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Maternal Neural Responses to Infant Cues: effects of caregiving experience, stress & retrospective remembrances of experienced parental care

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Abstract

Parents are central to the early development of their child and subsequently their future outcomes later in life. Some of the ways in which parenting behavior is expressed are more adaptive than others, such as responding in a sensitive & responsive manner when a child expresses their needs. How a given individual comes to parent in the way that they do is dependent on many different personal, social & contextual factors. In addition, emerging family structures provide an opportunity to study new variables within the mother—child relationship. Investigation into how these various factors interact is therefore necessary. In the current study, the functional brain responses to auditory infant cues were examined in 16 healthy lesbian mothers of 3 to 11 year old children. In response to infant cries, mothers showed neural activation in regions related to emotion regulation and abstract & sensory—motor representations of the cry stimulus itself in comparison to a control sound. In relation to measures of maternal behavior, it was found that moderate levels of maternal sensitivity are significantly associated with the highest level of activation within the Superior Temporal Gyrus. Brain responses were also observed for comparison between infant cries and baby laughs, as well as baby laughs and a control sound. Taken together, results from this study indicate that mothers recall memories related to infant cries presumably experienced with their own children. Additionally, current findings suggest that new stimuli be used in further research on mothers with children in middle to late childhood.

Keywords: fMRI, Parental Brain, Infant Cries, Infant Laughs, Stress

Introduction

There is large variability in the developmental trajectory that any given species takes to reach maturity. Upon birth some organisms, like deer, are tasked with learning "on the job" essentially being ready for challenges that their environment may pose rather quickly, whereas others, like humans, require an extended supervisory period before they are able to be entrusted with independence. Therefore, following birth, human infants require supervision and guidance as they become acquainted with their own abilities and the influence of their surroundings. In order to obtain the necessary knowledge required to guarantee survival and optimize well-being, adult figures must be present to provide protection, structure and encouragement towards further autonomy. Therefore, the ability of the adult (typically, parental) figure is of the utmost importance for anyone with concerns over child development and the maximization of human potential. This raises the questions of: What are the different skills & behaviors that are necessary for parents to provide to their children?; and, What makes one individual better at providing them than another?

History

The study of the relationship between a Parent and their Child in an empirical way, did not begin to emerge within the field of psychology until around the 1950s. This area of interest emerged largely due to the efforts of a British psychologist & psychiatrist by the name of John Bowlby, as well as an American-Canadian developmental psychologist Mary Ainsworth.

Despite being classically trained in psychoanalysis which was the predominant psychological practice of the time, Bowlby departed from these ideas during his time training at the British Psychoanalytic Institute when he realized that children's emotional problems were not just caused by internal conflicts but also by the external environment and, in particular, familial experience (Bretherton, 1992). Indeed, Bowlby published the first article concerning family interactions describing how he was able to make breakthroughs in his clinical work often via interviews with parents concerning their own previous childhood experiences while in the presence of their children (Bowlby, 1949). From this point forward, Bowlby focused his work on the phenomenon of mother–child separation and its effects on the child (Bretherton, 1992). The first empirical evidence that examines the early supervised period of child development came from a paper that Bowlby wrote on the mental health of homeless children in Europe where he summarized what the behavioral interactions in a healthy relationship between a mother (or permanent substitute) and their child would look like:

> *“During this phase of life, the child is therefore dependent on his mother performing [functions] for him. She orients him in space and time, provides his environment, permits the satisfaction of some impulses, restricts others… Gradually he learns these arts himself, and as he does, the skilled parent transfers the roles to him. This is a slow, subtle and continuous process, beginning when he first learns to walk and feed himself, and not ending completely until maturity is reached.”* (Bowlby, 1951, pg. 53)

This description of the parent–child relationship withstands the test of time, outlining the essential nature of the parental role in guiding a child in their development. However, through discussions with renowned ethologists, Bowlby came to realize the need for empirical evidence to back up his emerging theoretical view (Bretherton, 1992).

In 1950, Mary Ainsworth joined the work that Bowbly was performing at the Tavistock Clinic in London on the effects of maternal separation. Previously during her graduate dissertation work, Ainsworth conceptualized the idea that infants require a dependence on their parents early on in life, stating:

> *“Familial security in the early stages is of a dependent type and forms a basis from which the individual can work out gradually, forming new skills and interests in other fields. Where familial security is lacking, the individual is handicapped by the lack of what might be called a secure base from which to work.”* (Ainsworth, 1940, pg. 45)

Here emerges the idea that if an infant cannot be dependent on their parent because the parent is not appropriately providing security for the child’s needs then the child will develop deficits as they continue to mature. This interest leads to her unique contribution in Bowlby’s research where she developed the 3 main relationship patterns that can be observed between a parent and child upon reunion after being separated, they are as follows: (a) dyads which have reliable positive feelings toward each other, (b) dyads where the child displays ambivalence upon reunion and (c) dyads with indifferent or hostile feelings (Bowlby, Ainsworth, Boston & Rosenbluth, 1956). These early empirical patterns of attachment between mother–child dyads will be the foundation for what is later formalized as Attachment Theory.

Attachment Theory: Empirical Evidence

The first empirical studies observing infant–mother attachment were undertaken by Ainsworth utilizing her expertise in using narrative methods for data collection. The first project was performed in Uganda in 1953 where Ainsworth recruited 26 families with babies between the ages 1-24 months and observed them for 2 hours every 2 weeks over a period of 9 months. This study provided interview data on the qualitative individual differences of mother–infant dyads.From this, Ainsworth defined the behavioral measure of maternal sensitivity which described mothers who were responsive & informative with their infants in contrast to mothers deemed less sensitive who demonstrated imperceptiveness to the nuances of their infant's behavior. Additionally, the 3 attachment patterns were refined: (1) Securely attached infants were content to explore when the mother was present and cried little, (2) Insecurely attached infants did not explore much and cried frequently and, lastly, (3) not-attached infants who showed indifferent behavior towards their mothers. In the final analysis, securely attached infants showed to be significantly correlated with the mothers that were the most sensitive (Ainsworth, 1963, 1967). These data were used to back the original formulation of Attachment Theory.

The second empirical study was an extension of the work Ainsworth performed in Uganda but instead she recruited 26 families in Baltimore prenatally, scheduling 18 home visits lasting 4 hours and starting from the first month postpartum until 54 weeks. The data that was collected in the Baltimore study was in narrative report form which was later transcribed and grouped for analysis. This method of data collection was unique in that it focused not on the frequency of specific behaviors but instead on meaningful patterns of behavior within an ecological context. From this study, it was discovered that there was great variability in how mothers responded to their infants' signals within the first 3 months (Ainsworth et al., 1978, Ainsworth, 1982, 1983). Additionally, the behavioral construct of maternal sensitivity that was discovered in the Uganda study was associated with more harmonious interactions between mother and child later in the first year. For example, babies of mothers that were very responsive to their crying in the early months postpartum then showed a tendency to cry less and communicate more frequently with facial expressions, gestures & vocalizations later on (Bell & Ainsworth, 1972). These findings by Ainsworth show there are specific maternal behaviors, such as sensitively responding to infant cues, that are indicative of a healthier mother–child relationship.

Ainsworth's detailed observations of ecological interactions between a mother and their infant provided formidable evidence backing Bowlby's theoretical conceptualization of Attachment, as well as inspiring undergraduate & graduate students to pursue the topic thrusting the field of parent–child research into ascension in the decades that followed.

Attachment Theory: Formulation

Using the findings from Ainswoth's work in the Uganda study, Bowlby then set out to formalize their nascent ideas of mother–infant attachment in his book Attachment (1969). Before contextualizing attachment theory within the greater totality of human behavior, Bowlby felt it was necessary to have a theory of motivation and behavioral control that was up-to-date with the recent scientific progress that had been made. In his reformulation, he proposes that complex organisms with the ability of foresight are able to construct internal working models of their environment, and their actions within it, to form a model of the self. This enables an organism to simulate potential actions in their environment to understand the potential outcomes while avoiding any actual harm that may have resulted from carrying out an action on the premise of a poor internal working model. Being able to run these simulation-like models allows complex organisms to identify the best course of action before actually performing it. Bowlby offers that humans are among these organisms that formulate internal working models of their environment and of the self and additionally, due to our aptitude for language and complex communication, are able to intersubjectively share our internal working models with each other (Bowlby, 1969).

This is the context with which attachment and the importance of it sits within. Bowlby's broader idea of motivation and behavior is then applied to Attachment Theory, where he proposes that attachment serves to protect an infant from danger by keeping close proximity to the attachment figure and this behavior has its own unique motivation that is separate from other motivated behavioral systems (e.g., feeding, mating) (Bowlby, 1969). Once an infant is attached, they use the attachment figure as a secure base to then explore the environment from and subsequently, a safe haven to return to for solace (Ainsworth, 1967; Schaffer & Emerson, 1964). Bowlby describes different attachment interactions as follows:

> *"when interaction between a couple runs smoothly, each party manifests intense pleasure in the other's company and especially in the other's expression of affection.*

> *Conversely, whenever interaction results in persistent conflict each party is likely on occasion to exhibit intense anxiety or unhappiness, especially when the other is rejecting…Proximity and affectionate interchange are appraised and felt as pleasurable by both, whereas distance and expressions of rejection are appraised as disagreeable or painful by both"* (Bowlby, 1969, pg. 242)

How the social interaction described above is acted out, or more specifically how sensitive the attachment figure is with their infant then determines the quality of the attachment relationship between the dyad.

In his second book Separation (1973), Bowlby expands on his previous ideas that the working model of the self and the attachment figure are especially important and complementary to each other. For example, attachment figures that are able to simultaneously respect the infant's needs and enable them to independently explore, means that then there is a good chance that the child develops an internal working model of the self which is valued and self-reliant. On the contrary, attachment figures that often reject their child's need for exploration or comfort means that then the child may develop an internal working model of the self that is incompetent or unworthy (Bowlby, 1973). It is from this theoretical basis Bowlby espouses that these internal working models play a central role in the transmission of attachment patterns across generations. Children of parents who are supportive and encourage autonomy (i.e., an example of a secure attachment figure) typically become stable and self-reliant individuals. Bowlby hypothesizes that these parents are able to transmit beneficial internal working models of the self via straightforward communication of their own internal working models of the self but yet also admit that their working models are open to questioning and revision (Bowlby, 1973). Therefore, through adaptive parenting processes, children are able to construct their own working models of the world that allow them to be flexible to challenges in their environment while maintaining self-confidence and self-reliance in their pursuit.

In summation, Attachment Theory ignited the field of parenting research by providing evidence that parenting behaviors are variable and strongly influence the subsequent development of a healthy parent–child relationship. Additionally, the significance of the parent–child relationship is established by outlining at an abstract level how parents shape children's internal working model of the world. Based on this, it can be inferred that some parenting behaviors may be more adaptive than others and subsequently lead to better child outcomes.

Determinants of Parenting

As was identified in Attachment Theory through the works of Bowlby & Ainsworth (as well as the students inspired by their work), child-rearing strategies & behaviors have a substantial influence on the development of the parent–child relationship and consequently the child's development. As an example, sensitive–responsive parenting promotes attachment security early on during the formative infant-toddler years (De Wolff & van Ijzendoorn, 1997) which further advances the child's cooperation skills and conscience development (Kochanska et al., 2005). Even further into childhood, parenting strategies that emphasize that involvement of warmth & acceptance complimented by firm control & consistent boundary-setting allows the child to develop prosocial skills and positive peer relationships (Ackerman et al., 2004; NICHD, 2002; Skinner et al., 2005). Despite these influential findings which support the significance of positive parenting strategies, more needed to be discovered regarding how parents developed the parenting strategies that they did. This work was guided by Jay Belsky's process model on the conceptualization of the determinants of parenting which addressed social-contextual factors that influence parenting practices (Belsky, 1984).

Characteristics of Parents

Although Bowlby's work properly pointed to the importance of the intergenerational transmission of parenting, further research into this domain has revealed that in instances of both positive / growth-promoting and negative / maltreating parental relationships the subsequent outcome is not inevitable (Belsky & Jaffee, 2006). Perhaps unsurprisingly, research has found that personality characteristics influence the different ways in which parents respond to their children (Belsky & Barends, 2002). For example, extroverted parents who tend to experience more positive emotions from social engagement with people, display more responsive, sensitive & stimulating parenting behaviors throughout the childhood years (Belsky et al., 1995; Belsky et al., 2005; Losoya et al., 1997). On the other hand, disagreeable parents who tend to be more manipulative & cynical in their social interactions display less trusting & forgiving tendencies that lead to more controlling parenting behaviors in disciplinary situations (Clark et al., 2000). Studies like those described above lead to the conclusion that personality shapes the way that parents behave in response to their child. The possibility that these behaviors are shaped by childhood interactions with parents remains open (Belsky, 1984; Serbin & Karp, 2003) but contextual factors that influence a parents general behavioral functioning should continue to be included in studies that investigate how an adult's parenting behaviors operate the way they do.

Social Context: Marital / Partner Relationship

Besides an individual's personal characteristics, social relationships (e.g., spouse, partner) indirectly affects how parents determine the parenting practices they would like to enact on their children. Past research has demonstrated a link between problematic marriages and children's behavioral issues with at least some of the effect on the child's behavior being attributed to the effect of the marriage on parenting (Belsky, 1981; Belsky, 1984; Emery, 1989). It has been observed that the child can be affected by the status of the marital relationship by negative emotions spilling over from the partner relationship to the parent–child relationship (Goldberg et al., 2002), for example, anger stemming from the marital relationship can promote parental withdrawal which may be perceived by the child as rejection and cause knock-on negative outcomes (Lindahl & Malik, 1999). However, on a positive note, it must be noted that supportive marital relationships positively influence psychological well-being in general and subsequently facilitate more positive parenting behaviors (Belsky, 1984). Taken together, the configuration of the family structure and the status of the marital or partner relationship of parents should be considered as an influence on the parenting practices that are put in place.

In conclusion, the parent–child relationship does not exist within a vacuum. There are a myriad of historical, personal, social & contextual factors that influence how an individual decides to construct their parenting practices. Understanding the influence of a multitude of factors on parenting behaviors will enable psychologists to better assist parents with the demands of parenting with the goal of maximizing the potential of the child in mind.

Parental Brain Model

Overview

Up to this point, literature has focused on the behavioral factors that influence parents and the parent–child relationship. With the advent of neuroimaging technologies, a new frontier of research opened up to researchers enabling studies that attempted to link cognitive processes with the established behavioral findings. Studies in this field have led to the construction of a new model of parenting which concerns how a parent's brain responds to different audio or visual cues relating to child cues which would ideally require a parental response. The Parental Brain Model (Swain et al., 2011) is an emerging field of research that seeks to understand neural activity in human parents' brain response to different types of infant cues. Its creation stemmed from studies looking at functional and structural brain changes starting from pregnancy to the postpartum period. In this section the types of cues used to evoke activity, areas in which this activity takes place and how our behavioral & contextual variables of interest impact these areas will be reviewed.

Infant Cries

A common stimulus used in research that is aiming to investigate neural activation within the Parental Brain network is infant cries. Barry Lester (1984) described cries as a "biosocial phenomenon that directly reflects the status of the nervous system and indirectly mediates development through parental intervention". Indeed, a series of studies demonstrate that infant cries require more attention than a control sound and that mothers in particular show increased alertness to these vocalizations than nulliparous women (i.e., non-parents) which may indicate a mother's specialized ability to attune to their infant's needs (Tzourio et al., 1997; Purhonen, Paakkonen et al., 2001; Purhonen, Kilpelainen et al., 2001). Therefore, if cries are a signal that indicates the necessity for parental intervention it is reasonable to think it would cause a neural reaction in the Maternal Brain and subsequently justifies its use as a stimulus for fMRI research.

Lorberbaum and colleagues (1999) conducted the first study using fMRI to investigate parents' brain response to infant cries in a small sample. Results showed activation in an area from the right subgenual anterior Cingulate Cortex (ACC) to the right medial Prefrontal Cortex (mPFC). However, the interpretation of the results was not definitive, it is possible that the ACC activated in response to infant cries simply due to it being a more meaningful sound than a white noise control (Benedict et al., 1998). Although these results cannot substantiate any definitive claims of a parental brain response, it did justify further research. In a follow-up study, findings with respect to infant cry activations were expanded to show that Thalamocingulate (anterior & posterior Cingulate, medial Thalamic Nuclei), Prefrontal (mPFC, right Orbitofrontal Cortex) and auditory-related (anterior Superior Temporal Sulcus, Temporal Pole, inferior Frontal Cortex, Frontal Pole) areas were associated (Lorberbaum et al., 2002). In comparison with the first pilot study, the Cingulate Cortex was not solely activated for infant cries yet also activated for the control noise therefore authors speculated that the Cingulate's role may have been merely auditory, cognitive or emotional enhancement but this interpretation remained speculative. Moreover, the results indicate a brain response representative of vocal sound detection (rather than sound localization) and, additionally, the medial Thalamic Nuclei which were found activated have been implicated in other love-related (Bartels & Zaki, 2000; e.g., Hypothalamus, Nucleus Accumbens) and sadness-related (Lane et al., 1997; George et al., 1995; e.g., Hypothalamus, ventral Tegmental Area, Putamen) research. The nascent research conducted by Lorberbaum and colleagues demonstrates that the Maternal Brain may respond to the sounds of infant cries with a collection of auditory, emotional and executive sub-networks that enable a parent to appropriately intervene.

In the development of a model of the Maternal Brain response to infant cries, it is important to understand the nuance of which sub-networks activate in different contexts and for what reason. This can be disentangled by observing the brain response in mothers to infant cries over time and in comparison to brain responses by non-parents to the same stimuli. Research has shown that at 2 to 4 weeks postpartum, mothers show activation in the Midbrain, Basal Ganglia, Cingulate, Amygdala & Insula (Swain et al., 2003). When non-parents have been asked to listen to the same infant cries, they also show activation in the Amygdala & Insula, as well as the Auditory Cortex (Sander et al., 2003). Therefore, it seems that the Amygdala and Insula may uniquely activate to the emotional perception of sounds (e.g., cries, laughs) regardless of any maternal response or parental involvement. In the same group of 1st-time mothers previously observed, they were again asked to listen to cries while undergoing fMRI at 3 to 4 months postpartum and now showed activation in the mPFC & Hypothalamus (Swain et al., 2004). So, in the early postpartum period, mothers show activations in the Midbrain, Basal Ganglia & Cingulate but later into the postpartum period that activation shifts to the mPFC & Hypothalamus. It is hypothesized by the author that this shift in neural activation could reflect the mother–infant relationship developing from an initial point where the mother responds with alarm and anxiety to then learning to respond with more social and habit-related systems as the individual adapts to motherhood (Swain, 2007).

With a general foundation set on which sub-networks are involved in response to infant cries, we can use the latest research to better delineate and specify the neural mechanisms involved from perception to processing to planning / initiation when a mother listens to an infant cry (all implicated sub-networks can be identified in Figure 1).

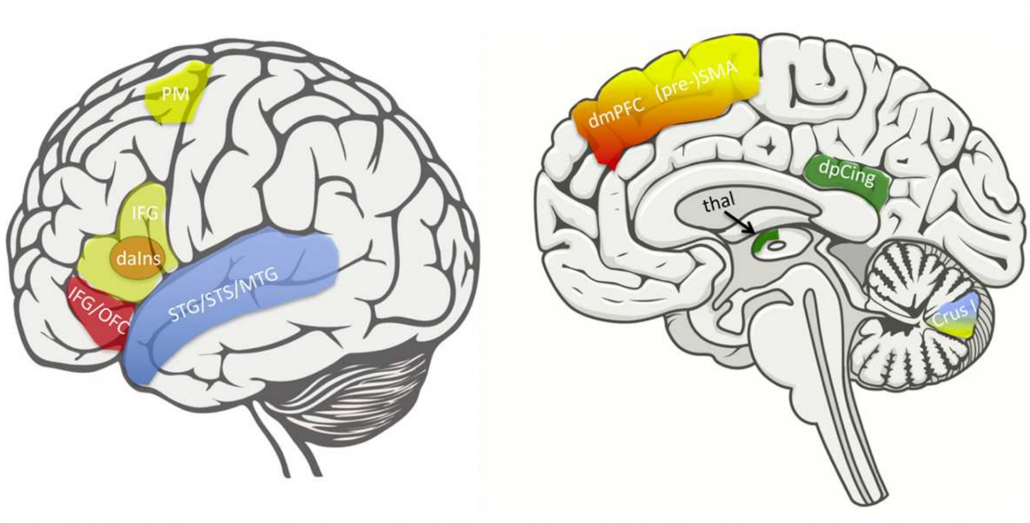


Figure 1

Schematic illustration of the circuits involved in infant cry perception

Note. Reprinted under the terms of the Creative Commons CC BY-NC-ND 4.0 DEED by Witteman et al. (2019).

Starting with the auditory perception of an infant cry, the Superior Temporal Lobe has been implicated specifically the Superior Temporal Gyrus (STG), Middle Temporal Gyrus (MTG) and the Superior Temporal Sulcus (STS) that demarcates the two gyri (Witteman et al., 2019). The ventral aspect of the auditory sub-system involves the bilateral STG & MTG constitute the 'What' pathway which processes the auditory and semantic aspects that identifies the perceived vocalization as an infant cry (Hickok & Poeppel, 2007; Lima et al., 2016; Witteman et al., 2019). Complimentary to this is the dorsal aspect which involves the bilateral Opercular Inferior Frontal Gyrus (IFG), pre-Supplementary Motor Area (pre-SMA) & right Premotor Area (at the level of the Larynx representation), all constituting the 'How' pathway which may speculatively simulate the acoustic properties of the heard vocalizations and subsequently aiding to identify the incoming information (Amodio & Frith, 2006; Hickok & Poeppel, 2007;

Lima et al., 2016; Sammler et al., 2015; Witteman et al., 2019). Furthermore, some studies have observed activation of Crus I of the Neocerebellum in the Maternal Brain and other auditory perception studies, however, the role of the Cerebellum is still largely unknown in the present context (Petracchi et al., 2005; Witteman et al., 2005). To recap, the dual-stream auditory pathway activates for the perception of an infant vocalization using Superior Temporal regions to process what kind of auditory stimuli is being received, in conjunction with, prefrontal, pre-motor & somatosensory areas that process how the vocalization was produced aiding in its identification.

Moving on to the processing of the auditory information, many areas are activated which are associated with emotional & cognitive processing of the infant cry. First, the dorsal anterior Thalamus in combination with the dorsal Posterior Cingulate Gyrus (forming the Thalamocingulate pathway) activate and are proposed to function as a 'neural alarm signal' alerting the mother to the presence of the infant cry (Rilling et al., 2013; Witteman et al., 2019). On top of that, the dorsal anterior Insula activates, presumably processing the integrated emotionally relevant information with motor & somatosensory information from the posterior Insula, in order to detect any salient emotional information (Deen et al., 2011; Uddin et al., 2014; Witteman et al., 2019; Zhang et al., 2018). Essentially, processing happening in the Thalamocingulate pathway & anterior Insula enable parents to 'experience' the emotion of the infant in order to understand their emotional state (Witteman et al., 2019). Second, the Triangular IFG & OFC activate, the Triangular IFG has been associated with social cognition, 'mentalizing' (i.e., understanding the mental state of oneself or someone else) and the OFC has been associated with making judgements based on semantic & emotional information it receives (Hartwigsen et al., 2018). These areas therefore work in tandem to assess the emotional valence and intensity of infant cries (Witteman et al., 2019). All of the above areas work in concert in order to experience and analyze the emotional properties of an infant vocalization so that the mother can better understand what action needs to be undertaken to intervene with her infant. Referencing back to the findings by Swain, this sub-network may be one that activates less as a mother has more experience later into motherhood and gains a better understanding of their infant's needs.

The final aspect of a Maternal Brain response to an infant cry, the medial Superior Frontal Gyrus (mSFG) has been implicated, specifically the dorsal medial Prefrontal Cortex (dmPFC) and the pre-SMA (Witteman et al., 2019). The gradient within the mSFG moves from the dmPFC which functions as abstract action monitoring to the particularly active pre-SMA where more absolute motor processing is purported to occur (Amodio & Frith, 2006). These prefrontal areas have been related to the initiation and planning of a parental response (Swain et al., 2007). Lastly, midbrain structures such as the right Caudate Nucleus & left Putamen activate (Witteman et al., 2019). The Caudate & Putamen are part of a motor loop which facilitate the initiation & planning of motivated action which are likely used often in routine parenting behaviors (Booth et al., 2007; Grahn & Rowe, 2009; Hove et al., 2013; Provost et al., 2010; Tricomi et al., 2004). In essence after perceiving & processing an infant cry a mother must then plan how they will respond appropriately and then execute it.

In summary, when a mother listens to an infant cry different sub-networks activate starting with an acoustic analysis of the stimulus to then shifting their attention to the perception of interest and evaluating its novelty & emotional significance while ending in the planning & initiation of a parental response. Some studies have also pointed to dopaminergic reward pathways that are activated in the Maternal Brain response indicating motivation in responding to their infant but the latest meta-analysis by Witteman and colleagues (2019) did not find solid evidence in support which may be due to a variety of factors that cause motivation-related areas to activate below the required significance threshold for their analysis. A final point, when discussing the interplay between sub-networks that have been correlated with a mother's neural response to listening to infant cries, it is important to note that the specific temporal sequence of events cannot be firmly concluded with current fMRI data due to the techniques poor temporal resolution. We can only state that these diverse spatial components' activation is correlated with a response to infant cries.

Maternal Sensitivity

The ability to properly interpret infant cries is a fundamental skill for parents, agreement between the cry signal and how it is interpreted by the parent is indicative of optimal development whereas the alternative (e.g., a normal cry perceived as aversive or an aversive cry perceived as normal) is non-optimal (LaGasse et al., 2005). In order to gain better understanding of how different dynamics within the Parental Brain are associated with mothers' ability to properly or improperly respond to their infant, some researchers have attempted to associate the neural response that mothers have to infants cries with other behavioral measures indicative of more optimal or non-optimal parenting behaviors. One of those parenting behaviors is referred to as Maternal Sensitivity – defined as “[a] mother's ability to perceive and to interpret accurately the signals and communications implicit in her infant's behavior, and given this understanding, to respond to them appropriately and promptly” (Ainsworth, 1969). Neural responses that positively correlate with increased maternal sensitivity could provide preliminary evidence of more adaptive responses within the Maternal Brain.

Although there are not many studies looking at the relationship between the response to infant cries and mother’s differing sensitivity, Kim & colleagues (2011) were the first to test any association. They found that mothers with greater activation in response to their own infants’ cries (relative to other cries) in the right Superior Frontal Gyrus (SFG) & right lateral Globus Pallidus–Amygdala area at 2-4 weeks postpartum showed greater maternal sensitivity measured later during dyadic interactions at 3-4 months postpartum. Based on previously reviewed research on infant cries, it is possible that the activation of the SFG could indicate that more sensitive mothers begin the transition to forming responsive motor behaviors earlier compared to less sensitive mothers. Additionally, research has shown that the Globus Pallidus is implicated in friendship-based love (Acevedo et al., 2012) and mediating reward & motivation (Smith et al., 2009). These findings may suggest that mothers identify cries as an emotionally-charged perception representative of a strong bond with their child which subsequently motivates them to respond. Nevertheless, nothing definitive can be drawn until there is further replication of these results.

Another study by Musser & colleagues (2012) collected data on a sample of 22 mothers with infants aged 15-18 months, they looked at the relationship between neural response to own infant cries (versus cries of other infants) and maternal sensitivity. Each dyad participated in a structured play task where their interactions were rated across a few domains intended to indicate the quality of the relationship. For the domain of maternal sensitivity, higher levels were associated with increased activation in the medial Prefrontal Cortex (mPFC) & Striatal regions (without controlling for the other behavioral domains), as well as, right Inferior Frontal Gyrus (IFG) & right Frontal Pole. More sensitive mothers’ activation of the mPFC & Striatal (i.e., Caudate & Putamen) regions supports previous findings of the Maternal Brain, demonstrating their role in initiation and planning of a parental response (Booth et al., 2007; Grahn & Rowe, 2009; Hove et al., 2013; Provost et al., 2010; Swain et al., 2007; Tricomi et al., 2004; Witteman et al., 2019). Because these regions were significant without controlling for other more specific behavioral aspects, these areas may represent common functions that operate across different dimensions of maternal behavior. Areas more specific to maternal sensitivity were the right IFG & right Frontal Pole where increased activations may help mothers to override negative emotions associated with their infant's cry, regulate their initial response and allow them to recognize their infant's emotional states in order to engage in sensitive responding (Musser et al., 2012). It is also important to note that activations of these regions are congruent with other findings linking their activity to maternal attachment behavior (Bartels & Zaki, 2004; Nitschke et al., 2004; Swain et al., 2008). Correlational evidence of specific neural activation for mother's that are more sensitive lends credence to further examination of sensitivity's instantiation within the Maternal Brain and its' role within the broader Mother–Infant relationship.

Although sensitivity is important to a mother's ability to form a secure attachment with their infant, it is not the only mechanism through which attachment is shaped (van Ijzendoorn, 1995). In fact, other aspects of maternal behavior such as Harmony (i.e., dyadic quality based on conflictual instances in interaction) and Non-intrusiveness (i.e., caregiver's ability to be stimulating and emotionally supportive) have shown to have similar effect sizes as maternal sensitivity (De Wolff & van Ijzendoorn, 1997). Notably, the sub-domains of Harmony & Intrusiveness were also associated with brain activations of the same mothers with 15-18 month old infants (Musser et al., 2012). Mothers with higher scores on Intrusiveness, showed increased activations in the left anterior Insula–Temporal Pole region. Because these areas have been previously associated with integrating sensory–emotional information and the empathetic experience when witnessing a loved ones' pain (Olson et al., 2007; Singer et al., 2004), authors presume that the present activation is attributable to intrusive mothers' perception of their infant's cries as a painful one and reacting accordingly which results in obtrusive behavior. In addition, mothers with higher scores on Harmony with their infants showed increased activation in the left Hippocampus–posterior Parahippocampal Gyrus area, right posterior Parahippocampal Gyrus–Lingual Gyrus area & right Precuneus. As will be discussed in-depth later on, the Hippocampus has been implicated in both memory and modulation of stress response via regulation of the HPA Axis (Dedovic et al., 2009). Therefore, authors suggest that harmonious interactions between mothers and their infants may be facilitated by the Hippocampus and the subsequent gyri leading to the Precuneus which enable mothers to recall past interactions and manage their stress responses in the face of challenging cues (e.g., infants' cries). This study by Musser and colleagues (2012) was one of the first to attempt to identify various regions within the Maternal Brain that play distinct roles which correlate with different sub-domains of maternal behavior.

In summary, studies that have explored the relationship between maternal behaviors and their respective neural dynamics show that mother's activation of dorsomedial Prefrontal Cortex (dmPFC) regions along with Striatal regions may indicate their readiness to respond in reaction to their infant's cries. Also, mothers that respond more sensitively to their infants may activate more anterior ventrolateral Prefrontal Cortex regions (vlPFC). Additionally, further investigation should examine whether it is advantageous for a mother to transition earlier from perceiving infant distress cues as alarming (i.e., evidence by activation of the Amygdala) to understanding the cue and engaging in a more habitual motor response (i.e., evidence by activation of dmPFC/pre-SMA/Striatal regions) while calibrating their appropriate response (i.e., via anterior vlPFC regions). Furthermore, other areas of maternal behavior may be related to other subsystems within the Maternal Brain, such as mothers who have more instances of harmonious interactions with their infants could be better at accessing positive memories of past shared experiences. Through more targeted and rigorous study design, confirmation of this relationship could be beneficial for new parents in the development of the relationship with their child. Although more replication of these findings is necessary and interpretation of the functions of each area should be cautioned, these studies do demonstrate that different regions with the larger Maternal Brain network facilitate different behaviors that constitute an overall maternal response to infant cues.

Stress Effects

It has been well-established that parent-child relationships have substantial influence on the outcomes of children, however, much remains on how other variables, such as stress, influence the dyad's relationship and subsequently the child's developmental trajectory (Ranson & Urichuk, 2008). New parenthood carries with it a new set of demands that have the potential to become especially challenging in environments where some mothers are exposed to severe stress (Belsky & Jaffe, 2006; Crnic & Low, 2002; Kettinger et al., 2000). Deater-Deckard (2004) was the first to formalize a domain-specific definition, Parenting Stress refers to a set of processes that lead to aversive psychological and physiological reactions arising from the attempts to adapt to the demands of parenthood. For example, although a supportive marriage can ameliorate stress from other sources, marital conflict can become a source of stress itself that affects the coping capability of those involved. Thus, parents who need to devote resources to a troubled marriage may not be able to fulfill the requirements of their children in a sensitive, supportive way (Belsky, 1984). Accepting the definition put forth by Deater-Deckard, enables accurate comparisons across studies and until new evidence arises to suggest that this conceptualization is insufficient, it should be embraced. Following its conception, researchers further differentiated the effects of Parenting Stress based on differing levels. Moderate levels of stress benefitted maternal motivation and were associated with how a parent evaluated their success in the parental role and properly perceived their child's cues (Henderson et al., 2012). However, high levels of stress are a detriment to the parent-child relationship, the mother's well-being & the child's outcomes via harsh and reactive caregiving which leads to cold and unresponsive parenting (Lupien et al., 2009; Chan et al., 2018). More recent research has further supported negative impact of high levels of parenting stress by specifically associating stressful experiences with alterations in the maternal brain, therefore further impacting the approach to parenting and consequently the dynamics of the mother-child relationship (Azhari et al., 2019; Feldman et al., 2019; Kim et al., 2014; Levy et al., 2019b; Olsavsky et al., 2019; Schechter et al., 2012). Evidence from both animal models, as well as human neuroimaging studies has shown that the harmful effects of stress lead to both structural & functional changes in neuroendocrine and neurobiological systems (Veenema, 2009; Kim et al., 2021). In this section, brain areas that have been implicated to be involved in both adaptive & maladaptive responses to stress in parents will be reviewed.

HPA Axis & Cortisol

In the presence of a stressor, one of the main neurobiological components to respond to physical or psychological stress is the Hypothalamic-Pituitary-Adrenal Axis (i.e., HPA Axis). It has been shown that early life experience (e.g., early caregiving experiences) shapes the future functioning of the HPA Axis in both non-human primates (Sanchez, 2006) and children (Hostinar et al., 2014; McEwen et al., 2012). In order to better understand the relationship between stress and the maternal brain, as well as its impact within the dyadic parent-child relationship, an understanding needs to be reached on the dynamics of the HPA Axis and its differential activation for both the parent & child in the context of stressful situations. The HPA Axis' pathway is a cascade of neuroendocrine hormones, from the Hypothalamus to the Adrenal Glands, which results in the production of Cortisol. In the studies that follow, HPA Axis activation references the following mechanism: (1) Release of Corticotropin-Releasing

Hormone (CRH) & Vasopressin from the Paraventricular Nucleus of the Hypothalamus (PVN) into the anterior Pituitary Gland, here, CRH and Vasopressin stimulate the secretion of Adrenocorticotropic Hormone (ACTH) into the blood (2) ACTH then stimulates the Adrenal Glands to produce & release Glucocorticoids (i.e., Cortisol in humans) (Veenema, 2009). Activation of the HPA Axis is not entirely maladaptive, its function can be supportive, but when the hormone release is sustained or excessive then it can become harmful (de Kloet, Joels & Holsboer, 2005). This is evidence by findings which demonstrate that there is a positive relationship between levels of Cortisol and negative-intrusive parenting behavior (Mills-Koonce et al., 2009), meaning that higher levels of Cortisol are associated with more negative-intrusive parenting behavior, therefore understanding the influence of stress on HPA Axis activation is relevant within the broader study of the Mother-Child relationship.

In behavioral research the measurement of stress is assessed through Cortisol (which is a proxy for HPA Axis activation). By measuring Cortisol, it has been demonstrated that each part of the dyad influences the others' Cortisol levels within the dyadic relationships throughout the developmental range from infancy (Middlemiss et al., 2012) to adolescence (Papp et al., 2009). Further, Gordon & colleagues (2010) found that a mother's engagement in synchronous processes (e.g., gaze, affect, proximity position, touch) during a triadic interaction with a father and child is likely shaped by the Oxytocin & Cortisol hormonal systems. These researchers found that maternal Cortisol was related to lower synchrony in an observed free-play triadic interaction (Gordon et al., 2010). So, within a Mother-Child relationship, HPA Axis activation can be influenced by the other individual in the dyad; but how are these dynamics influenced by contextual factors? In a study by Atkinson & colleagues (2013) with mothers and their 16-17 month old infants, these contextual factors are rigorously tested. It is also important to note that it is not the baseline levels of Cortisol that are significant but instead the trajectories (i.e., timing & shape) of Cortisol response (Atkinson et al., 2013; Laurent et al., 2011, 2012). Atkinson & colleagues (2013) assessed Cortisol dynamics over multiple time points in different stress-inducing challenges for both Mother-Infant dyads where the mother is highly sensitive or less sensitive. They found that infants of highly sensitive mothers showed a more flexible, adaptive Cortisol response to different challenges, whereas infants of less sensitive mothers showed a blunted, more rigid response to stressful challenges. Additionally, highly sensitive mothers showed greater Cortical attunement with their infants than less sensitive mothers. These findings suggest that the quality of Mother-Infant relationship has an influence over how adaptive a response an infant has to stress.

In the context of how stress affects the Maternal Brain, it is plausible that a mother with low maternal sensitivity that is confronted with stress could transmit it via Cortisol response to their child which subsequently has a negative impact on the child's development. However, this is highly speculative and would require further research. None of the above studies are meant to indicate a direction of influence from one individual to the other. Instead, that stress influences not just the primary individual but also the interaction between each individual within a dyad which then may have further impact on the secondary individual within a dyadic relationship. One could imagine a scenario where one's HPA Axis in the presence of stress could act as either a risk or protective factor (depending on the quality of the relationship & other contextual factors) for the other's HPA Axis function.

Although it is clear that there is much nuance in the HPA Axis' response to stress and how that influences the Parent-Child relationship, the HPA Axis is not the only component in a mother's neurobiological reaction to stress. A theme that persists through many other areas of study within neuroscience is the brains' expansive levels of complexity. Here, it is no different; the response to stress is not solely dependent upon the HPA Axis but also various Limbic & Cortical areas each uniquely contributing to what eventually culminates to a behavioral stress response.

Limbic System

The HPA Axis is also regulated by other components within the Central Nervous System. Animal studies have shown that brainstem & limbic structures are involved in the regulation of the HPA Axis (Herman et al., 2003). In humans, structural & functional studies have implicated the Amygdala, Hippocampus and Prefrontal Cortex areas in regulatory response to stressors (Pruessner et al., 2008; Pruessner et al., 2007; Tessner et al., 2008; Wang et al., 2007; Wang et al., 2005) but only indirect connections between these areas and the PVN of the Hypothalamus have been found (Fernandes et al., 2007; Floyd et al., 2001; Herman et al., 1996; Hurely et al., 1991).

In regards to the Hippocampus, research on animal models has found that activity in the Hippocampus (HC) dampens the release of CRH from the neurons in the PVN of the Hypothalamus (Herman et al., 1992), therefore HC acts as a negative feedback loop which modulates glucocorticoids by exercising inhibitory effects on the HPA Axis (de Kloet et al., 1998). Therefore, the Hippocampus is implicated as an important Limbic System structure that participates in stress regulation, and it is known that both structural alterations & volumetric reduction of the Hippocampal formation is associated with stress exposure and interferes on the activity of the HPA Axis (Fuchs & Flügge, 2003). This association has been confirmed in human studies where associations between Cortisol stress response, Hippocampal volume & self-esteem were examined. Pruessner & colleagues initially found that only subjects with low self-esteem were shown to have a significant Cortisol response in an acute stress task (Pruessner et al., 1999b) and then they further expanded this finding by demonstrating in both young & old samples that self-esteem & HC volume were positively correlated and that, together, they were inversely correlated with Cortisol stress response when exposed to a psychosocial stressor (Pruessner et al., 2005). In other words, these researchers found that individuals with low self-esteem showed reduced Hippocampal volume and also had a higher Cortisol stress response, which may suggest Hippocampal volume as a vulnerability factor in stress response, falling in line with findings from the animal research literature. It is important to note that these findings do not suggest the Hippocampus as having a causal role in stress regulation in humans, additionally, the studies performed by Pruessner & colleagues were performed on both men & women not taking into account any potential gender differences which limits its generalizability to the context of the maternal brain. Lastly, although there has been some research performed in animal models looking at the specific mechanisms of change within the Hippocampus in response to stress; these studies often look at mechanisms during pregnancy or in the very early postpartum period so there is no evidence in either the animal or human research that suggests preliminary evidence for mechanistic adaptations within the Hippocampus in mothers in the late postpartum period or well into motherhood.

In regards to the Amygdala, animal research has shown that it is implicated in stress response by activating the HPA Axis, glucocorticoid receptors within the Amygdala play a ‘feed forward’ role where they facilitate HPA responses rather than inhibit them (Herman et al., 2005). When there is a threat cue present, or even an anticipated threat cue, the Amygdala sends a signal to the PVN of the Hypothalamus which then subsequently activates the HPA Axis resulting in these two structures correlated activation (Rodrigues, LeDoux & Sapolsky, 2009). Critically it should be noted that there is discrepancy between animal and human studies on the role of the Amygdala in stress response, Dedovic & colleagues (2009) suggest that this could be due to the fact that animal studies are often fear-based stress tasks, whereas in humans, neuroimaging studies commonly use paradigms that use more psychosocial-based stressors.

This is highlighted in a human study where researchers looked at stress response and found that the Amygdala deactivated in the presence of a psychosocial stressor which is contrary to the animal literature (Pruessner et al., 2008). In the previous study, the authors do suggest limitations in the functional MRI technique used where poor spatial resolution may lead to an inability to differentiate between the Amygdala and nearby Hippocampus or alternatively, poor temporal resolution may not have been able to identify ephemeral changes in activity. Unfortunately, there is a shortage of information from human studies in the general population that would allow better understanding of the dynamic activation within the Amygdala in the presence of a psychosocial stressor. This would allow a more nuanced view on the similarities & differences in stress response between humans & animals under variable contextual circumstances.

However, fortunately within the specific domain of the maternal brain, there is preliminary research to give insight into the role of the Amygdala for mothers in the presence of infant cues. Neuroimaging studies that observed mothers brain response to infant cues have demonstrated that the Amygdala activates in the presence of an infant distress cue (e.g., crying) when compared to laughing (Seifritz et al., 2003) but it also has greater activation when mothers viewed their own infant's positive faces compared to unfamiliar infant's positive faces (Barrett et al., 2012). Therefore, there is evidence of activation within the context of mother's response to both negative (e.g., cries) and positive (e.g., happy faces) infant cues from the Amygdala. This contradiction is not entirely unfounded as the Amygdala has been associated with both stress reactivity and reward processing (Feder et al., 2009). Thus, depending on the context, increased activation of the Amygdala to infant cues could be suggestive of either sensitive parenting or stress reactivity and intrusive parenting (Atzil et al., 2011; Kim et al., 2017a). In the context of the maternal brain, not many conclusions can be drawn on how the Amygdala reacts to different infant cues, more research is required to better understand when the Amygdala activates whether it is due to stimulus salience or a reaction to stress and what each of those activation profiles may look like.

Although there is no clear evidence for activation of the Hippocampus from human mothers and the evidence for the Amygdala is mixed, there is evidence from studies looking at animal models or studies on the general population and their response in the context of a psychosocial stressor. Until a confluence of evidence suggests that these structures are not implicated, their potential roles in activating with the maternal brain as a response to infant-specific psychosocial stressors such as infant cries should continue to be considered.

Cortical Areas

Up to this point, most neuroimaging studies that observe a mother's response to their infant's cues & consider the Parenting Stress levels of those mothers focus on activations that take place in cortical areas of the brain.

Initially, animal models suggested the Prefrontal Cortex as a strictly regulatory region that would aim to inhibit a stress response (Herman et al., 2003). This role has been further supported by human neuroimaging research, where acute psychosocial stress increased the resting-state functional connectivity between the medial Prefrontal Cortex (mPFC) and the Amygdala which could be induced by substantial bi-directional anatomical connections between these two areas (Ghashghaei et al., 2007; Ghashghaei & Barbs, 2002; Veer et al., 2011). These findings lend preliminary evidence to the idea that the mPFC regulates the Amygdalar response in the presence of a psychosocial stressor. However, these models quickly evolved to show that different regions within the Prefrontal Cortex (PFC) serve different functions in the presence of stressors (Herman et al., 2005). For example, it was found that individuals with a significant stress response showed less activity in the Orbitofrontal Cortex (OFC) & anterior Cingulate Cortex (ACC) which the authors suggested to be involved in the appraisal / evaluation of social threats and providing a sense of stress perception, although, it should be noted that these areas did not specifically correlate with Cortisol (Pruessner et al., 2008).

In recent years, researchers that are interested in the maternal brain have used infant cries as a context-specific stimuli that ideally elicits a neural response in line with other research on response to psychosocial stressors. Laurent & colleagues (2011) were the first study to bridge the gap between HPA Axis reactivity and the Cortical response in mothers. In this study, 1st time mothers of 15-18 month old infants had their Cortisol sampled throughout participation in the Strange Situation in order to establish a stress-response profile and then this profile was associated with brain activations when listening to infant cries. Their findings show that mothers who had a more reactive HPA profile (i.e., more delayed, prolonged Cortisol response) showed activation in the right Frontopolar Cortex, right Angular / Supramarginal Gyri & left Occipital Pole. Although these areas have been suggested to be involved in attentional shifting

& sensory processing, for mothers who represent those with a less adaptive response to stress these activations are novel findings which have not been previously found and any interpretation remains speculative until further replication. For mothers with a less reactive HPA response representing a more adaptive stress response to their infant's distress, activation was seen in the right anterior & posterior Insula, left lateral OFC, left / right ACC, left / right Periaqueductal Grey (PAG), left / right Cerebellum and left / right dorsomedial PFC (dmPFC). With activation found in the dmPFC, this provides further evidence that the mPFC plays a top-down regulatory role in stress reactivity in individuals that show an adapted response. Activation of the lateral OFC & ACC also further justifies Pruessner & colleagues (2008) that these areas evaluate the emotional perception of the stressful stimuli at hand and generate a thoughtful response, and as suggested by the authors, further expand this network to include the Insula which may elaborate the emotional aspect of a stimulus providing an "Empathic Awareness" (Laurent et al., 2011). Lastly, activation in the PAG & Cerebellum were novel findings in this context and had not been previously demonstrated in the literature. This study demonstrated that the PFC, as well as other cortical areas play various roles in an adaptive stress response to infant distress cues.

The specific mechanism of some of these cortical areas is further delineated by Noriuchi & colleagues (2019), in this study mothers provided self-report data on their levels of Parenting Stress and watched videos of their children's feeding behavior in the scanner. Although observing feeding behavior is not a direct distress cue, feeding behaviors have been found to elicit both feelings of joy & stress (Lewinsohn, 2005). Researchers found that the right OFC was negatively correlated with mothers' sense of their own parenting competence, meaning that the more dysfunctional a mother regarded their own parenting competence the less activated their right OFC was. Therefore, in regards to Parenting Stress the role of the OFC may additionally be taking the mother's own sense of competence into account during evaluation of the emotional stimuli. Additionally, activation in the right anterior Cerebellum was found to be negatively correlated with stress that is associated not to the parent but instead the characteristics of the child, so the less the Cerebellum activates the more stress the mother feels due to the temperament of their child. This study by Noriuchi & colleagues (2019) further confirms & expands the involvement of the OFC and the Cerebellum discovered by Laurent et al. (2011). Lastly, a hyper-scanning study where researchers used fNIRS to scan both mothers and their child while participating in a passive joint attention task found that self-reported parenting stress was significantly associated with activity in a left mPFC cluster. Specifically, the left inferior Frontal Gyrus, frontal Eye Field & dorsolateral PFC (dlPFC) had decreased synchrony between the mother & child as Parenting Stress increased (Azhari et al., 2019). Whilst this study does not measure a response to a psychosocial stressor directly and consequently only serves as a proxy for synchronous activation of mother-infant dyads with different levels of overall Parenting Stress, it does suggest that there are more brain areas involved in the dyadic relationship between mother-child than just the HPA Axis with regards to stress.

In summation, literature from animal models and human neuroimaging studies show that the brain's response to psychosocial stress involves a series of perceptual, emotional & executive functions that contribute to the resulting activation of the HPA Axis and release of the neuroendocrine hormone Cortisol. The dance of neural activation at each level of the brain from the Cortex to the midbrain seems to determine either an adaptive or maladaptive response to stress which can have an outsized influence on a person's behavior and subsequent social relationships like those between a mother and their child.

Perceived Quality of Maternal Care Effects

To this point, concepts that qualitatively assess maternal behavior (e.g., maternal sensitivity) and a factor (e.g., stress) that influences the ability of mothers to provide higher quality maternal behavior have been reviewed. However, there are other environmental influences that impact the quality of maternal behavior that mothers provide to their child. One of which is an individual’s social relationships; more specifically, how a given individual views their previous attachment with their own parents may influence their current parental abilities. Indeed, researchers have been using animal & human studies to understand how the quality of mothering one receives from their own mother then later influences how their current maternal behavior is expressed.

Although this remains an emerging idea in the scientific literature, the basis for intergenerational transmission of maternal behaviors was laid through the work of animal studies. When observing rats, scientists have discovered that pup grooming (e.g., licking) is one of the main components of maternal behavior and that licking in particular shows a wide amount of variation which then affects their offsprings quality & intensity of licking behavior as mothers themselves (Champagne & Meaney, 2001; Numan & Insel, 2003). Essentially, the offspring of high-licking moms then become high-licking moms themselves which, as demonstrated by rats, substantiates the idea that maternal behavior is transmitted across generations (Champagne & Meaney, 2001). Additionally, rat pups that were reared without a mother (i.e., in isolation) and did not receive the required maternal stimulation, show deficits in licking and grooming as mothers (Gonzalez et al., 2001). The findings from rat studies provides evidence that an individual's experiences with their mother, either positive or negative, has an effect on their own maternal behavior upon becoming a parent which justifies further research in humans.

In human research, behavioral studies began to investigate this idea by examining attachment classifications in different generations. In fact, one study found that about two-thirds (65%) of grandmother–mother–infant triads had correspondent attachment styles (Benoit & Parker, 1994). However, it should be noted that the authors recognize the distribution of their sample skewed towards securely attached dyads which may inflate the likelihood of correspondence across generations compared to more insecure attachment styles. Many behavioral studies have identified a relationship between adult & infant attachment styles (van Ijzendoorn, 1992; Serbin & Karp, 2004); even so the mediational factors, let alone the specific maternal behaviors, that perpetuate the transmission of maternal behaviors still remains unclear. Yet it is commonly accepted that maternal care influences the organization of a brain circuit, which then operates differentially based on the quantity & quality of care and expresses a variety of emotional, perceptual and cognitive functions that later affect how one expresses caregiving behavior (Barrett et al., 2011).

One of the first studies to examine the relationship between attachment style and the brain was conducted by Strathearn and colleagues (2009), who found differential neural activations in secure vs insecure-dismissing mothers when they viewed their own infant faces compared to unknown infant faces. For securely-attached mothers, they experienced increased activation in Striatal (i.e., ventral Striatum, Nucleus Accumbens), Inferior Frontal Gyrus & Superior Frontal Gyrus to both their own infants' happy and sad faces (compared to those of unknown infants). These results suggest that secure mothers may experience their own infants' cues as a signal of incentive salience (Berridge, 2007) – meaning a cue that elicits a desire or motivation to pursue – which then reinforces their responsive care. Conversely, for insecure-dismissing mothers, they experienced increased activation in the dorsolateral PFC & anterior Insula to their own infants' sad faces. This suggests that insecure-dismissing mothers may experience more cognitive control over an affective response that is more negative (Greene et al., 2004; Sanfey et al., 2003) and rather than feel motivated as secure mothers do, may interpret their infants' sad face as a missed opportunity for reward. Consequently, this could lead to an avoidant maternal response to their infants cues rather than an approach response (Sanfey et al., 2003). Although this study does not address neural activations of mothers across generations, it does provide a foundation for neural activations in mothers of differing attachment styles which is necessary for further research on intergenerational transmission. Additionally, direct comparison of this studies results with the current study and previously reviewed work thus far should be cautioned as Strathearn & colleagues (2009) used visual infant cues (i.e., faces) rather than auditory infant cues (i.e., cries).

Lastly to connect this literature with the present work, Kim and colleagues (2010) investigated the relationship between neural activation of infant cries and mothers' retrospective perception of maternal care when they were younger. In this study, mothers previous experience of care with their own mothers was assessed using the Parental Bonding Instrument (PBI) which is a retrospective self-report measure assessing retrospective maternal care with items that ranged from warmth & affection to indifference & neglect (Parker, 1979). For mothers who scored higher on their previous perceived maternal care, researchers found increased functional activation, as well as larger grey matter volume in the Medial Temporal Gyrus, Superior Temporal Sulcus & middle Frontal Cortex. As we have seen with previous findings on neural response to infant cries, this pattern of activity may indicate that mothers with a more positive reflection of their care as a child can then carry a better ability to perceive the auditory infant cues of their child and subsequently plan & respond to them into their own mothering. Alternatively for mothers who scored lower on their previous perceived maternal care, increased functional activation in the left Hippocampus in response to infant cries, as well as, reduced grey matter volume in the Orbital Gyrus was found. From the literature on stress effects, the functional activation of the Hippocampus could be indicative of these mothers regulating their stress reactivity by inhibiting the HPA Axis (Dedovic et al., 2009). The authors suggest that current mothers whose perception of their care when they were children is represented as being more indifferent or possibly neglectful, may then consequently experience more stress reactivity in the early postpartum in response to infant cues when they become mothers. Additionally, the reduced grey matter volume in the Orbital Gyrus may culminate in a compromised ability to evaluate & process social and emotional stimuli for appropriate responding (Kringelbach, 2005). By using retrospective self-reports of mothers perceived quality of maternal care and comparing these behavioral scores with mothers' neural response to infant cries, this study by Kim and colleagues (2010) provides early preliminary neurobiological evidence for potentially variable maternal behaviors according to their own care as children and simultaneously providing a proximal reference point for the current study to extend findings in this domain.

Current Study

In the present study, a novel sample of lesbian mothers will be asked to listen to unfamiliar infant cues while undergoing a functional Magnetic Resonance Imaging (fMRI) scan. Various behavioral measures will also assess the quality of interaction between the mothers and their child (3-11 years old), as well as their self-reported level of parenting stress and reported previous acceptance–rejection of their own past experience of maternal care. The aims of this study are to: (a) extend the knowledge of the parental brain model, through observation of a different type of family structure, to mothers that have greater caregiving experience through their neural response to infant cries, (b) further extend knowledge of the parental brain model by preliminarily observation of mothers', in the late postpartum period, neural response to a new auditory stimulus of baby laughs, (c) investigate associations between sub-components of the brain response to infant cues with different aspects of maternal behavior during dyadic interaction (i.e., sensitivity, structuring, intrusiveness & hostility), (d) assess the influence of parenting stress on the brain response to infant cues and the quality of dyadic interaction and lastly (e) understand the influence of previous parental acceptance–rejection on current levels of mothers parenting stress and behaviors within dyadic interaction with their children.

Hypotheses

1. It is hypothesized that different brain regions will activate for infant cries, relative to control noise and baby laughs.
2. It is expected that brain responses to infant cries when compared to control sounds will produce activation in prefrontal (i.e., SFG, IFG, OFC), temporal (i.e., STG, Insula) and midbrain regions (i.e., Hypothalamus, Caudate, Putamen, Cerebellum) (Witteman et al., 2019).
3. It is predicted that mothers with higher levels of sensitivity will display increased neural activations in the IFG & Frontal Pole, and that mothers with low levels of non-intrusiveness will display increased activations in the Insula & Temporal Pole (Musser et al., 2012).
4. It is hypothesized that mothers with low levels of parenting stress will exhibit more adaptive neural responses with increased activity in memory (e.g., Hippocampus) & emotional processing-related areas (e.g., OFC, Insula, ACC).

5. It is hypothesized that mothers who perceived more acceptance from their own mothers in their childhood will display increased neural activation in the Medial Temporal Gyrus, Superior Temporal Sulcus & middle Frontal Cortex (Kim et al., 2010)

Methods

Participants

16 healthy lesbian mothers (*M* age = 44.5 years, sd = 5.34; education level range = 13 - 21 years) and 8 of their full-term, healthy children (range = 3 - 11 years; *M* age = 5.53 years, sd = 2.64) participated in the study. Mothers were recruited via public advertisement and word of mouth at the University of Padova. Inclusion criteria included being a lesbian family and having children between the ages of 3-11. Exclusion criteria included neurological or psychiatric disorders, psychotropic medications, pregnancy & non-compatibility with MRI scan. All participants gave informed consent to participate, and the study was approved by the ethical committee for experiments at the University of Trento.

Stimuli

The auditory stimuli used in the scanner included 3 categories of sound: (1) infant cries (IC; hunger cries from 1-year-olds), (2) baby laughs (BL; from 1 to 2-year-olds) and (3) control noise sounds (CS). Each category consists of 10 sounds with a duration of 15 seconds. Human vocalizations (IC & BL) were retrieved from Oxford Vocal (OxVoc) Sounds database Parsons et al., 2014), as well as, online public databases (sounddogs, www.sounddogs.com/; soundbible, soundbible.com/; audio4fun, www.audio4fun.com/; freesound, https://freesound.org/). CSs were derived from ICs by generating white noise sounds and then, so that the morphological features of ICs would be preserved, the temporal pattern (i.e., shape & form) of the control noise were modulated using ICs as a reference. All stimuli were equalized for volume. All acoustic files were edited using the computer software Audacity 2.1.0 (www.audacity.sourceforge.net) and Adobe Audition CC 2015 (Adobe Systems Incorporated, https://creative.adobe.com/products/audition).

Measures

Emotional Availability Scales (EAS)

The Emotional Availability Scales (EAS, 4th Edition; Biringen, 2008) were used in order to assess the emotional availability of maternal behavior during a dyad interaction. The EAS is used in order to assess the relational dynamic of a parent–child interaction based on each of the actor's emotional responsiveness and attunement to the other. The 15-20 minute interaction was recorded on a video call where mothers were instructed to aid their child in completing a puzzle. Each family was sent the same puzzle, mothers were instructed to help their child as they normally would in order to complete the puzzle but without completing it themselves.

After working together for about 15 minutes, the mother received a text message which instructed her not to interact with their child for a few minutes while they continued working on the puzzle. The video-recorded interactions were then rated by a trained researcher who was blind to any descriptive information, as well as the results of other behavioral questionnaires.

Based on the dyadic interaction, all six subscales were scored on a scale from 1 to 7, with higher scores indicating higher prevalence of the specific behavior. In the present study, only the 4 parental subscales were considered. The 4 adult subscales are: (1) Adult Sensitivity, referring to the parent's appropriate responsiveness (e.g., attunement, timing, flexibility) to the child's emotional expression; (2) Adult Structuring, referring to the ability of the parent to guide and scaffold the child's activities; (3) Adult Non-Intrusiveness, referring to parental behaviors (e.g., over-direction, over-stimulation, interference) that deny a child their autonomy; (4) Adult Non-Hostility, referring to the parent's absence of hostile responses (e.g., raising one's voice, subtle signs of anger, impatience, boredom). The EAS has shown to have robust psychometric properties including validity and reliability specifically within Italian samples, as well as samples with children in middle childhood (Biringen, 2014).

Parenting Stress Index (PSI)

The Parenting Stress Index–Short form (PSI; Abidin, 1995) was administered to parents in this study to assess their levels of parenting-related stress. The PSI-short form is a 36-item self-report questionnaire with the following three subscales: (1) parental distress, referring to the stress that is attributable to their self-perception of inadequate parenting, conflict with the other parental figure or lack of social support; (2) parent–child dysfunctional interaction, referring to the stress that is attributable to the parent's perception that the child is not meeting their expectations and may consequently feel rejected, exploited or alienated by the child; (3) difficult child, refferring to the stress that is attributable to the characteristics of the child's behavior (often originating from their temperament). The questionnaire was administered to both parents using statements such as, "My son / daughter rarely does things that gratify me" (parental distress), "At times I feel that my son / daughter does not like me and he / she does not want to be near me" (parent–child dysfunctional interaction) or "My son / daughter remains mad easily even for the smallest things" (difficult child). Each statement was rated using a 5-point Likert Scale ranging from [5] "Strongly Agree" to [1] "Strongly Disagree". Raw scores were converted to percentiles based on the Italian population statistics and the child's age, the normal range for parenting stress is between the 25th and 75th. The measure has been translated and validated for the Italian population using a normative sample of 1352 parents (age range = 18-54 years; children age range = 0-12 years) (Gaurino et al., 2008).

Parental Acceptance–Rejection Questionnaire (PARQ)

The Parental Acceptance–Rejection Questionnaire (PARQ; Rohner, 2005b) was administered to parents in this study to assess the remembrances of their mothers' and fathers' accepting or rejecting behaviors when they were children. The PARQ-short form is a 24-item self-report questionnaire designed to assess the following four subscales: (1) warmth / affection, referring to a parent–child relationship being remembered as emotionally supportive & nurturing or alternatively emotionally cold & unaffectionate; (2) hostility / aggression, referring to a parent–child relationship where caregivers are remembered for being angry, bitter or resentful or also physically, verbally or psychologically harmful in some way; (3) indifference / neglect, referring to a parent–child relationship where caregivers are remembered for being unconcerned or emotionally unavailable; (4) undifferentiated rejection, referring to a parent–child relationship where caregivers are remembered for being unwanting, unloving & unappreciative but there are no objective signs that they were cold, neglecting or aggressive with the adult as a child. The questionnaire was used to assess the retrospective relationship with both the mother and father, using statements such as, "My mother / father made me feel wanted and needed" (warmth / affection) or "My mother / father paid no attention to me" (indifference / neglect). Each statement was rated using a 4-point Likert Scale ranging from [4] "almost always true" to [1] "almost never true". The total score of the PARQ-short form ranges from 24 to 96, with higher scores indicating that the adult remembers their past relationship with their parent as more rejecting. The PARQ has been shown to be a reliable and invariant scale that has been confirmed within the Italian population (Senese, 2016).

fMRI Paradigm

Before beginning the experimental phase of the fMRI scan, few technical sequences were acquired to center the participant, as well as calculate the dishomogeneity of the static magnetic field in order to correct the data acquisition. Then the experimental task (see Figure 2) began with a fixation cross with a duration of 8 seconds when first presented, then the fixation cross was presented with an 8-10 second jittered interstimulus interval between each trial. Following the initial fixation cross, each of the three sound conditions (IC, BL, CS) was played for a duration of 15 seconds. The order of the sounds was randomized. Following the experimental trial was a control task where the subject was asked if the presented stimulus was either: "Positive?" or "Negative?", with a yes or no response displayed on the bottom left and right of the screen respectively. This screen appeared for a duration of 2 seconds followed by a 4 second window for response time where the subject would indicate their answer with a button box. This control task is inserted randomly and does not appear after every sound, the task occurs about 5 times during the listening session. Participants were asked to respond to the control task as fast as possible.

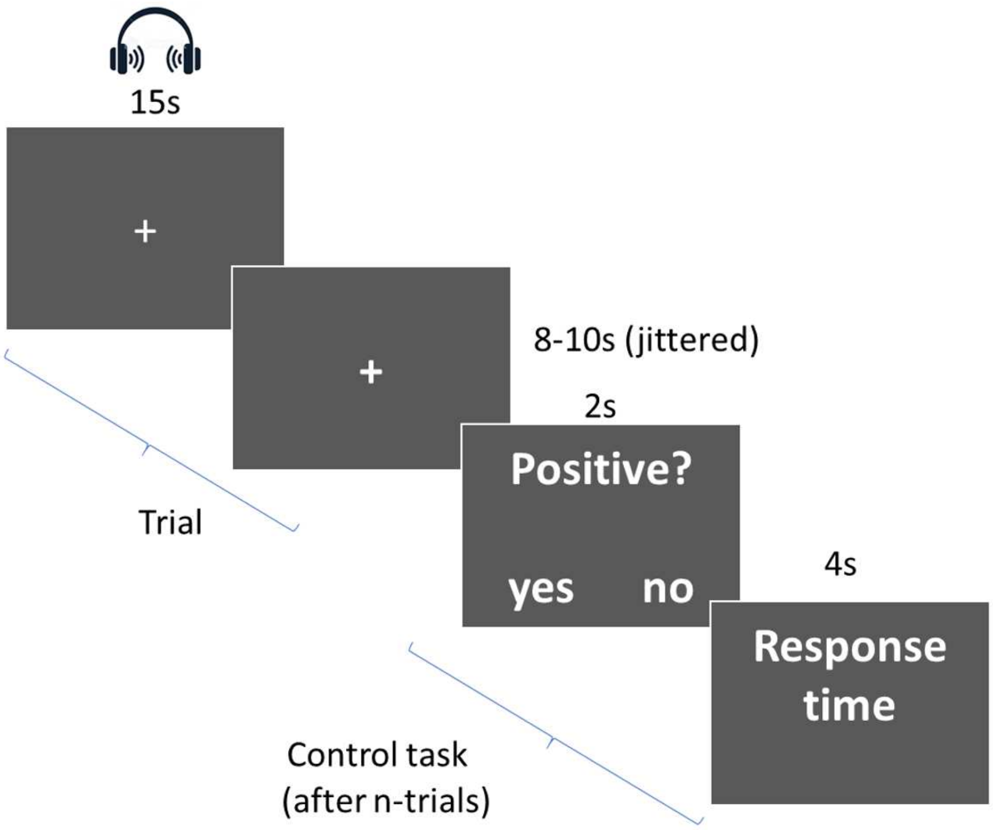


Figure 2

Schematic illustration of the auditory task presented during the fMRI

fMRI Specifications & Data Pre-Processing

A Siemens Prisma Whole Body 3.0 T MR System was employed for the scanning. Functional T2*-weighted images were acquired using an Echo Planar Imaging (EPI) sequence with the following parameters: 33 slices, FoV=192x192 mm 2 , voxel size = 3.×3.×3 mm, flip angle (FA) = 75°, TE = 33 ms, TR = 2000 ms per volume. Additionally, high-resolution T1-weighted anatomical images were obtained (3D MPRAGE, 192 slices, matrix size 256x256, TE = 2.34, TR = 2530ms) were acquired for spatial registration with the functional scans. The experimental session consisted of 368 whole brain images per participant, including 2 dummy scans at the start of each time series to allow for T1 equilibration.

The functional neuroimaging data were preprocessed using SPM12 (Statistical Parametric Mapping 12; Wellcome Department of Neurology, London, UK; https://www.fil.ion.ucl.ac.uk/spm/), a free and open-source software within MATLab (R2023a). After importing the DICOM files and converting them to NIFTI, the functional images were realigned in reference to the first collected volume with the aim of correcting for any head motion artifacts that may have occurred during scanning. Participant re-alignment was accepted if the translation did not exceed 3 mm and the rotation was no greater than 2°. Next using the average functional image from the previous step, the realigned functional images were co-registered with the subjects high-resolution T1 anatomical image. Then the co-registered images were normalized to the SPM12 standard MNI brain template using the default settings which enables for comparisons across subjects due to the brain's anatomical individual variability. Lastly, in order to reduce the rate of false positives, the normalized functional images were spatially smoothed using a Gaussian filter with a full-width half-maximum value of 8 mm.

fMRI Data Analysis

Once the fMRI data was prepped, General Linear Models (GLMs) were implemented at the individual and group level to assess the neural activation in response to infant cries (ICs), baby laughs (BLs) and control sounds (CS). In this analysis, neural activity is represented by the BOLD signal – the total amount of deoxygenated hemoglobin within an area of the brain – which is dependent on the extraction of oxygen by nearby active neurons. Therefore, measuring the BOLD signal, although not a direct measure of neural activity, serves as a proxy which indicates active brain regions.

For the analysis at the individual level (1st-Level), the GLM was used to estimate the effect of the stimulus type (ICs, BLs, CSs) on the BOLD signal within each individual. The GLM defines a model which creates a prediction (i.e., regressor) of the response to each auditory stimulus. These regressors are then convolved with the typical hemodynamic response which accounts for the natural properties of the BOLD signal. The regressors for each condition with its first temporal derivative is then combined with each of the six head motion correction parameters and essentially creates the expected activation function that would be observed for each stimulus type. Using a least squares approach, the GLM estimates the parameters that best fit the observed BOLD signal in each voxel within each subject's brain. Then, in order to test the hypotheses, the following contrasts are created to compare neural responses between different stimuli: Infant Cry vs. Control + Baby Laugh vs. Control + Infant Cry vs. Baby Laugh. Finally, statistical thresholds are used to identify clusters of activation where neural activity (activation or deactivation) is different from baseline in response to the different auditory stimuli. Activated brain clusters were mapped to their anatomical regions using the SPM12 toolbox xjView (https://www.alivelearn.net/xjview).

For the analysis at the group level (2nd-Level), the aim is to make inferences on whether a given region activates more or less to one stimulus versus another across all participants. Accordingly, a paired t-test was performed for each contrast of interest. This test enables the acceptance or rejection of the null hypothesis (i.e., there is no difference between the compared stimuli). The significance threshold for each *t*-test at the cluster level was set at a minimum value of $p < .005$ (uncorrected). As a part of the 2nd-level analysis, a random effects analysis was conducted in order to account for variability within- and between-subjects. Therefore, results will be more generalizable from the current sample to the broader population.

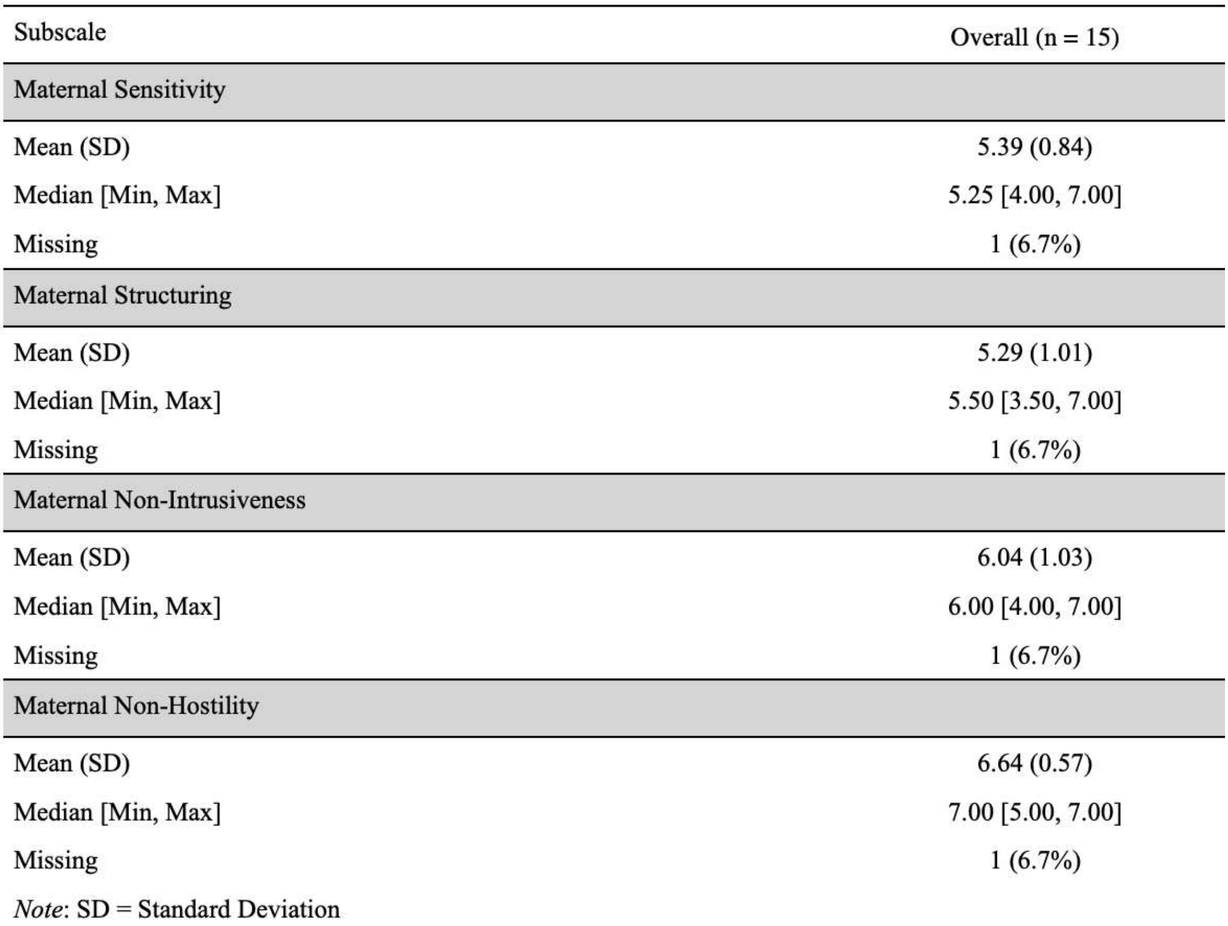
Results

Means & Standard Deviations of Variables

In this section, the means and standard deviations of each self-report measure will be reviewed.

Emotional Availability Scales (EAS)

Table 1 EAS Descriptive Statistics



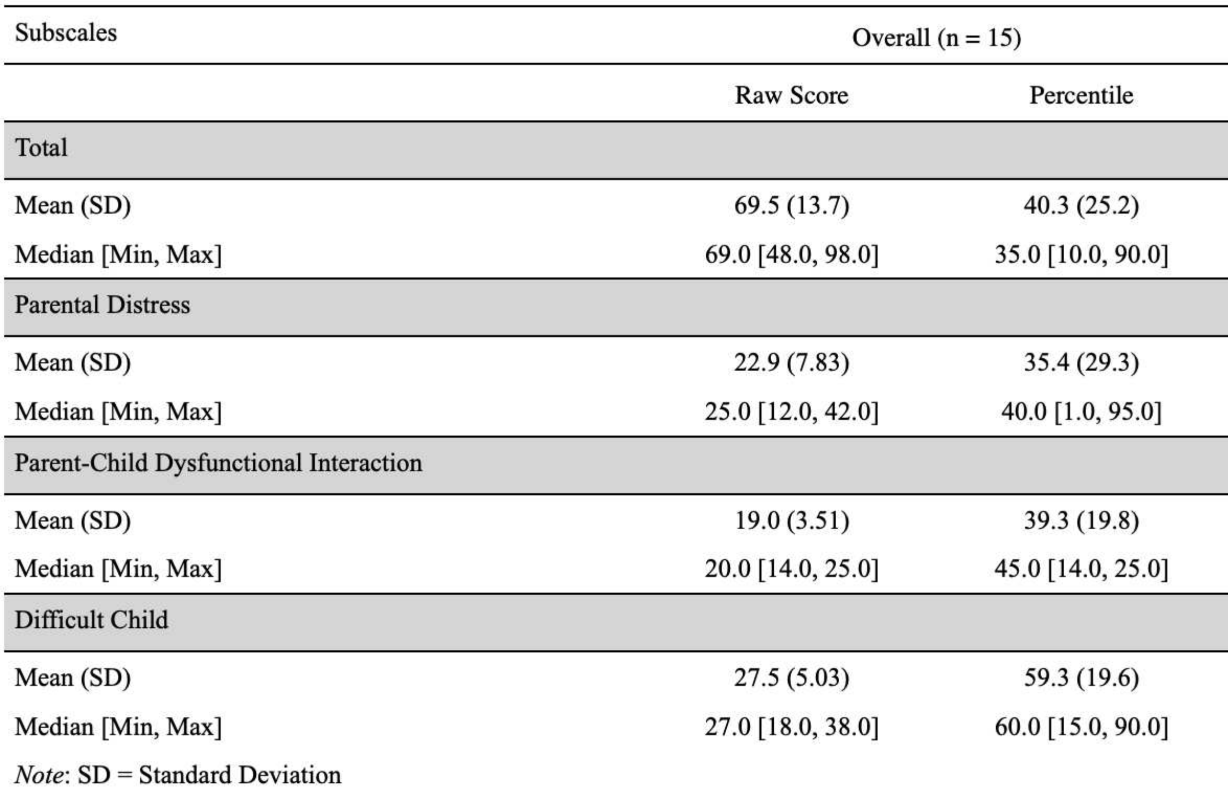
Subscale	Overall (n = 15)
Maternal Sensitivity	
Mean (SD)	5.39 (0.84)
Median [Min, Max]	5.25 [4.00, 7.00]
Missing	1 (6.7%)
Maternal Structuring	
Mean (SD)	5.29 (1.01)
Median [Min, Max]	5.50 [3.50, 7.00]
Missing	1 (6.7%)
Maternal Non-Intrusiveness	
Mean (SD)	6.04 (1.03)
Median [Min, Max]	6.00 [4.00, 7.00]
Missing	1 (6.7%)
Maternal Non-Hostility	
Mean (SD)	6.64 (0.57)
Median [Min, Max]	7.00 [5.00, 7.00]
Missing	1 (6.7%)

Note: SD = Standard Deviation

Table 1 displays the mean and standard deviations for the EAS sub domains. As shown, one participant failed to complete the EAS so only 14 participants were analyzed on this measure. Highest and most robust scores were observed on the sub scale of Maternal Non-Hostility. Lowest scores were observed on the Maternal Structuring dimension. The most variance was shown on the Maternal Non-Intrusiveness subscale.

Parenting Stress Index (PSI)

Table 2 PSI Descriptive Statistics



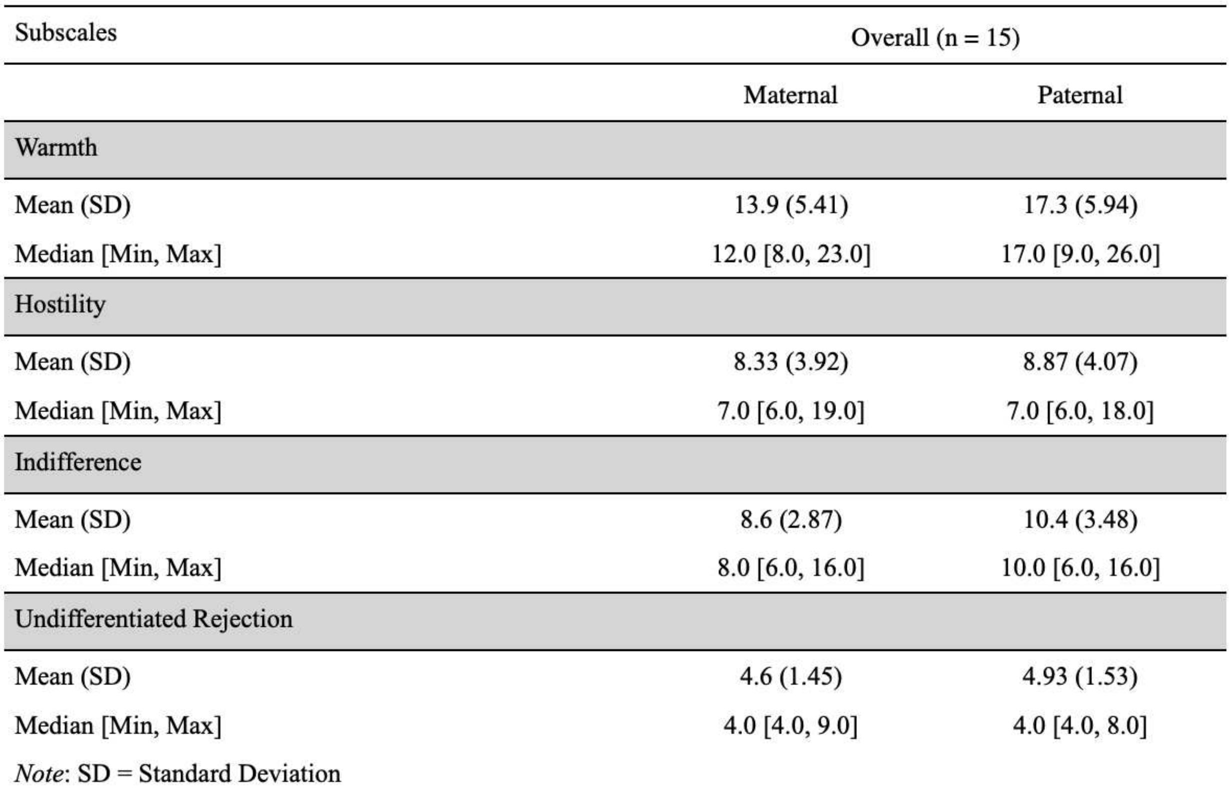
Subscales	Overall (n = 15)	
	Raw Score	Percentile
Total		
Mean (SD)	69.5 (13.7)	40.3 (25.2)
Median [Min, Max]	69.0 [48.0, 98.0]	35.0 [10.0, 90.0]
Parental Distress		
Mean (SD)	22.9 (7.83)	35.4 (29.3)
Median [Min, Max]	25.0 [12.0, 42.0]	40.0 [1.0, 95.0]
Parent-Child Dysfunctional Interaction		
Mean (SD)	19.0 (3.51)	39.3 (19.8)
Median [Min, Max]	20.0 [14.0, 25.0]	45.0 [14.0, 25.0]
Difficult Child		
Mean (SD)	27.5 (5.03)	59.3 (19.6)
Median [Min, Max]	27.0 [18.0, 38.0]	60.0 [15.0, 90.0]

Note: SD = Standard Deviation

Table 2 displays the mean and standard deviations for the PSI, both raw scores and standardized percentile scores are reported for both the total and sub domain scores. Total parenting stress scored a mean of 69.5 (±13.7) with scores ranging from 48-98. This sample of mothers, on average, scored below the median on their level of parenting stress. The Difficult Child subscale reported the highest scores at 27.5 (±5.03) with least variability. It was the only subscale to score above the population median. However, all subscales of Parenting Stress fell within the interquartile range. The Parenting Distress subscale showed the greatest variance among all subscales.

Parental Acceptance–Rejection Questionnaire (PARQ)

Table 3 PARQ Descriptive Statistics



Subscales	Overall (n = 15)	
	Maternal	Paternal
Warmth		
Mean (SD)	13.9 (5.41)	17.3 (5.94)
Median [Min, Max]	12.0 [8.0, 23.0]	17.0 [9.0, 26.0]
Hostility		
Mean (SD)	8.33 (3.92)	8.87 (4.07)
Median [Min, Max]	7.0 [6.0, 19.0]	7.0 [6.0, 18.0]
Indifference		
Mean (SD)	8.6 (2.87)	10.4 (3.48)
Median [Min, Max]	8.0 [6.0, 16.0]	10.0 [6.0, 16.0]
Undifferentiated Rejection		
Mean (SD)	4.6 (1.45)	4.93 (1.53)
Median [Min, Max]	4.0 [4.0, 9.0]	4.0 [4.0, 8.0]

Note: SD = Standard Deviation

Table 3 displays the mean and standard deviations for the PARQ, because the PARQ reports three negative subscales (i.e., Hostility, Indifference, Undifferentiated Rejection) along with one positive subscale (i.e., Warmth) total scores were not reported due to ambiguity in interpretability. All four subscales referencing past relationships with both the mother and father are reported. It is observed that, on average, the mothers in this sample rated their own father's warmth (17.3 ±5.94) as higher than their mothers (13.9 ±5.41). In reference to Hostility, mothers in this sample rated their own fathers (8.87 ±4.07) higher than their mothers (8.33 ±3.92). In reference to Indifference, mothers rated their own fathers (10.4 ±3.48) higher than their own mothers (8.60 ±2.87). Lastly for Undifferentiated Rejection, mothers rated their own fathers (4.93 ±1.53) higher than their own mothers (4.60 ±1.45).

fMRI Activations by Contrast

In this section the significant clusters of activation will be reported following the pre-defined contrasts: Infant Cry vs. Control, Baby Laugh vs. Control & Infant Cry vs. Baby Laugh.

Infant Cry vs. Control

The brain clusters that showed a significant difference (at a threshold of p = .0001 uncorrected) in activation when mothers listened to unfamiliar infant cries compared to the white noise control sound are reported in Table 4. When mothers listened to unfamiliar infant cries for a duration of 15 seconds, increased activation was observed in the right and left Hippocampus / Midbrain area, right Temporal Pole, right Superior Temporal Gyrus & left Cerebellum compared to listening to the control sound.

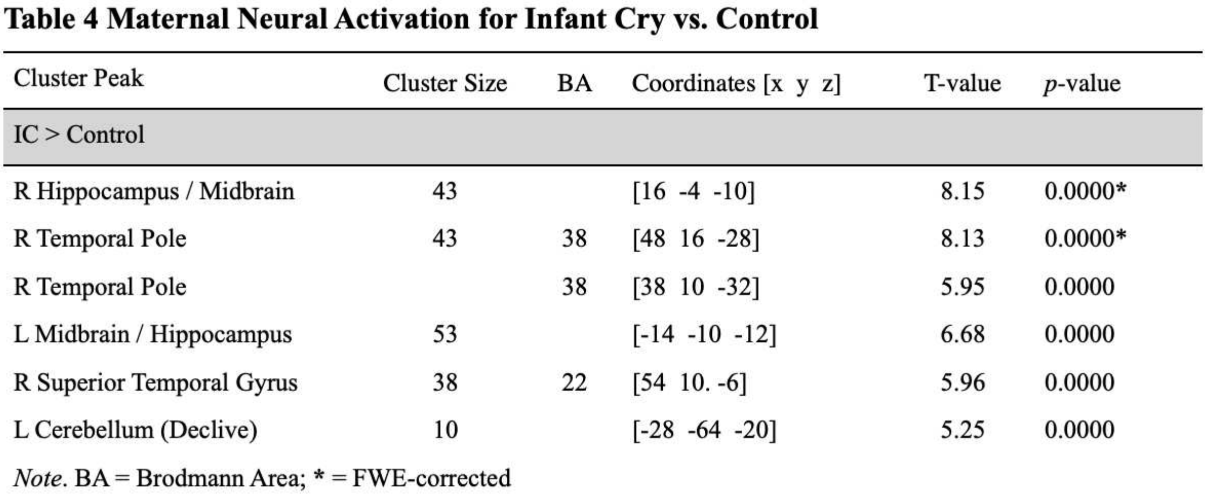


Table 4 Maternal Neural Activation for Infant Cry vs. Control

Cluster Peak	Cluster Size	BA	Coordinates [x y z]	T-value	*p*-value
IC > Control					
R Hippocampus / Midbrain	43		[16 -4 -10]	8.15	0.0000*
R Temporal Pole	43	38	[48 16 -28]	8.13	0.0000*
R Temporal Pole		38	[38 10 -32]	5.95	0.0000
L Midbrain / Hippocampus	53		[-14 -10 -12]	6.68	0.0000
R Superior Temporal Gyrus	38	22	[54 10. -6]	5.96	0.0000
L Cerebellum (Declive)	10		[-28 -64 -20]	5.25	0.0000

Note. BA = Brodmann Area; * = FWE-corrected

Infant Cry vs. Baby Laugh

The brain clusters that showed a significant difference (at a threshold of $p = .0001$ uncorrected) in activation when mothers listened to unfamiliar infant cries compared to unfamiliar baby laughs are reported in Table 5. When mothers listened to unfamiliar infant cries for a duration of 15 seconds, increased activation was observed in left Mid Occipital Gyrus–Cuneus, right Cerebellum Crus 1 & 2, left Occipital Lobe–Mid / Inf Occipital Gyrus, right Mid Occipital Gyrus, left Supramarginal Gyrus, right Subcallosal Gyrus & right Cerebellar Declive compared to listening to baby laughs.

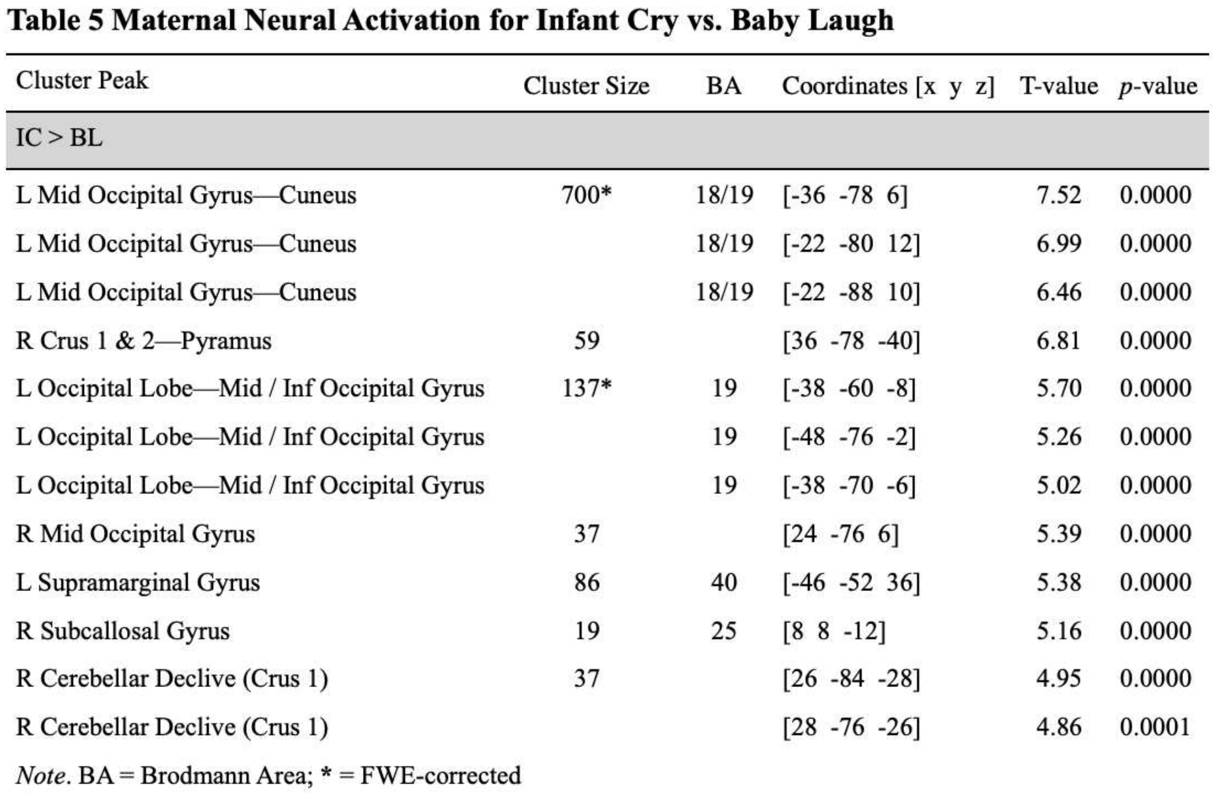


Table 5 Maternal Neural Activation for Infant Cry vs. Baby Laugh

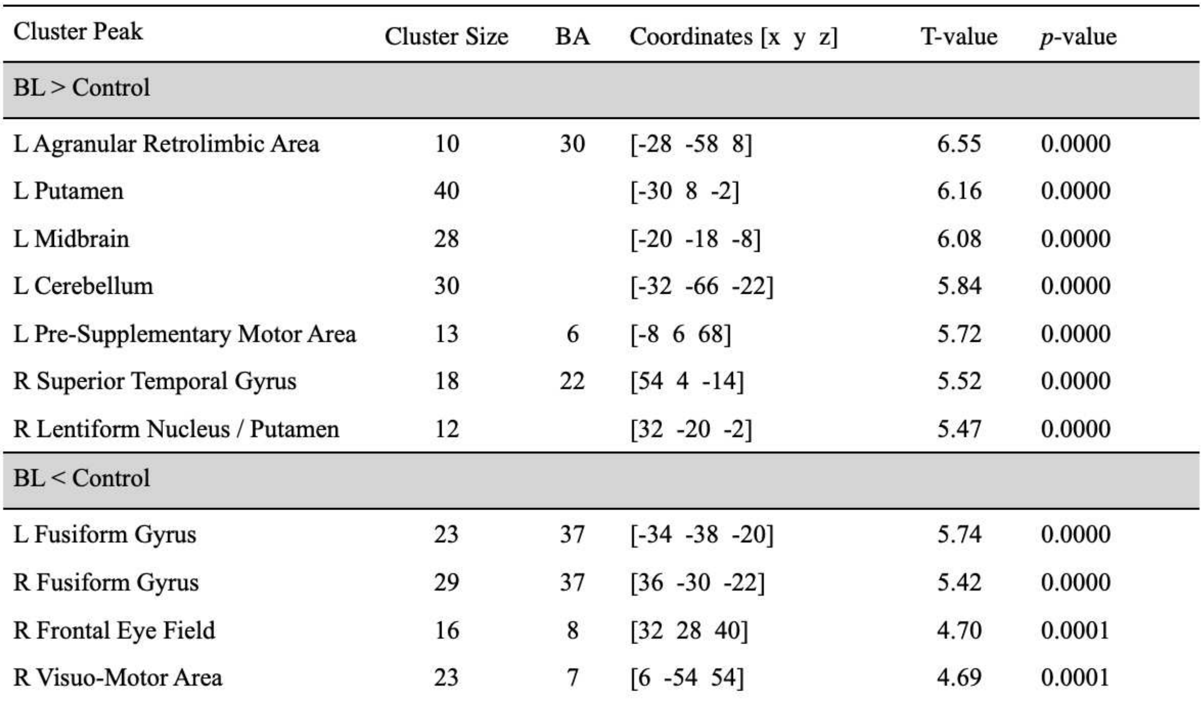
Cluster Peak	Cluster Size	BA	Coordinates [x y z]	T-value	*p*-value
IC > BL					
L Mid Occipital Gyrus—Cuneus	700*	18/19	[-36 -78 6]	7.52	0.0000
L Mid Occipital Gyrus—Cuneus		18/19	[-22 -80 12]	6.99	0.0000
L Mid Occipital Gyrus—Cuneus		18/19	[-22 -88 10]	6.46	0.0000
R Crus 1 & 2—Pyramus	59		[36 -78 -40]	6.81	0.0000
L Occipital Lobe—Mid / Inf Occipital Gyrus	137*	19	[-38 -60 -8]	5.70	0.0000
L Occipital Lobe—Mid / Inf Occipital Gyrus		19	[-48 -76 -2]	5.26	0.0000
L Occipital Lobe—Mid / Inf Occipital Gyrus		19	[-38 -70 -6]	5.02	0.0000
R Mid Occipital Gyrus	37		[24 -76 6]	5.39	0.0000
L Supramarginal Gyrus	86	40	[-46 -52 36]	5.38	0.0000
R Subcallosal Gyrus	19	25	[8 8 -12]	5.16	0.0000
R Cerebellar Declive (Crus 1)	37		[26 -84 -28]	4.95	0.0000
R Cerebellar Declive (Crus 1)			[28 -76 -26]	4.86	0.0001

Note. BA = Brodmann Area; * = FWE-corrected

Baby Laugh vs. Control

The brain clusters that showed a significant difference (at a threshold of $p = .0001$ uncorrected) in activation when mothers listened to unfamiliar baby laughs compared to the white noise control sound are reported in Table 6. When mothers listened to unfamiliar baby laughs for a duration of 15 seconds, increased activation was observed in the left Agranular Retrolimbic Area, left Putamen, left Midbrain, left Cerebellum, left Pre-Supplementary Motor Area, right Superior Temporal Gyrus & right Lentiform Nucleus / Putamen compared to listening to the control sound. Alternatively, decreased activation was observed in the left & right Fusiform Gyrus, right Frontal Eye Field & right Visuo-Motor Area.

Table 6 Maternal Neural Activation for Baby Laugh vs. Control



Cluster Peak	Cluster Size	BA	Coordinates [x y z]	T-value	*p*-value
BL > Control					
L Agranular Retrolimbic Area	10	30	[-28 -58 8]	6.55	0.0000
L Putamen	40		[-30 8 -2]	6.16	0.0000
L Midbrain	28		[-20 -18 -8]	6.08	0.0000
L Cerebellum	30		[-32 -66 -22]	5.84	0.0000
L Pre-Supplementary Motor Area	13	6	[-8 6 68]	5.72	0.0000
R Superior Temporal Gyrus	18	22	[54 4 -14]	5.52	0.0000
R Lentiform Nucleus / Putamen	12		[32 -20 -2]	5.47	0.0000
BL < Control					
L Fusiform Gyrus	23	37	[-34 -38 -20]	5.74	0.0000
R Fusiform Gyrus	29	37	[36 -30 -22]	5.42	0.0000
R Frontal Eye Field	16	8	[32 28 40]	4.70	0.0001
R Visuo-Motor Area	23	7	[6 -54 54]	4.69	0.0001

Note. BA = Brodmann Area; * = FWE-corrected

Brain–Behavior Correlations

After analyzing the significant clusters of brain activity for each contrast between stimuli, the significant clusters were further correlated with all behavioral questionnaires (EAS, PSI, PARQ). Using Pearson's correlation coefficient, a significant negative relationship was found between the activation of the right Superior Temporal Gyrus and the EAS subscale of Maternal Sensitivity (Figure 1; r = 0.79, *p* = .037) when mothers listened to unfamiliar infant cries compared to the white noise control sound. No other significant correlations were found.

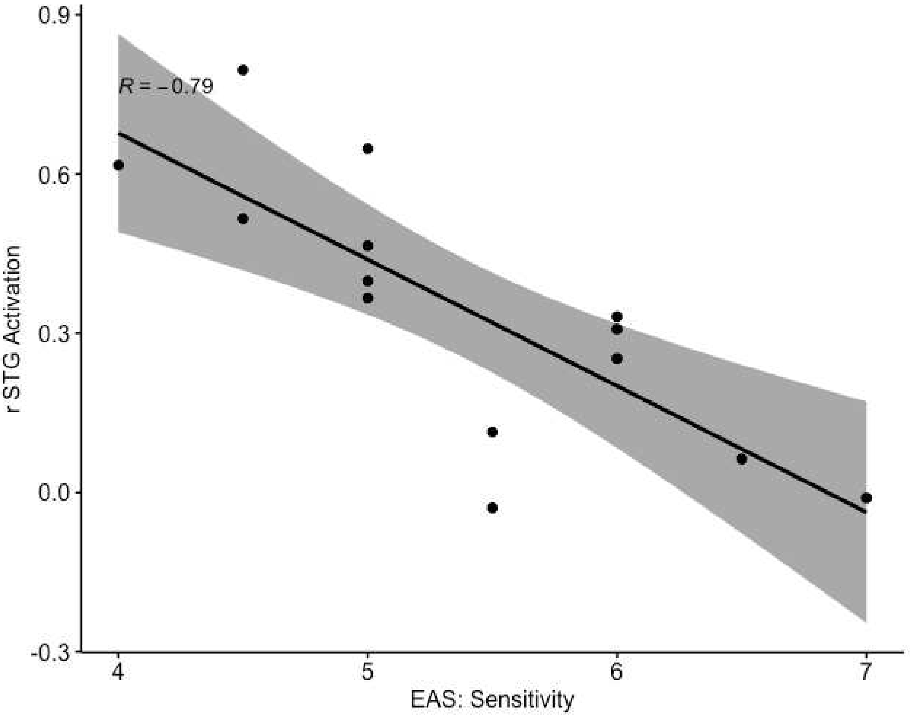


Figure 3

Correlation between right STG activation and EAS: Sensitivity for Infant Cry vs. Control Sound

Discussion

Children’s vulnerability in the precursory stages of life requires experienced parental figures to guide and nurture them as they learn and explore the world around them. The responsibility of a mentor substantiates the importance of the parent–child relationship and yet, open questions still remain on what specific maternal behaviors constitute more adaptive parenting practices and how these may change as the parent gains more caregiving experience and the child grows older. For this reason, it is also important to understand how contextual factors affect parenting behaviors in positive or negative ways. In addition, societal changes have reshaped our conception of traditional family structures, posing a new opportunity for researchers to investigate the interplay between caregiving role and gender within the mother–child relationship. Therefore, in the present study the aim was to analyze the maternal neural response to infant cries in a novel sample of lesbian mothers with children later into childhood than has been observed in the literature, as well as understand how these responses are related to different maternal behaviors, change in the context of parenting stress and previous remembrance of parental care.

Supporting the 1st hypothesis, unique clusters of neural activation were identified for both infant cries and baby laughs, in relation to control sounds as well as to each other. However, the 2nd hypothesis regarding the specific areas that activated for infant cries relative to control sounds was only partially supported by the current data. Activation of the Superior Temporal Gyrus and Cerebellum was confirmed, but additional activation was also seen in the Hippocampus / Midbrain region and Temporal Pole. Based on the reviewed literature, activation of the Superior Temporal Gyrus could indicate the involvement of the ‘What’ auditory pathway that activates upon perceiving & processing the auditory and semantic aspects of infant vocalizations (Hickok & Poeppel, 2007; Lima et al., 2016; Witteman et al., 2019) and activation of the Temporal Pole has also been attributed with auditory-related processing of infant cries (Lorberbaum, 2002). Furthermore, the current data provides more evidence for activation of the Cerebellum in response to infant cries and more broadly auditory perception in general (Petracchi et al., 2005; Witteman et al., 2005). Literature that reviews the involvement of the Cerebellum in auditory processing suggests that the left lateral anterior lobe of the Cerebellum (seen activated in the current study) is associated with pitch discrimination (Holcomb et al., 1998). In combination with the Pons, the pathway may match auditory inputs with spectrotemporal memory templates which are then further associated with the symbolic identity of the sound in the secondary auditory cortex (i.e., Superior Temporal Gyrus) (Davis

& Johnsrude, 2003; Schwartze & Kotz, 2016). According to the present MNI coordinates of the bilateral clusters identified as the Hippocampus / Midbrain region, the activation falls on the border between the Hippocampus and, perhaps more interestingly, the Crus Cerebri region of the Pons. This interpretation falls in line with research that indicates a Cortico-Ponto-Cerebellar pathway which stores sensory–motor memories of commonly occurring sequences in the Cerebellum and further enables automatic cognitive processing when presented with said stimulus (i.e., infant cries) as a form of embodied cognition (Mahon & Caramazza, 2008). Although purely speculative, the observed pattern of activation may demonstrate that spectrotemporal templates of infant cries are stored in the left lateral anterior lobe of the Cerebellum and upon perceiving an infant cry mothers identify & recall the sensory–motor memory of the sound via the Pons and associate it with a more abstract symbol of an infant cry in the Superior Temporal Gyrus. This would account for the pattern of activation seen in the present data with the activation of the Temporal Pole potentially indicating some sensory-emotional information processing related to the recalled infant cry template.

Additionally, the overall response to infant cries for this sample of mothers should be equated to the patterns of activation observed in other mothers that were earlier in the postpartum period. To reiterate, previous research has shown that mothers early in the postpartum period demonstrate activation in brain areas that may indicate a more emotionally arousing response (i.e., Midbrain, Cingulate & Basal Ganglia activity; Swain et al., 2003) whereas later in the postpartum period mothers demonstrate activation that better represents initiation & planning of a parental response (i.e., medial Superior Frontal Gyrus; Swain et al., 2007).This transition indicates the effects of early caregiving experience where mothers initially respond with alarm to the new arousing infant cries but then as they gain repeated exposure to these situations, they learn how to respond appropriately and prepare their motor system accordingly. Interestingly none of these areas are activated in this sample. Tentatively, this could mean that once the child reaches middle childhood and subsequently gains more independence, the stimulus of an infant cry is no longer salient so therefore does not elicit anxiety and no longer requires preparation & planning of a motor response because children do not cry in the same way that infants and toddlers do. So, when mothers of this sample perceive infant cries, they simply activate sensory–motor memories of the cry but do not activate any other cognitive, emotional or executive processes because the stimulus is no longer relevant when their child reaches this stage of development. These results need further replication but if the current data stand to be confirmed it may indicate that different stimuli should be used once mothers reach more advanced stages of motherhood in order to properly evaluate their maternal behavior as they gain more experience and as their children gain more independence.

Regarding the 3rd hypothesis concerning the relationship between neural activations to infant cries and mothers' behavior during a dyadic interaction with their child, the expected activation was not supported. However, there was one significant negative relationship between neural activation in the Superior Temporal Gyrus and the EAS subscale for maternal sensitivity. As a result, the current sample of mothers showed that increased activation to infant cries relative to control sounds was associated with lower scores on maternal sensitivity. However, because the lowest score on maternal sensitivity within our sample was a 4 on a 7-point scale, this indicates that the current set of mothers are grouped on the upper end of this scale. Therefore, moderately sensitive mothers associating with higher levels of activation of the STG may indicate that the overall pattern has a U-shaped distribution. Whether or not moderate levels of maternal sensitivity are therefore optimal would remain in question and would require further study taking into account child behavioral outcomes. But if the STG is responsible for holding the symbolic representation of infant cries for mothers when listening to infant cries then its abstract form may influence or may be influenced by how sensitive mothers are with their children. Importantly, it must be acknowledged that this is the first finding of this relationship and there are very few studies looking at neural activation and maternal behaviors as mentioned in the literature review. Accordingly, not much should be definitively concluded from the finding and interpretation found here and more studies should continue to examine neural activation in reference to observed maternal behaviors to better establish a consensus on what can be expected. Otherwise, no other significant relationships were found between neural activations to infant cries and the other EAS dimensions of maternal behavior so previous findings of this type are not supported here.

Regarding the 4th & 5th hypotheses concerning the relationship between neural activations to cries from unfamiliar infants and behavioral measures looking at levels of parenting stress, as well as, retrospective remembrances of parental care, the expected activation was not supported. In reference to parenting stress, one of the reasons why the current data does not show any significant relationships with neural activations may be because of the characteristics of the sample. The sample of mothers studied here showed parenting stress levels that were below the population median and only 1 mother showed stress levels that were above the 85th percentile cut-off of being critically stressed. It is possible that a sample with mothers that are more representative across the entire spectrum of parenting stress would better elucidate any potential relationship between neural activation to infant cries and parenting stress. In reference to the retrospective remembrances of parental care, it is difficult to make a determination on where the current sample falls relative to others largely as a consequence of the absence of population-level statistics for the PARQ measure. Not only that, but also the construction of the PARQ with three subscales that assess negative remembrances (i.e., hostility, indifference, undifferentiated rejection) and one subscale that assess positive remembrances (i.e., warmth) makes the interpretation of the total PARQ score, which would ideally indicate the overall memory of an accepting or rejecting past relationship, challenging. Better measurement of how current mothers view the totality of their past relationship with their parents as a child to then associate with the neural activations to infant cries may lend more power and subsequently lead to a higher likelihood of any potential more significant relationships being found. On the other hand, even if a significant relationship had been found between neural activation and the PARQ, interpretation and generalization would have proved difficult due to the various measures (e.g., PBI, AAI, PARQ) which are used to evaluate current mothers past experience with their own parents. In order to better understand mechanisms of intergenerational transmission of parenting behaviors, first it would be advantageous to identify the standard measure for assessing the transmission of attachment behaviors before relating it to functional neuroimaging data.

In addition to analysis addressing the hypotheses, additional exploratory analysis was carried out. The first exploration examines the neural activation from infant cries relative to baby laughs, therefore these activated regions are uniquely activated when mothers listen to infant cries while taking into account the activation when listening to baby laughs. Many large clusters of activation were found in the left posterior Occipital lobe (Cuneus, middle Occipital Gyrus, inferior Occipital Gyrus), a cluster was found in the left Supramarginal Gyrus and, finally, multiple clusters were found in the right Cerebellum Crus 1 & 2. With regards to the activation seen in the Occipital Lobe, it may seem contradictory that brain areas classically associated with visual perception are activated during an auditory perception task. However, recent research has recognized the idea of involuntary associative mental imagery where eventual visual images are influenced or triggered by current neural representations and this involuntary imagery involves the corresponding sensory cortices (e.g., primary visual areas shown activated in this study) (Koenig-Robert & Pearson, 2019; Pearson, 2019). Also, the inferior Occipital Gyrus – also referred to as the Fusiform Face Area – has been shown to be selectively tuned to face processing (de Haas et al., 2021). This could potentially lend evidence to the notion that mothers are experiencing non-voluntary associative visual imagery of a face (presumably their child) when listening to infant cries. On top of that, the left Supramarginal Gyrus has been shown to be selectively involved in the retention & maintenance of pitch memory (Schaal et al., 2014; 2017) and similarly, the Cerebellum Crus 1 & 2 have been implicated in encoding and retrieving rhythmic information (Konoike et al., 2012). Therefore, mothers may also be retrieving and maintaining acoustic information related to infant cries from their memory when listening to infant cries. Putting this all together one could speculate that when mothers listen to infant cries, they essentially run a simulation of a past experience with their own child by constructing mental images of their child's face while recalling the acoustic properties of their own infants' cry while listening to the unfamiliar cry stimulus. Moreover, because infant cries are being contrasted with baby laughs, this pattern of neural activation may indicate that infant cries are a potentially more potent stimulus to activate visual mental imagery and recall past interactions with their children instead of baby laughs.

In the second exploratory analysis, neural activations of baby laughs compared to control sounds were examined. When comparing the baby laugh vs control contrast to the infant cry vs control contrast, there are some overlapping regions which can be identified. As previously discussed, the activations in the Superior Temporal Gyrus, Midbrain & Cerebellum may represent the sensory–motor memories of the baby laugh, as well as, the higher-order abstract symbol. Additionally, as discussed in the literature review the activation of the Putamen and pre-Supplementary Motor Area could indicate the initiation of a planned motivated action which could be representative of routine parenting behaviors (Amodio & Frith, 2006; Booth et al., 2007; Grahn & Rowe, 2009; Hove et al., 2013; Provost et al., 2010; Tricomi et al., 2004). Next, activation was seen in the Agranular Retrolimbic Area. Although one study which investigated judgements of visually affected auditory intensity changes significantly implicated the Agranular Retrolimbic Area (Li et al., 2011) which may be applicable to the current context of baby laughs, there is not enough evidence in research to make definitive claims on the functional role of this area in the present study. Lastly, deactivation was observed in the bilateral Fusiform Gyrus, right Frontal Eye Field & right Visuo-Motor Area. It could be interpreted that these areas are involved in visual attentional orientation and recognition but because of the obscure nature of deactivation, understanding the function of these areas within the context of the maternal neural response to baby laughs remains challenging. However, based on the activation observed in the pre-SMA and Putamen when mothers listened to baby laughs compared to control sounds, it may be that when children reach later developmental stages and into middle childhood the baby laugh could be a more proper stimulus to evaluate the quality of maternal caregiving behavior than infant cries due to activation of areas which may be more representative of routine parenting behaviors.

Limitations & Future Research

The findings should be interpreted in relation to the following limitations. First, results in this study risk being underpowered due to a small sample size and generalizability may be limited on account of the characteristics of the sample. As the majority of the literature investigating the neural response to infant cues has been performed on samples of heterosexual mothers, studying the current sample of homosexual mothers without any comparison group makes it difficult to bridge the existing literature with the results identified here. Future studies should examine the neural response to infant cries in a demographically-matched sample of homosexual–adoptive, homosexual–donor insemination, heterosexual–adoptive and heterosexual mothers during early and late stages of the postpartum to identify any differences in caregiving status (i.e., primary or secondary), gender or any effects of the biological status of the child to the mother across motherhood. Additionally, in an attempt to find significant links between levels of parenting stress and mothers' neural response to infant cues, the sample used here was largely ineffective by virtue of parenting stress levels all falling close to or below the population median with very few mothers displaying critically high levels of stress. If a majority of mothers report stress levels within a small range of each other with very few out on the ends of the entire distribution then within the regression analysis where stress is associated with the neural response, the behavioral variable will act as a constant and no significant relationship will be found. Future studies should recruit a sample of mothers that are more representative across all levels of parenting stress to better understand the relationship between stress and neural responses to infant cues.

Second, although the use of unfamiliar infant cries as stimuli aids in bridging the current results to the literature and allowing for some generalization to previous findings in the field, this choice in itself brings complications. As the current sample observes mothers with greater caregiving experience, due to their children being past the preverbal stage of development it may mean that infant cries are not the most appropriate way to assess parenting behaviors at this point in motherhood. The choice of using infant cries as a stimulus to link the current explorations with previous research on neural responses to infant cues is important but it does suggest that future research may want to use new stimuli (e.g., baby laughs) that could better assess parenting behaviors of mothers with children that have surpassed the preverbal stage. Furthermore, it may be beneficial if a future study surveyed mothers with children from childhood up until puberty asking about specific salient behaviors that their children display in order to factor analyze the most prominent child behaviors following the preverbal stage (e.g., tantrums, laughs). Therefore, researchers could construct stimuli to present that would evoke neural responses which could better evaluate a mothers parenting behavior across time.

Third, despite the attempt to explore the transmission of parental behaviors, the use of the PARQ self-report questionnaire may not have provided the appropriate measure to significantly identify patterns between mothers' retrospective remembrance of their relationship with their own parents and their current neural response to infant cues. Two factors contribute to difficulty in contextualizing scores from the PARQ questionnaire; (1) there is no population level data to identify where a given mother may fall relative to others outside of the observed sample, (2) within the sample, comparisons on overall past relationship with mothers or fathers is difficult because total scores are summed containing both positive & negative subscales making the interpretation of the total score difficult to attribute much validity. Future research should focus on identifying questionnaires that can most accurately report mothers' previous relationships with their own parents. Understanding the different mechanisms underlying the transmission of parenting behaviors would be especially informative as a critical point of intervention to address maladaptive parenting practices.

Lastly, there are natural limitations in the fMRI specifications used. For example, the outer reaches of the specified field of view (i.e., the extent of the total three-dimensional observed within the scanner) carry with them increased noise relative to the inner portions, therefore brain areas such as the Cerebellum or Frontal Pole may have more noise than the rest of the brain. Also, fMRI studies do not allow conclusions to be drawn on the sequence of observed activations due to the poor temporal resolution of the technique so none of the above areas deemed to have significant activation should be interpreted in sequential relation to each other. Future studies should also incorporate electrophysiological methods using EEG to assess the temporal aspect of the neural response to better understand which areas activate in what sequence when an infant cry is presented. In combination, fMRI & EEG data can provide information on both the spatial and temporal dynamics of parental brain structures that are involved in responding to infant cues. Finally, all findings from this study are simply associative and no causal inferences should be made based on the results of this study.

Conclusion

Within a greater context investigating caregiving behaviors in emerging modern family structures, the current study examines the neural responses to infant cries as well as baby laughs in lesbian mothers with 3-11 year old children. It was found that infant cries activate brain areas that are associated with both abstract and sensory–motor representations of infant cries, as well as emotion regulation regions which partially supported previous findings in the field. Also, when contrasted with baby laughs, mothers demonstrated a neural response that may represent the simulation of a past experience with their own infant reconstructing it with mental imagery and acoustic properties of their own infants' cry. Therefore, during this stage of motherhood the stimulus of an infant cry may elicit a response more similar to memory recall than a parental behavioral response. Additionally, maternal sensitivity was found to be associated with activation in the Superior Temporal Gyrus showing a negative association where moderate scores on sensitivity correlate with the highest levels of activation which had not been previously found in the literature. Lastly in an exploratory analysis, neural responses to baby laughs were identified for the first time substantiating further research using a more positively valenced stimulus. Much remains to be found with regards to the neural responses in reaction to infant cues of mothers with greater caregiving experience. It may be the case that new stimuli need to be implemented for further investigation into various groups of mothers with children at every stage of childhood development.

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