in the left supramarginal gyrus (**Table 5**). In order to decompose findings, post-hoc analyses examined findings by dividing the sample into

low oxytocin and high oxytocin overprotection groups. In the high oxytocin group, higher paternal overprotection was associated with decreased activation in the left supramarginal gyrus in response to infant cry sounds compared to matching white noise sounds (r = -.46, p = .024). In the low oxytocin group, higher paternal overprotection was associated with increased activation in the left supramarginal gyrus in response to infant cry sounds compared to matching white noise sounds (r = .44, p = .027). Exploratory analyses revealed that greater activation in the left supramarginal gyrus during cry vs. noise was associated with increased sensitivity (r = .31, p = .032) and increased non-intrusiveness (r = .32, p = .023).

A significant two-way interaction of **Paternal Overprotection x Sound** (Cry, White noise) was identified in the right medial frontal gyrus and right inferior frontal gyrus (**Table 5**). For both clusters, higher paternal overprotection was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed that greater activation in the right medial frontal gyrus (cluster 1) during cry vs. noise was associated with rating infant cry as less comforting compared to noise (r = -.30, p = .039) and less aversive compared to noise (r = -.33, p = .023).

A significant two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus, right precentral gyrus, and right inferior frontal gyrus (**Table 5**). Please see **Appendix C** for additional analyses.

A Priori Regions-of-Interest Analysis

Neural activation was extracted from the left and right amygdala ROIs and averaged across values. Repeated measures ANOVAs were conducted for the left and right amygdala. Within-subjects variables were brain response across conditions (Sound, Identity) and continuous, between-subjects variables tested were: 1) Paternal Care, 2) Paternal Overprotection, 3) Oxytocin 4a) Paternal Care and Oxytocin, and 4b) Paternal Overprotection and Oxytocin. Covariates included were scanner type, postpartum months, and income-to-needs ratio.

Paternal Care

Repeated measures ANOVA revealed no significant findings for the right amygdala. Repeated measures ANOVA revealed a significant interaction for **Paternal Care x Sound x Identity** ($F = 5.208$, $p = .027$) in the left amygdala. This interaction was at trend level with the inclusion of additional covariates maternal psychiatric history and state anxiety ($F = 3.819$, $p = .058$). To decompose findings, repeated measures ANOVAs revealed significant contrasts for own infant cry vs. control cry, ($F = 5.140$, $p = .028$) and control cry vs. matched noise ($F = 6.233$, $p = .016$). Higher paternal care was associated with greater left amygdala activation in response to own cry vs. control cry and reduced activation to control cry vs. matched control noise. Exploratory analyses revealed no significant findings.

Paternal Overprotection

No significant findings.

Oxytocin

No significant findings.

Paternal Care x Oxytocin

Repeated measures ANOVA revealed no significant findings for the right amygdala. Repeated measures ANOVA revealed a significant interaction for **Paternal Care x Sound x Identity** ($F = 5.082$, $p = .029$) in the left amygdala. Please see **Appendix D** for additional analyses.

Paternal Overprotection x Oxytocin

No significant findings.

Discussion

The current study is one of the first, to our knowledge, to show that perceived childhood paternal care and paternal overprotection are related to maternal parenting behaviors and brain response to infant stimuli. The present study also deepens our understanding of how neurobiological factors alter the influence of childhood experiences on maternal behavior. Findings suggest a differential effect of perceived childhood paternal overprotection on maternal behavior, depending on maternal salivary oxytocin levels. Recollections of overprotective fathering are associated with dampened activation in the supramarginal gyrus among mothers with high oxytocin levels, but heightened activation among mothers with low oxytocin levels, when listening to infant cry sounds. Further, exploratory analyses reveal that greater activation in the supramarginal gyrus during infant cry was associated with increased maternal sensitivity and decreased intrusiveness. Thus, perceptions of childhood paternal overprotection may indirectly

signal neural risk or protection for maternal parenting behaviors, depending on the individual's oxytocin level.

Paternal Care

The main effects of childhood paternal affectionate care revealed that higher levels of care were associated with dampened brain response in the precentral and postcentral gyrus, superior temporal gyrus, insula, and precuneus regions during presentation of infant cry sounds. This finding was surprising and not consistent with prior research on childhood maternal care, which demonstrated enhanced brain response in the superior temporal gyrus (Kim, Leckman, Mayes, Newman, et al., 2010). Exploratory analyses suggest that dampened activation in these areas may be related to poorer parenting outcomes, but elevated maternal anxiety and depressive symptoms. Dampened activation in the superior temporal gyrus and insula, specifically, were related to increased maternal intrusive behaviors. The association between paternal care and dampened brain activation during infant cry may be protective for maternal mental health, while also conveying potential risk for parenting. This is consistent with research suggesting that neural changes during the postpartum period promote responsivity to infant cues, but heighten risk for postpartum mood difficulties. For example, mothers' insula response increases across the postpartum period; however, insula activation is related to increased risk for anxiety and depressive symptoms (Gingnell et al., 2015). In the current sample, perceived childhood paternal care was related to decreased maternal state anxiety and trend-level decreased depressive symptoms. Exploratory analyses further showed that childhood paternal care decreases neural activation in areas positively related to depression (i.e.,

precentral and postcentral gyrus, precuneus) and anxiety (i.e., superior temporal gyrus, postcentral gyrus, precuneus). Said differently, mothers with low paternal care may exhibit hypersensitive responding to infant cry, consistent with their high state anxiety. This fits with a growing body of literature suggesting that anxious mothers exhibit prefrontal and motor cortex hyperactivation to infant and adult affective stimuli (Gingnell et al., 2015; Kim et al., 2015; Noriuchi et al., 2008; Roos et al., 2011; Yatziv et al., 2021). Elevated pre- and post-central gyrus activation to emotional stimuli (e.g., fearful or sad faces) has also been observed among depressed individuals (Chen et al., 2006; Scheuerecker et al., 2010). Although hyperactivation of these regions may help to facilitate empathy and mentalizing with regards to infant distress (and thus decrease intrusive behaviors), there is a trade-off in that mothers may also exhibit enhanced anxiety and disrupted mood.

In addition to clusters identified in the whole brain analysis, an a priori amygdala region-of-interest (ROI) analysis demonstrated that higher childhood paternal care was associated with greater left amygdala activation during exposure to own cry vs. control cry and reduced activation during exposure to control cry vs. matched control noise. Greater amygdala activation to own infant cry (compared to control cry) may reflect heightened saliency and attunement towards own infant, and has previously been associated with higher maternal sensitivity (Kim et al., 2011). By contrast, greater amygdala activation to control cry among mothers with lower childhood paternal care may reflect greater maternal negative emotion (e.g., experiencing angry or aversive feelings) (Firk et al., 2018; Riem, Bakermans-Kranenburg, et al., 2012). Unfamiliar infant

cry may be particularly distressing for mothers with poorer childhood parenting experiences, as they may be unsure how to interpret or respond to the novel infant cry. By contrast, mothers with perceptions of warm childhood paternal care may be more flexible in their ability to attend to new infant cry stimuli without becoming overwhelmed.

Paternal Overprotection

Higher childhood paternal overprotection was related to attenuated activation to infant cry in prefrontal areas important for emotion regulation and social cognition (i.e., medial and inferior frontal gyrus). Interestingly, this finding was observed only when paternal overprotection was examined within a model that included oxytocin. This suggests the importance of considering individual oxytocin levels before interpreting childhood caregiving findings. Mothers typically show enhanced prefrontal cortical response during exposure to infant stimuli; this may support mothers' mentalization capacities via enhanced emotional salience (e.g., medial PFC) and empathy processes (e.g., inferior frontal gyrus) (Leibenluft et al., 2004; Lenzi et al., 2009; Lorberbaum et al., 2002). Dampened prefrontal activation has been reported among mothers experiencing depressed mood, using substances, or with insecure adult attachment (Landi et al., 2011; Laurent & Ablow, 2012b; Moses-Kolko et al., 2010; Strathearn et al., 2009). Although no parenting findings were observed in this study, prior research suggests that dampened brain response in regions such as the inferior frontal gyrus are related to decreased maternal sensitivity (Kim et al., 2011; Musser et al., 2012). Listening to infant cry likely activates higher-level maternal mentalization processes, such as recalling past memories of care and inferring the infant's emotional state and needs. Attenuated activation in

prefrontal areas may reflect disrupted responsivity to infant cues for mothers reporting overprotective and controlling fathering in childhood.

Oxytocin

Higher maternal oxytocin during the mother-infant interaction was associated with suppressed activation in the superior temporal gyrus, precentral gyrus, and inferior frontal gyrus during exposure to infant cry. These are all regions typically activated by infant cry and known to play a role in emotion regulation, mentalization, and empathy (Kim et al., 2011; Laurent & Ablow, 2012a; Swain, 2011; Swain et al., 2011). This was somewhat surprising as some prior research suggests that plasma oxytocin and intranasal oxytocin are related to elevated frontal and temporal gyrus activation to infant-stimuli (Atzil et al., 2012; Riem et al., 2011; Voorthuis et al., 2014). Of note, however, Elmadih and colleagues (2016) found that, among high sensitive mothers, higher maternal plasma oxytocin following a mother-infant interaction was associated with reduced activation in the superior temporal gyrus, when viewing own infant videos. This relation between elevated oxytocin and dampened neural activity is likely consistent with oxytocin's known anxiolytic effects during times of stress (Kanat et al., 2015; Ma, Ran, et al., 2020; Petrovic et al., 2008; Tops et al., 2007). Although the mother-infant interaction was not designed to be a stress task, aspects of infant play (e.g., fussy infant behaviors, crying) and the research visit itself (e.g., unfamiliar researchers visiting the home) could elicit social stress. Elevated oxytocin can be an index of heightened interpersonal stress broadly, and specifically increased interactive stress during mother-infant play (Feldman et al., 2011). Further, oxytocin release can help to reduce parenting stress and promote

social affiliation (Elmadih et al., 2014; Feldman, 2012). High oxytocin levels may help some mothers to manage social or infant-related stress, while also contributing to dampened neural response to infant-relevant stimuli.

Paternal Overprotection & Oxytocin

The interaction of perceived childhood paternal overprotection and maternal salivary oxytocin revealed a striking pattern of activation in the supramarginal gyrus (SMG). Among mothers with lower oxytocin, higher paternal overprotection was associated with *increased* activation in the SMG during infant cry; by contrast, among mothers with higher oxytocin, higher paternal overprotection was related to *decreased* activation in the SMG. The SMG is located within the inferior parietal lobule and involved in neural networks underlying emotion perception and empathy for pain (Lawrence et al., 2006; Naor et al., 2020). SMG activity is shown to be critical for overcoming emotional egocentricity (Silani et al., 2013). Further, SMG response to infant cry is observed among healthy maternal populations (Bornstein et al., 2017; Laurent & Ablow, 2012a). In the current study, recruitment of the SMG during infant cry appeared to relate to positive parenting behaviors during play, specifically increased maternal sensitivity and reduced maternal intrusiveness. As discussed previously, high maternal oxytocin could be an index of high interpersonal or parenting stress. These findings suggest that perceptions of fathers as overprotective may convey neural risk for poorer parenting in the context of high oxytocin (i.e., high stress). Stated differently, risk for parenting difficulties appears elevated among mothers with two risk factors present (i.e., both high oxytocin and high childhood paternal overprotection). Although neural activation in the SMG was related to

parenting outcomes, it is critical to highlight that paternal overprotection and oxytocin were not interactively related to parenting differences within this sample. Thus, SMG neural activation may thus represent a more proximal and subtle neural correlate of risk.

Limitations and Future Directions

The current findings should be considered in light of several limitations. First, perceptions of childhood paternal caregiving were assessed retrospectively and were subjective in nature. The current study evaluated associations between perceptions of childhood caregiving and potentially confounding factors, such as current mood, and included them as covariates when relevant. There was possible suggestion of mood bias in the current study as maternal anxiety and depressive symptoms were related to poorer perceptions of childhood paternal care; thus, these variables were included as covariates in the whole brain model. It is also possible that unexamined third variables, such as participants' relationship quality with their father in adulthood, influenced ratings. Additionally, the current study assessed participants' perceptions of childhood care, rather than objective measurements of caregiving (e.g., observed paternal behaviors in childhood). Although the parental bonding instrument has demonstrated long-term stability and validity (Kapçi & Küçüker, 2006; Wilhelm et al., 2005), it cannot be equated with observational measures of caregiving quality or to adult attachment security (Manassis et al., 1999; Roisman et al., 2007). Despite this, perceptions of childhood caregiving have a unique and predictive influence on adaptation to motherhood and are worthy of investigation in their own right (Fukui et al., 2021; Grant et al., 2012). Prospective studies with large sample sizes are needed to tease out the similar and

different influences of perceptions of childhood care, observed parenting in childhood, and attachment security.

Second, the present study assessed measures concurrently, making interpretations of causality impossible. It is possible that associations between perceived childhood paternal care, neural activation, and parenting behaviors were related because they were assessed within a similar time frame. However, research by Ohara and colleagues (2018) suggests that perceived childhood care assessed prior to the postpartum period is predictive of mother-infant bonding. Future research using a longitudinal design will be important to investigate perceived childhood paternal care and brain response to infant cry and how these prospectively predict vulnerability or resilience during the postpartum period.

Third, the range of perceived childhood paternal caregiving and observed parenting was constrained in the current sample. According to defined PBI cut-offs (Parker et al., 1979), only 36.7% of the sample would be classified as experiencing low childhood paternal overprotection. Although a continuous measure of childhood care and overprotection was used, it is important to note the uneven distribution of parenting styles. Study implications for individuals with low paternal overprotection should be made with particular caution, due to the small number of such participants in this study. In addition, the nonsignificant associations between paternal care, paternal overprotection, and salivary oxytocin with parenting behaviors should be interpreted within the context of this specific sample. It is possible that detection of individual differences in parenting were reduced due to the modest sample size (N=49) and constrained range in assessments. It is also important to note that no participants

exhibited extreme intrusiveness or insensitivity to their child's signals. Additionally, no participants reported moderate or severe depressive symptoms and only 14 mothers (28.6%) reported clinically significant trait anxiety. Findings highlight the influence of perceived paternal childhood caregiving among a community sample of healthy postpartum mothers. However, future investigation is needed to explore the generalizability of findings among high-risk and clinical samples.

Fourth, the present study did not find a significant change in maternal oxytocin level following the infant play interaction. This is consistent with some prior work showing high individual stability and no overall change in maternal OT levels during infant interaction (Altemus et al., 2001; Elmadih et al., 2014; Gordon et al., 2010c; Levine et al., 2007). It is also possible that the current study paradigm did not sufficiently elicit an oxytocin response. Maternal oxytocin was assessed during a home visit, when mothers could interact with their infants prior to the mother-infant interaction. Perhaps the mother-infant interaction was not sufficiently novel, and thus did not elicit a clear oxytocin response. Future research could conduct the mother-infant play interaction in a laboratory setting to control for differences in home environments. Researchers could also briefly remove the infant from the mother's care before starting the infant play interaction (Elmadih et al., 2016; Feldman, Gordon, Schneiderman, et al., 2010; S. Kim et al., 2014; Strathearn et al., 2009). Although postpartum months were included as a covariate, it is possible that oxytocin differences by postpartum age may have reduced detection of individual differences within this modest sample size. Some studies also assess the longitudinal course of oxytocin during pregnancy and postpartum as a

predictor of maternal mood and mother-infant bonding, which may be more meaningful than a single assessment (Jobst et al., 2016; Levine et al., 2007).

Finally, the current study found differences in how mothers responded to the identity of infant cry stimuli (i.e., own infant cry vs. control infant cry) only for the amygdala ROI analysis but not the whole brain analysis, which contrasts with prior literature (Kim et al., 2011; Laurent & Ablow, 2012a, 2012b; Musser et al., 2012; Swain et al., 2008). In other words, the majority of neuroimaging findings in the present study were related to the general processing of infant cry stimuli (i.e., maternal brain response combined across own infant and control infant cry conditions). In the current sample, 66.7% of mothers correctly identified their own infant cry sound per post-scanner ratings. Infant cry sounds were collected at the home visit and then played at the fMRI visit, which was on average 1 month later (but varied between 0 and 6 months). It is possible that the infant's cry changed significantly during this time period, leading to difficulties identifying the cry sound at later visits. Future research could collect and present infant cry sounds concurrently to eliminate this potential issue. Additionally, researchers could inform mothers of the identity of own and control infant cries prior to scanning.

Research on maternal brain and behavior has often neglected the importance of childhood caregiving experiences with fathers. The current findings demonstrate that perceptions of childhood paternal care as affectionate (vs. cold) and autonomy-granting (vs. overprotective) relate to maternal brain response during the postpartum period, with downstream impacts for maternal mood and behavior. Further, this relationship appears to be modulated by maternal oxytocin levels, such that the impact of childhood

overprotection depends on individual differences in oxytocin levels. Research is needed to further understand the role of fathers in promoting the neurobiological adaptation to parenthood.

Tables and Figures

Table 1. Sample Characteristics

Maternal Characteristics	N(%)	Mean ± SD	Range
Age at home visit (years)	--	25.90±5.56	18-37
Age at fMRI Scan (years)	--	25.99±5.55	18-37
Ethnicity			
Hispanic/Latinx	23(46.9)		
Race			
White/Caucasian	25 (51.0)		
Black/African American	2 (4.1)		
Asian	1 (2.0)		
Multiracial	4 (8.2)		
Other/Unspecified [a]	17 (34.7)		
Income-to-needs ratio (last 12 months)	--	2.64±1.51	0.43-6.24
Years of education	--	14.18±2.41	9-20
Handedness (right) [b]	42 (85.7)	--	--
Relationship status (Married/engaged/common law marriage/long-term relationship)	39 (79.6)	--	--
Index of maternal intelligence (FSIQ on the WASI-II)	--	98.73 ± 11.75	73-125
Breastfeeding exclusively (Yes)	20 (40.8)	--	--
Time between home visit and fMRI visit (months)	--	1.08±1.10	0.07-6.25
State anxiety symptoms (STAI-State)	--	31.43±7.42	20-54
Trait anxiety symptoms (STAI-Trait)	--	35.04±10.07	20-60

Depressive symptoms (BDI)	--	6.78±4.81	0-17
Self-reported history of psychiatric disorder (Yes) [c]	17 (34.7)	--	--
Current anxiety or depression medication use (Yes)	3 (6.1)	--	--
Perceived Paternal Care	--	22.47±10.67	1-36
Perceived Paternal Overprotection	--	15.84±8.89	0-37
Sensitivity	--	5.41±1.17	3.5-7.0
Non-intrusiveness	--	5.61±1.24	3.0-7.0
Baseline oxytocin	--	41.00±17.50	7.03-91.23
Post-interaction oxytocin	--	37.01±17.34 (N=48)	9.26-86.03
Average oxytocin	--	38.90±15.09	8.15-69.81

Infant Characteristics	**N(%)**	**Mean ± SD**	**Range**
Sex (female)	30 (61.2)	--	--
Gestational age at birth (weeks)	--	39.44±1.53	37-42
Age at home visit (months)	--	3.53±1.72	0.72-7.00
Age at fMRI Visit (months)	--	4.61 ± 2.08	0.89-10.65

[a] Of the 17 participants who identified their race as "Other", 10 participants self-identified their race as "Hispanic/Latinx", 4 participants as "Mexican/Mexican-American", 1 participant as "West Indian", 1 participant as "American", and 1 participant did not self-identify.

[b] 2 participants missing handedness data

[c] Participants self-reported a history of Anxiety (N=4), Depression (N=4), Depression and Anxiety (N=5), Postpartum Depression (N=1), Anorexia (N=1), PTSD (N=1), OCD and Anxiety (N=1)

Table 2. Significant Brain Areas from Whole Brain Analysis: Paternal Care x Condition (Sound, Identity)

Regions	BA	Side	x	y	z	Cluster size	F
Paternal Care x Sound							
Precentral gyrus	43	L	-49	-7	11	97	36.14
Postcentral gyrus	42	R	62	-10	14	91	30.93
Insula	13	R	44	-31	20	61	21.89
Precentral gyrus	4	R	47	-10	50	54	22.70
Precuneus	31	L	-7	-67	23	51	18.27
Superior temporal gyrus	13	L	-40	-37	17	45	32.42

Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

Table 3. Significant Brain Areas from Whole Brain Analysis: Oxytocin x Condition (Sound, Identity)

Regions	BA	Side	x	y	z	Cluster size	F
Oxytocin x Sound							
Superior temporal gyrus	21	R	59	-22	2	50	31.71
Precentral gyrus	6	R	35	-4	32	38	23.30
Inferior frontal gyrus	45	R	47	20	2	36	23.15

Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

Table 4. Significant Brain Areas from Whole Brain Analysis: Paternal Care x Oxytocin x Condition (Sound, Identity)

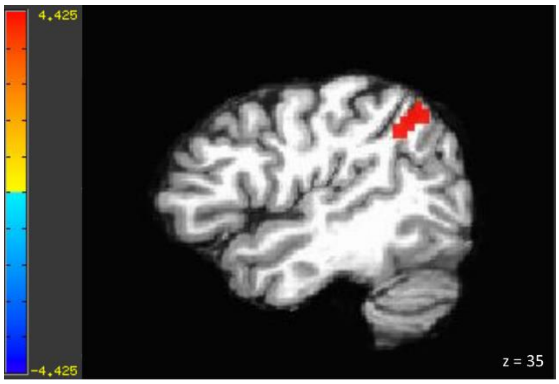
Regions	BA	Side	x	y	z	Cluster size	F
Paternal Care x Sound							
Precentral gyrus	43	L	-49	-7	11	88	35.65
Postcentral gyrus	42	R	62	-10	14	79	30.05
Insula	13	R	44	-31	20	74	21.95
Precuneus	31	L	-7	-67	23	54	18.72
Superior temporal gyrus	13	L	-40	-37	17	50	35.23
Precentral gyrus	4	R	47	-10	50	50	21.44
Oxytocin x Sound							
Superior temporal gyrus	21	R	59	-22	2	44	27.77
Inferior frontal gyrus	45	R	47	20	2	34	22.21
Precentral gyrus	6	R	35	-4	32	34	23.18

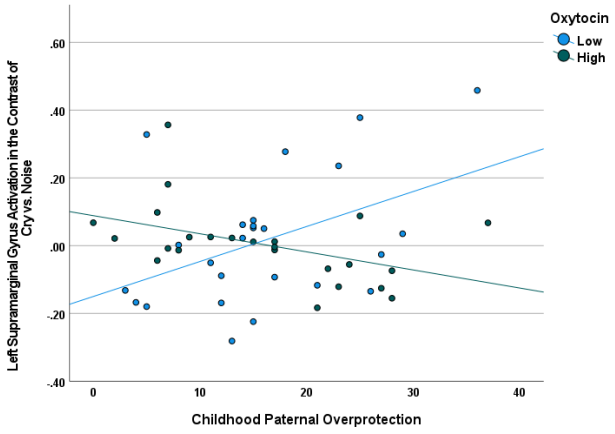
Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

Table 5. Significant Brain Areas from Whole Brain Analysis: Paternal Overprotection x Oxytocin x Condition (Sound, Identity)

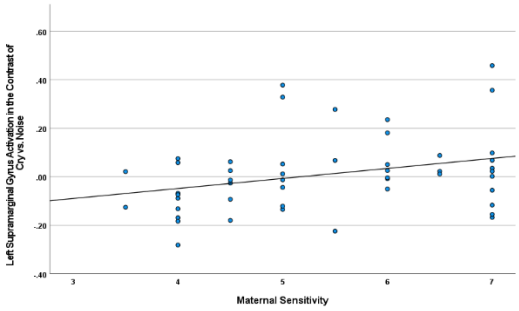
Regions	BA	Side	x	y	z	Cluster size	F
Paternal Overprotection x Oxytocin x Sound							
Supramarginal gyrus	40	L	-46	-49	35	47	20.55
Paternal Overprotection x Sound							
Medial frontal gyrus	8	R	8	32	41	56	20.27
Inferior frontal gyrus	45	R	53	20	14	34	19.74
Oxytocin x Sound							
Superior temporal gyrus	21	R	59	-22	2	50	29.37
Precentral gyrus	6	R	35	-4	32	45	26.34
Inferior frontal gyrus	45	R	47	20	2	43	23.17

Note. $p < 0.05$, corrected; BA = Brodmann area, R= right, L = left; x, y, z are Talairach coordinates, and F-statistics represent the voxel with maximum signal intensity (i.e. peak value) for each cluster.

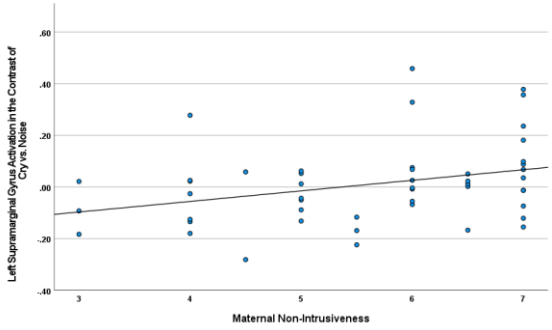




a)



b)



c)

Figure 1. Left supramarginal gyrus (x, y, z = -46, -49, 35, k = 47, $p < .05$ corrected) showing a Paternal Overprotection x Oxytocin x Sound interaction. a) Scatterplot showing the association between paternal overprotection and activation to infant cry vs. noise when dividing the sample into low oxytocin and high oxytocin groups (by dividing around the mean). b) Scatterplot showing the association between higher sensitivity and increased activation during cry vs. noise ($r = .31$, $p = .032$). c) Scatterplot showing the association between higher non-intrusiveness and increased activation during cry vs. noise ($r = .32$, $p = .023$).

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Appendix A.

Demographics Correlation Table

	Childhood Paternal Care	Childhood Paternal Overprotection	Average Oxytocin	Sensitivity	Non-intrusiveness
Maternal Characteristics					
Age at home visit (years)	-0.050	-0.083	0.055	.288*	0.143
Age at fMRI scan (years)	-0.052	-0.084	0.059	.287*	0.144
Hispanic ethnicity	0.179	0.226	0.101	-0.191	-.285*
Non-Hispanic White	-0.132	-0.159	-0.053	0.048	0.194
Income-to-needs ratio (last 12 months)	0.152	-.370**	.283*	0.131	0.022
Years of education	-0.009	-0.199	0.110	.361*	0.174
Handedness (right)	0.014	-0.209	-0.151	0.022	-0.078
Relationship status (Married/long-term relationship)	0.057	-0.094	-0.073	-0.003	-0.089
Index of maternal intelligence (FSIQ on the WASI-II)	-0.216	-0.128	0.037	.426**	.327*
Breastfeeding exclusively (Yes)	0.089	-0.192	.290*	0.066	0.211

Time between home visit and fMRI visit (months)	-0.103	-0.102	0.251	-0.101	0.034
State anxiety symptoms (STAI-State)	-.301*	0.010	-0.057	0.037	-0.046
Trait anxiety symptoms (STAI-Trait)	-0.205	0.155	-0.047	0.087	0.229
Depressive symptoms (BDI)	-0.271	0.026	0.044	0.160	0.224
Self-reported history of psychiatric disorder (Yes)	-.381**	0.174	-0.130	.299*	0.177
Current anxiety or depression medication use (Yes)	-0.084	-0.121	-0.122	0.020	0.046
Time between eating and oxytocin sampling	0.120	-0.192	-0.151	0.141	0.117
Infant Characteristics					
Infant sex (female)	-0.203	-0.039	-0.122	0.118	0.090
Gestational age at birth (weeks)	0.065	0.146	0.177	0.136	0.208
Child age at home visit (months)	0.072	-0.186	0.032	0.005	-0.207
Child age at fMRI visit (months)	0.005	-0.207	0.159	-0.049	-0.153

*$p < .05$. **p <.01

Appendix B.

Paternal Care x Oxytocin Model: Additional Analyses

A significant two-way interaction of **Paternal Care x Sound** (Cry, White noise) was identified in the left precentral gyrus (including left insula), right postcentral gyrus (including right transverse temporal gyrus), right insula (including right inferior parietal lobule), left precuneus, left superior temporal gyrus, and right precentral gyrus (**Table 4**). Higher paternal care was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed that greater activation in the right insula (cluster 3) (r = .37, p = .009) and left superior temporal gyrus (cluster 5) (r = .32, p = .024) during infant cry vs. noise was associated with increased non-intrusiveness. With regards to infant cry ratings, greater activation in left precuneus (cluster 4) during cry vs. noise was associated with rating infant cry as more pleasant compared to noise (r = .30, p = .038). Greater activation in the right postcentral gyrus (cluster 2) during cry vs. noise was associated with rating infant cry as less aversive compared to noise (r = -.35, p = .014). Greater activation in the left precentral gyrus (cluster 1) (r = .31, p = .029), right postcentral gyrus (cluster 2) (r = .51, p < .001), left precuneus (cluster 4) (r = .33, p = .022), and right precentral gyrus (cluster 6) (r = .41, p = .003), were related to higher maternal depressive symptoms. Greater activation in the postcentral gyrus (cluster 2) (r = .32, p = .024), left precuneus (cluster 4) (r = .36, p = .010), and left superior temporal gyrus (cluster 5) (r = .30, p = .037) were related to higher state anxiety.

A significant two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus (including right middle temporal gyrus), right inferior frontal gyrus, and right precentral gyrus (**Table 4**). For all clusters, higher oxytocin was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed no significant associations.

Appendix C.

Paternal Overprotection x Oxytocin Model: Additional Analyses

A significant two-way interaction of **Oxytocin x Sound** (Cry, White noise) was identified in the right superior temporal gyrus, right precentral gyrus, and right inferior frontal gyrus (**Table 5**). For all clusters, higher oxytocin was associated with less activation in response to infant cry sounds (both own and control infant cry sounds) compared to matching white noise sounds. Exploratory analyses revealed no significant associations.

Appendix D.

Paternal Care x Oxytocin Amygdala ROI: Additional Analyses

Repeated measures ANOVA revealed no significant findings for the right amygdala. Repeated measures ANOVA revealed a significant interaction for **Paternal Care x Sound x Identity** ($F = 5.082$, $p = .029$) in the left amygdala. This interaction was no longer significant with the inclusion of additional covariates maternal psychiatric history, state anxiety, and breastfeeding status ($F = 3.443$, $p = .071$). To decompose findings, repeated measures ANOVAs revealed significant contrasts for own infant cry vs. control cry, ($F = 5.076$, $p = .030$) and control cry vs. matched noise ($F = 6.195$, $p = .017$). Higher paternal care was associated with greater left amygdala activation in response to real cry vs. control cry and reduced activation to control cry vs. matched control noise. Exploratory analyses revealed no significant associations.

Chapter Four: Conclusion

As both papers described the findings in detail, the purpose of this conclusion is to provide an overview and tie together the two papers conceptually.

Across the two studies, higher perceived parental overprotection was related to dampened activation in prefrontal regions which play a role in emotion regulation, mentalization, and emotional empathy (e.g., medial and superior frontal gyrus). Blunted activation was additionally related to finding infant cry more aversive, suggesting decreased regulation of negative emotion in response to infant cry. Conceptually, parental overprotection models a caregiving style that does not readily take into account the child's interests or autonomy. Overprotective parents may experience their child's distress as highly aversive, and thus seek to quickly fix any problems that arise. Unfortunately, this limits the child's ability to problem-solve independently or with the help of parental scaffolding. Mothers who have recollections of this parenting style during childhood may also exhibit greater alarm in response to infant distress and may be less likely to consider the infant's mental state before responding. It follows that these mothers may then be less likely to recruit regions involved in emotion regulation (e.g., regulating their own emotional state) and mentalization (e.g., considering the infant's mental state) when responding to infant distress signals.

Although there were not main effects of childhood maternal care, paternal care was related to dampened neural response in circuits important for empathy and auditory

recognition. The direction of these findings was initially surprising; however further investigation revealed that this finding may be driven by associations between low paternal care and increased anxiety and depressive symptoms. It appeared that reduced activation may be protective, in the sense that it was related to decreased maternal depressive and anxiety symptoms. Mothers with memories of fathers as cold and unaffectionate during childhood appeared highly anxious and potentially hypersensitive to infant distress signals. Uncaring or harsh fathers could contribute to unsafe feelings during childhood. A hypervigilant style of responding may be adaptive within this context. Hyperactivation of these regions may help to facilitate empathy and mentalizing with regards to infant distress, thus contributing to fewer observed intrusive behaviors in the current study. However, there is a trade-off in that these mothers also exhibited enhanced anxiety and disrupted mood. Additionally, of note, a priori amygdala region-of-interest (ROI) analysis revealed that higher childhood paternal care was related to greater amygdala activation to own cry compared to control cry, potentially suggesting heightened saliency and attunement towards own infant.

Importantly, the current project demonstrates that perceptions of childhood caregiving and oxytocin level interactively relate to mothers' neural response. Higher maternal oxytocin level was related to dampened neural activation in regions typically stimulated by infant cry. This may be consistent with the known anxiolytic role of oxytocin in situations of social stress (Feldman et al., 2011; Olff et al., 2013). Broadly, high basal oxytocin may be an index of interpersonal and parenting stress (Feldman et al., 2011; Tabak et al., 2011; Taylor et al., 2006; Weisman et al., 2013), and relatedly less optimal

neural response to infant cry. Despite this, when mothers exhibited high oxytocin and reported positive perceptions of childhood maternal care, they demonstrated more optimal neural response (i.e., activation in the anterior cingulate cortex). This suggests a potential protective role of perceived childhood maternal care. A different pattern emerged for childhood paternal caregiving, in that the more optimal neural response (i.e., activation in the supramarginal gyrus) was related to both low oxytocin and high paternal overprotection. In this situation, higher paternal overprotection related to reduced neural response when mothers also exhibited high oxytocin. Although contrasting, these findings are similar to many of the contradictory findings existing in the oxytocin literature (Bakermans-Kranenburg & van IJzendoorn, 2013; Bartz et al., 2010; Julian et al., 2018; Riem et al., 2014, 2020; Schwaiger et al., 2019; Van Ijzendoorn et al., 2011). As described in detail in the prior papers, the functional meaning of high oxytocin may depend on caregiving experiences, such that high oxytocin is beneficial (and a marker of increased affiliation) in the context of positive childhood caregiving, but disadvantageous (and a marker of increased stress) in the context of negative childhood caregiving.

An alternative explanation for the oxytocin interaction findings is that high endogenous oxytocin is an indicator of sensitivity to social environment, such that individuals with high oxytocin show enhanced susceptibility to positive *and* negative caregiving experiences (McQuaid et al., 2013). Certain oxytocin receptor gene polymorphisms are known to be related to differential susceptibility to the environment, such that some individuals benefit more from supportive environments but are far more impacted by early adversity (Belsky et al., 2009; Cataldo et al., 2020; McQuaid et al.,

2013). This genetic variation could influence the current findings as oxytocin receptor gene polymorphisms have been associated with individuals' salivary oxytocin levels (Fujiwara et al., 2019; Nishizato et al., 2017; Rybicka et al., 2021). Thus, high salivary oxytocin in the current study may be an indicator of underlying "for better *and* for worse" oxytocin receptor genotypes. Future research is necessary to integrate study of genetic and hormonal markers of the oxytocin system.

Surprisingly, there were no direct associations between perceived childhood caregiving and observed parenting behaviors. This contrasts with prior research (Barrig Jo, 2008; Brown, 2019; Burrous et al., 2009; Madden et al., 2015). As alluded to previously, the present sample may have been under-powered to detect individual differences related to perceptions of caregiving and parenting behaviors. In addition to this, perceptions of caregiving exhibited limited range and were at times highly skewed in the current sample (e.g., few participants reported very low childhood maternal care). Continued research in larger and higher risk samples is necessary to make broader conclusions about these findings.

If continued studies demonstrate nonsignificant (or modest) associations between PBI and parenting outcomes, this could be due to a few reasons. First, individuals can reflect on their childhood experiences and choose to practice different parenting styles. This is consistent with research showing that individuals can have negative caregiving experiences, but still demonstrate secure adult attachment (i.e., a classification termed "earned-secure", as opposed to "continuous-secure") (Pearson et al., 1994; Roisman et al., 2002). Continuous-secure mothers demonstrate positive parenting behaviors and can

form a secure attachment relationship with their infant, although they may be at a slightly higher risk for depressive symptoms compared to continuous-secure mothers (Pearson et al., 1994; Saunders et al., 2011). Second, it is likely that the predictive value of the Parental Bonding Instrument (PBI) is limited it some ways, as a it is a subjective, self-report measure. The individuals who reported on poorer parenting quality may have already gone through the process of reflecting on their negative childhood experiences and conceptualized their own role as parent, such that they could exhibit positive parenting with their own child. Rather, it is the individuals who reported positive perceptions of caregiving, when their caregiving experiences were actually quite negative, who would have more negative parenting outcomes. This follows from research suggesting that the PBI is not comparable to the Adult Attachment Interview when individuals show idealization or anger towards their caregiver (Manassis et al., 1999). In sum, although perceptions of childhood caregiving may convey risk for postpartum adaptation, the associations with parenting behaviors may be more complex than previously thought.

The current project provides important clinical implications and suggests avenues for future research. It is recommended that clinicians screen for perceptions of childhood maternal and paternal caregiving during the perinatal period, as these relate to postpartum adaptation. Importantly, providers should not neglect the importance of caregiving received from fathers, as it uniquely predicts outcomes. Building insight around the care received from parents and forming a new conceptualization of self as parent is an important target of therapeutic intervention (Dozier et al., 2014; Erickson et al., 2019;

Marvin et al., 2002; Narayan et al., 2016). The current project also challenges the early view of oxytocin as the “love hormone” and suggests that oxytocin may have beneficial or detrimental influences for neural response depending on context and caregiving history. Although these findings contribute to our understanding of neurobiological mechanisms, further research is needed to illuminate the complex interactions of biology and social environment in the development of parental behaviors.

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