TOWARD AN UNDERSTANDING OF HUMAN CAREGIVING: INVESTIGATIONS OF BRAIN, AFFECTIVE, AND ATTITUDINAL RESPONSES TO INFANTS AND CHILDREN

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Lay Abstract

The work presented in this thesis adds to literature on human caregiving. In different studies we investigated brain, emotional, and attitudinal responses to human babies and children in people with and without depression as well as in people with different levels of caregiving experience. In the first two studies, we measured brain response to smiling baby pictures in depressed and non-depressed mothers and non-mothers. The amygdala is a brain region that is involved in the neurobiology underlying both depression and maternal behaviour. We found that amygdala response was the highest among mothers with postpartum depression. We also found that the coupled activity of the left and right amygdalae and another brain region called the insula was altered in mothers with postpartum depression. In the third study, we measured facial features of the baby faces presented in the first two studies to develop a measure of cuteness. We also measured emotional responses to the baby faces. We found that cuter infants elicited more positive and less negative emotional responses. In the fourth study, we measured differences in attitudes about children and caregiving between men and women who did and did not own and care for pets—specifically dogs and/or cats. We found that compared to men who did not own and/or care for pets, men who had more experience caring for pets had more positive attitudes about children and childcare.

Abstract

Optimal responsiveness to infant cues, an integral component of parental caregiving, is thought to be determined by multiple factors including maternal mood, previous experiences of caregiving, and infant characteristics. This thesis builds on previous work and details novel investigations of brain, affective, and attitudinal responses to infants/children. In the first two studies, we investigated the effects of maternal mood and parity (previous experiences of caregiving) on brain response to affectively positive infant pictures using functional magnetic resonance imaging (fMRI). We found that mothers with postpartum depression showed an elevated right amygdala response to infant pictures in comparison to mothers without PPD and depressed non-mothers. Further, functional connectivity between the bilateral amygdalae and the right insular cortex was negatively correlated with clinical symptoms (self-reported depression and anxiety). Therefore, as depression and anxiety symptoms increased amygdala to insular cortex connectivity decreases and vice versa. In the third study, we developed a novel data-driven infant cuteness (DDIcute) metric using the infant pictures presented in the first two studies. In line with ethological postulations on cuteness (infant characteristics), we found that infant pictures with a higher DDIcute score were associated with increased positive/approach-related affective responses and decreased negative/avoidant-related affective responses. In the fourth study, we investigated whether the sex differences in attitudes about children and childcare were moderated by pet ownership/care (previous experiences of caregiving). We found that pet ownership and care eliminated sex differences in attitudes about children and childcare. This effect was driven by males; compared to males with low levels of experience caring for pets, males with high levels of experience caring for pets had more positive attitudes about children and childcare.

“Research is what I am doing when I don’t know what I’m doing”

-Werner von Braun

Preface and Authors' Contributions

- **Ms. Aya Dudin:** contributed to the study design, data collection, entry and analyses, and to writing the report for **study 1.** Conceived and designed the study and analyses; collected the data; performed the analysis; wrote the report for **study 2 & 3**. Contributed to the conception design; performed data analyses and wrote the report for **study 4.**

- **Dr. Mayra L. Almanza-Sepúlveda:** contributed to the conception design, data collection and analyses, and to writing the reports for **studies 3 and 4**.

- **Dr. Kathleen E. Wonch**: For **study 1,** conceived and designed the study; collected the data; performed the analysis; wrote the report. For **study 2,** conceived and designed the study; collected the data. For studies 1, 2, and 3, collected infant pictures; edited infant pictures to processed for standardization purposes.

- **Dr. Alison S. Fleming**: For **studies 1, 2, 3, and 4** conceived and designed the study, contributed to the statistical analyses and to writing the papers.

- **Dr. Geoffrey B. Hall**: contributed to the conception, design, analyses, and writing of **studies 1, 2 and 3**; developed the affect rating task used during the fMRI sessions in **studies 1 and 2** (used during the fMRI session to elicit brain response to baby faces). Contributed to discussions on data analyses and interpretation of results of **study 4**.

- **Dr. Jennifer A. Barrett**: contributed to the conception and design of **study 1**.

- **Ms. Cynthia B de Medeiros**: contributed to the conception and design of **study 1**; collected the data for **study 1**.

- **Dr. William A. Cunningham:** contributed data analyses tools and methodologies for **study 1**.

- **Dr. Meir Steiner:** conceived and designed the **studies 1 and 2**; mothers with postpartum depression in the study were being seen and treated by Dr. Steiner.

- **Dr. Andrew D. Davis**: contributed to the data analysis pipeline and data analysis methods and tools for **study 2**.

- **Dr. David R. Feinberg**: contributed data analyses methods and tools, and to the design of **study 3**.

- **Dr. Katherine T. Cost:** contributed to data analysis methods, tools and to the writing of the paper of **study 4.**

- **Dr. Jonathan Freedman:** conceived and designed the study; collected the data; contributed to analyses and discussions on interpretations of results; contributed to writing the paper for **study 4**.

List of Publications Arising from this Thesis

1. **Study 1.** Wonch, K. E., de Medeiros, C. B., Barrett, J. A., Dudin, A., Cunningham, W. A., Hall, G. B., Steiner, M., Fleming, A. S. (2016). Postpartum depression and brain response to infants: Differential amygdala response and connectivity. *Social neuroscience*, *11*(6), 600-617. DOI: 10.1080/17470919.2015.1131193
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3. **Study 3.** Almanza-Sepúlveda, M. L., Dudin, A., Wonch, K. E., Steiner, M., Feinberg, D. R., Fleming, A. S., & Hall, G. B. (2018). Exploring the morphological and emotional correlates of infant cuteness. *Infant Behavior and Development*, *53*, 90-100. https://doi.org/10.1016/j.infbeh.2018.08.001
4. **Study 4.** Dudin, A., Almanza-Sepúlveda, M. L., Cost, K. T., Hall, G. B., Fleming, A. S., Freedman, J. (2022). Interactions between sex and pet ownership on attitudes toward children. *People and Animals: The International Journal of Research and Practice, 5(1),* Article 7. Available at: https://docs.lib.purdue.edu/paij/vol5/iss1/7

The data presented in studies 1 and 2 were collected from the same study; data collection started on April 28, 2011 (upon receiving consent from the first participant) and ended on August 27, 2013 (upon final participant's exist). The pictures of infants used to explore the morphological and emotional correlates of infant cuteness in study 3 were collected from the aforementioned study. Subjective cuteness and emotional rating data for study 3 were collected from Feb-March, 2017. Data for study 4 were collected (including information on pet ownership, extent of pet care, and attitudes about children and childcare) from May-June, 2013.

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Chapter 1

General Introduction

1.1 Overview

It may appear that human infants are born helpless. However, infants are equipped with 'potent protective mechanisms' that greatly aid in their survival and development. Given that human infants are born without the ability to care for themselves, most of these protective mechanisms are geared to attract and sustain the attention of their caregiver (Kringelbach, Stark, Alexander, Bornstein, & Stein, 2016). Before the development of language, infants and children communicate their needs and internal states via auditory and facial expressions including cries, laughter, smiles, and cooing (Hrdy, 2009). Maternal sensitivity includes appropriate and contingent responsiveness to infant cues—a marker of optimal and high-quality caregiving (Ainsworth & Wittig, 1969; Mesman & Emmen, 2013; Moss et al., 2011). Responding to those cues is the infant's primary caregiver—usually, but not necessarily, the mother. Optimal responsiveness to infant cues is affected by multiple factors including maternal mood, previous experiences of caregiving, and infant characteristics (Barrett & Fleming, 2011; Belsky, 1984). This is an area of ongoing research. The studies presented in this thesis add to the literature by investigating responsiveness to infant cues as a function of several factors including depression (maternal mood), maternal status (experiences of caregiving), infant cuteness (properties of the infant), and interactions between sex and pet ownership (experiences of caregiving). In different studies, we evaluated human brain, affective, and attitudinal responses to human infants and children. In chapter 2, we investigated brain (amygdala) response and connectivity as well as affective responsiveness to positive pictures of infant faces comparing mothers with and without postpartum depression (PPD). In chapter 3, we investigated brain (amygdala) and affective responsiveness to positive pictures of infant faces as a function of depression and maternal status; comparing depressed and non-depressed mothers and non-mothers. In chapter 4, we investigated the morphological and emotional correlates of infant cuteness and developed a novel data-driven metric of infant cuteness. In chapter 5, we investigated whether sex differences in attitudes toward children and caregiving were moderated by pet ownership and lifetime experiences of pet care.

1.2 Belsky's model: determinants of parenting

Beyond the survival of an infant, optimal human parenting is defined by the ability to produce competent offspring. In 1984, psychologist Jay Belsky proposed an integrated model of the complex and dynamic processes involved in the parenting system. Belsky proposed three major domains that can influence the quality of parenting that the child receives: (1) the personal and psychological resources of the parent, (2) the characteristics of the child, and (3) the contextual sources of stress and support. The weight by which each subsystem influences the quality of the parenting is not equal. Belsky postulated that the personal and psychological resources of the parent is the most influential subsystem, followed by the contextual sources of stress and support, and finally the least influential subsystem is the characteristics of the child. Personal and psychological resources of the parent are proposed to be influenced by the parent's own developmental history. There is also a proposed bidirectional relationship between the parent's personal/psychological resources and environmental sources of stress and support including the: marital relationship, social support network, and work/employment. For instance, social support networks have a protective influence on the parent's psychological well-being and in turn a parent's personality and psychological well-being influences their ability to build and mobilize social support networks when needed. Therefore, each node in this complex and dynamic system is postulated to add a degree of protective and/or stressful influence onto the parenting system (Belsky, 1984).

1.3 Brain response to infants: healthy mothers

1.3.1 Non-human mammals. Most of the knowledge on the neurobiology underlying maternal behaviour as well as the neuroplasticity that accompanies the transition to motherhood has been gathered using non-human mammalian models. In the non-human mammalian literature, it is well established that the sensory cues of young offspring (including olfactory and auditory cues) are particularly salient (i.e., attracting notice or attention and thus relevant) to the mother (Lonstein, Levy, & Fleming, 2015; Numan, 2020; Numan, Fleming, & Levy, 2006; Numan & Insel, 2003). Hormonal changes during pregnancy and parturition prime neural brain circuits for approach-related behaviours toward rat pups instead of the avoidant or aggressive behaviours displayed by virgin female rats. After hormonal fluctuations return to pre-gestational levels, it is the mother's ongoing experience and constant interfacing with her young offspring (and therefore their cues) that contributes to the maintenance of the neural pathways underlying maternal behaviour. Most work in the area has focused on the final common path for the expression of maternal behaviour, which includes the hypothalamic medial preoptic area (MPOA) and its downstream projections into the midbrain ventral tegmental area (VTA) and hindbrain (periaqueductal gray) as well as sensory, limbic (amygdala and striatal regions), and cortical systems that project into the MPOA. The MPOA contains receptors for all the hormones involved in the activation of maternal behaviours (Numan, 2020; Numan & Insel, 2003). The neurons projecting to and from the MPOA are situated in brain regions associated with several psychological processes including: affect (projections from amygdala, anterior cingulate cortex (ACC)), reward and motivation (VTA, projections from ventral striatum (vST) including the nucleus accumbens (NAc)), and attention (vST, medial prefrontal cortex (mPFC)). Some of these brain regions (amygdala, mPFC) also contain hormone receptors (e.g., estrogen, progesterone, oxytocin) and are likely the regions where hormones of birth act to change behaviour at the time of parturition (Numan, 2020; Numan & Insel, 2003). As aforementioned, this understanding of the complex neurobiology of maternal behaviour is based predominantly on work done in non-humans mammals including: rodents, voles, rabbits, sheep, and non-human primates (Lonstein et al., 2015; Numan, 2020; Numan et al., 2006; Numan & Insel, 2003). This has been the impetus to the growing literature on investigations of the human maternal brain. Thus far, evidence points to largely conserved neural underpinnings of maternal behaviour across mammalian species—including human mammals (Lonstein et al., 2015; Numan, 2020; Numan et al., 2006).

1.3.2 Human mammals. A human mother's response to her infant's cues requires an orchestration of several neural circuits involved in processing affective and cognitive information to help her choose an appropriate behavioural response in the face of competing internal, external, and infant related demands (George & Solomon, 1999; Shafritz, Collins, & Blumberg, 2006; Solomon & George, 1996).

Non-invasive brain imaging techniques have made it possible to study the neurobiology underlying human maternal behaviour. This is mostly done by investigating brain responsiveness to sensory infant cues using *in vivo* neuroimaging technologies. The knowledge presented here stems from studies using functional magnetic resonance imaging (fMRI) (Paul et al., 2019; Swain, 2011). During the fMRI scans, mothers were presented with infant stimuli (own and/or unfamiliar infant) such as infant pictures (Bartels & Zeki, 2004; Leibenluft, Gobbini, Harrison, & Haxby, 2004; Nitschke et al., 2004; Strathearn, Li, Fonagy, & Montague, 2008), recorded infant distress cries (Kim et al., 2011, 2010; Musser, Kaiser-Laurent, & Ablow, 2012; Swain et al., 2008), and videotapes of interactions with infants (Noriuchi, Kikuchi, & Senoo, 2008; Ranote et al., 2004). Most studies converge on the involvement of hypothalamic, subcortical (including limbic such as amygdala and striatal regions), and cortical regions in the maternal response to infant cues. These regions are implicated in motivation and reward (striatal and limbic structures), emotion regulation (limbic, paralimbic, and cortical structures), social (face) processing, executive function such as inhibitory control and attention (medial prefrontal cortex (mPFC)), as well as empathy (cortical: insular cortex (IC), orbitofrontal cortex (OFC)) (Kim, Strathearn, & Swain, 2016; Lonstein et al., 2015; Noll, Mayes, & Rutherford, 2012; Numan, 2020; Paul et al., 2019). Importantly, similar regions were found to be involved in the maternal neural circuitry in non-human mammals (Lonstein et al., 2015).

1.4 Brain responses to infants: depressed mothers

1.4.1 Overview. The pathophysiological mechanisms underlying postpartum depression (PPD) are not well understood (Payne & Maguire, 2019). Non-invasive neuroimaging methodologies hold the promise to elucidate the neurobiology underlying postpartum depression (Fiorelli et al., 2015; Moses-Kolko, Horner, Phillips, Hipwell, & Swain, 2014). Neuroimaging methods also hold the promise to develop biologically-based diagnostic tools such as biomarkers for early detection and intervention of psychopathological conditions including postpartum depression (Moses-Kolko et al., 2014). The published studies presented in chapters 2 and 3 contribute to these efforts using fMRI. The amygdala is a brain region that is implicated in both the maternal neural network (Kim et al., 2016; Lonstein et al., 2015; Swain, 2011) as well as the affective (depression) neural network (Jaworska, Yang, Knott, & Macqueen, 2015; Price & Drevets, 2010) (see Amygdala subsection below). As such, we specifically investigated amygdala responsiveness and connectivity to positive infant pictures of varying familiarity in mothers with clinically determined PPD compared to mothers without PPD (Non-PPD) (Chapter 2). Further, in an effort to identify the specificity of the PPD neural response to infant pictures, we investigated amygdala responsiveness to positive infant pictures as a function of depression and maternal status by comparing four groups of women: mothers with and without postpartum depression (PPD, Non-PPD) and non-mothers with and without depression (MDD, Non-MDD) (Chapter 3). In this section, I provide a clinical overview of PPD, describe the need for a biomarker, and review fMRI studies investigating PPD.

1.4.2 Clinical overview of postpartum depression. Postpartum depression (PPD) is a mental health condition that is recognized as the most common maternal birth complication (Howard et al., 2014; Ross, Dennis, Blackmore, & Stewart, 2005). The prevalence of PPD ranges from 13 to 20% (Carothers & Murray, 1990; Cooper &

Murray, 1995; Cox, Connor, & Kendell, 1982; Horowitz & Goodman, 2004; Marcus, 2009; Moses-Kolko & Roth, 2004; O'Hara & McCabe, 2013). PPD is characterized by the same symptoms that occur during a major depressive episode (MDE) outside the postpartum period. Characterization of a major depressive episode includes depressed mood and/or anhedonia lasting for two or more consecutive weeks, as well as some combination of sleep or eating disturbances, restlessness or agitation, lack of energy, inability to concentrate, and feelings of hopelessness, worthlessness and guilt experiences (American Psychiatric Association, 2013; Cox, Murray, & Chapman, 1993; Dennis, Heaman, & Vigod, 2012; O'Hara & McCabe, 2013). Psychological, social, and environmental risk factors of PPD are similar to those of major depressive disorder (MDD) or depression occurring outside of the postpartum period (O'Hara & McCabe, 2013). Risk factors include having a history of MDD or PDD, low social support during the postpartum period, recent stressful life events, inter-marital conflict, a history of interpersonal violence, poor perceived maternal health, low self-esteem, and neuroticism (Dennis et al., 2012; Milgrom et al., 2008; O'Hara & McCabe, 2013; O'Hara & Swain, 1996).

Despite similarities with MDD, PPD is differentiated by timing of onset during the peripartum period (i.e., prior to, during, and after giving birth). Further, many of PPD symptoms occur in the context of the mother-infant dyad including excessive worry and/or guilt surrounding parenting abilities (American Psychiatric Association, 2000, 2013; Beck, 2001; Cox et al., 1993; Dennis et al., 2012; O'Hara & McCabe, 2013; Ross, Dennis et al., 2005). Compared to MDD, PPD presents greater comorbidity with anxiety (Altshuler, Hendrick, & Cohen, 2000), and for a subtype is associated with a greater risk of converting to bipolar disorder if PPD symptoms start within 1-14 days postpartum (Munk-Olsen, Laursen, Pedersen, Mors, & Mortensen, 2006). Evidence from an experimental study suggests that a sensitivity to hormonal fluctuations in a subset of women may be responsible for differences between women who develop depression for the first time during the postpartum period compared to women with a history of depression outside the peripartum period who go on to develop PPD (Bloch et al., 2000; Payne & Maguire, 2019). An epidemiological study found that approximately 40% of women will develop their first depressive episode during the postpartum period (Wisner et al., 2013). Despite phenotypic and pathophysiological differences between PPD and MDD (Batt, Duffy, Novick, Metcalf, & Epperson, 2020; Brummelte & Galea, 2016), the Diagnostic and Statistical Manual of Mental Disorders-5 does not classify PPD as an independent condition separate from MDD (American Psychiatric Association, 2013). Rather, the patient must meet criteria of a MDE with "peripartum onset" as a classifier (American Psychiatric Association, 2013).

1.4.3 Need for a biomarker. PPD affects the mother's ability to bond with her infant (Badr, 2005) and impairs sensitive parenting (Field, Diego, & Hernandez-Reif, 2006). In turn, the condition has a pervasive impact on the developing infant (Goodman et al., 2011; Kumar & Robson, 1984) at a time when they are most vulnerable (Field, Diego, & Hernandez-Reif, 2009; Field et al., 2007, 2000). Beyond the mother-infant dyad, PPD affects the entire family unit (O'Hara & McCabe, 2013). Despite its widespread impact, PPD is an understudied, underdiagnosed, and undertreated mental health condition. This is, in part, due to the heterogeneity of the condition (Kettunen, Koistinen, & Hintikka, 2014; Putnam et al., 2015, 2017). This poses a challenge to studying, screening, and diagnosing PPD. Several studies outline the inadequacy of the current syndromic characterization of PPD at detecting biological-based heterogeneity and thus highlight the need for a psychobiological characterization (Batt et al., 2020; Pawluski, Swain, & Lonstein, 2021; Payne & Maguire, 2019; Putnam et al., 2017; Silverman et al., 2011, 2007). Understanding the neural correlates of PPD using neuroimaging tools, such as fMRI, holds the promise of developing a biologically targeted diagnostic and treatment plan that is more sensitive to the heterogeneity of mental health conditions compared to the current syndromic characterization.

The studies presented in chapters 2 and 3 contribute to these efforts using fMRI. The study presented in chapter 2 investigated the amygdala response and connectivity while mothers (with and without PPD) viewed pictures of their own and an unfamiliar infant. The study presented in chapter 3 investigated the amygdala response to positive infant pictures comparing four groups of women, mothers with and without PPD and non-mothers with and without MDD.

1.4.4 In search of a neural signature for PPD. Compared to the more extensive literature on the neural correlates of MDD (Jaworska et al., 2015; Price & Drevets, 2010), there is a dearth of research on the neural correlates of postpartum depression (PPD). At the time of collecting the data for studies 1 and 2 (presented in chapters 2 and 3), there were 8 fMRI studies on PPD (Fiorelli et al., 2015; Moses-Kolko et al., 2014). Most studies investigated the PPD neural response to emotionally provocative negative non-infant stimuli. In general, they found dysregulations in fronto-limbic-striatal regions in mothers with PPD compared to mothers without PPD (Non-PPD). In this section, I present a detailed review of the aforementioned studies.

Silverman and colleagues (Silverman et al., 2007) evaluated the neural response to emotional words in mothers with and without clinically determined PPD at approximately 2 months postpartum. Using a functional region of interest approach, they found differential responsiveness to emotional words in front-limbic-striatal (orbitofrontal cortex (OFC), insular cortex (IC), amygdala, striatum) regions as a function of depression status in mothers in the early postpartum period. Compared to the Non-PPD group, mothers with PPD showed a decreased response to negative emotional words in the right amygdala (limbic region) and the bilateral posterior OFC (frontal region). Also, in response to negative emotional words, the PPD group showed increased response in the bilateral insula compared to Non-PPD. In response to positive emotional words, the PPD group showed decreased response in striatal regions compared to Non-PPD. This is similar to studies showing a hypoactive striatal response to positive stimuli in MDD compared to non-depressed participants (Epstein et al., 2006; Lawrence et al., 2004). Striatal regions are implicated in processing motivational and rewarding stimuli (Bhanji & Delgado, 2014; Cox & Witten, 2019). However, the hypoactive amygdala response to negative emotional words observed in the PPD is in contrast to the hyperactive amygdala response typically observed in MDD (depression occurring outside the peripartum period) (Jaworska et al., 2015). These results suggest that despite syndromic similarities between MDD and PPD, the neural signature of PPD may be unique compared to depression occurring outside of the peripartum period. Specifically, amygdala hyporesponsiveness may be pathognomonic of PPD. Therefore, Silverman and colleagues investigated PPD-specific amygdala responsiveness to negative emotional words in a follow-up study using an anatomical region of interest approach. Similar to the results of the previous study, Silverman and colleagues (2011) found decreased right amygdala responsiveness to negative emotional words (threatening-neutral words) in PPD compared to Non-PDD. Further, this amygdala response was negatively associated with depression symptom severity measured using the Edinburgh Postnatal Depression Scale (EPDS) (Cox, Holden, & Sagovsky, 1987); as depression scores increased the amygdala response decreased. Overall, these results show a blunted fronto-limbic-striatal response to emotional words in PPD and point to the potential importance of amygdala hypoactivity as a neural signature specific to PPD.

Moses-Kolko and colleagues (2010) evaluated the PPD neural response to pictures of adult faces expressing negative emotions (fear and anger) comparing mothers with and without clinically determined PPD at 1-3 months postpartum. They used an anatomical region of interest approach to investigate neural response to emotional adult faces in the dorsomedial prefrontal cortex (dmPFC) and the amygdala. They found that compared to Non-PPD, mothers with PPD showed a decreased response to adult faces (negative facial expression-shapes) in the dmPFC. Although there were no group differences in amygdala response to the emotional adult faces, left amygdala response to the emotional faces was negatively associated with symptom severity assessed by EPDS and the right amygdala response to the emotional faces was positively associated with the absence of infant related hostility. In other words, more severe depression symptoms and more self-reported hostility towards the infant were associated with decreased amygdala (left and right, respectively) response to emotional adult faces. These results corroborate the findings by Silverman and colleagues showing decreased amygdala response to negative emotional words in PPD (Silverman et al., 2011, 2007). Moses-Kolko and colleagues (2010) also investigated functional connectivity—using a measure of effective connectivity called granger causality —and found that in response to faces dmPFC response preceded left amygdala response in the non-depressed mothers but not in mothers with PPD. These results show a blunted PPD neural response to emotional faces in the dmPFC and the amygdala as well as a reduced functional connectivity between those regions in PPD relative to the Non-PPD group. A subsequent study by Moses-Kolko et al (2011) specifically investigated the ventral striatal response during a monetary reward paradigm in PPD at 1-3 months postpartum. Mothers were asked to guess the number of a hidden card, guessing correctly or incorrectly results in monetary gains or losses, respectively. The gains and losses can be low, medium, or high. They found that compared to the Non-PPD group, the ventral striatum response to the high reward (monetary gain) showed a faster rate of decay in the PPD group. They also found that the ventral striatal response to reward was negatively correlated with depression symptom severity (assessed by EPDS); as depression severity increases the ventral striatal response to reward decreases. These results also corroborated findings from Silverman and colleagues (Silverman et al., 2007) showing blunted striatal response to positive words in PPD relative to Non-PPD.

Given that PPD occurs within the context of transitioning into motherhood along with interactions with the infant, it is important to consider the neural response to infant cues. Laurent and Ablow (2012, 2013) were the first to investigate the neural response to infant cues in mothers with and without PPD at 15-18 months postpartum—notably later in the postpartum period relative to previous studies. Depression status was determined by history of a major depressive episode (MDE) during their most recent pregnancy or postpartum period. Further, current depression symptomatology was assessed by using a self-report measure (Center for Epidemiologic Symptoms Depression (CES-D) scale (Radloff, 1977)). In their first study, Laurent and Ablow (2012) investigated the neural response of mothers to their own infant's recorded distress cries compared to recorded distress cries of an unfamiliar infant. In their second study and using the same group of women, they investigated the neural response to pictures of their own and an unfamiliar infant's face displaying either joy or distress (Laurent & Ablow, 2013). Overall, the PPD group showed a blunted neural response to infant cues in cortical and subcortical structures associated with the maternal neural network as well as the affective neural network. In response to own infant distress cries, mothers in the PPD group showed a blunted response in subcortical striatum regions (caudate and NAc) and the medial thalamus compared to mothers in the Non-PPD group. Similarly, in response to own infant cries contrasted to an unfamiliar infant's cries, mothers in the PPD group showed a blunted response in the occipital fusiform and the lingual gyrus compared to mothers in the Non-PPD group. With regard to current depression symptomology, they found that the neural response to own infant cries (percent signal change) was negatively correlated with depression symptom severity in the dorsal ACC, left OFC, medial superior frontal gyrus (SFG), left ventral striatum; higher depressive symptoms were associated with lower responsiveness to own infant cry sounds in those regions (Laurent & Ablow, 2012). Results were similar for the response to visual infant cues. Compared to the Non-PPD group, the PPD group showed a blunted left dorsal ACC response to pictures of infants in distress (own vs unfamiliar infant in distress) (Laurent & Ablow, 2013). Further, current depression symptom severity was negatively associated with neural response to joyful pictures of infants (own-unfamiliar joyful infant faces) in the right insula and the left OFC; greater depression symptoms were associated with a decreased response to joyful infant faces in those regions. In response to mothers' own infant's joyful versus distressed face, Laurent & Ablow (2013) found a negative association between current depression symptomology and the activation of the dorsal ACC, left-putamen, and insula. Taken together, these results suggest that the aberrant PPD neural response to auditory and visual infant cues is a blunted neural response in cortical and subcortical structures implicated in affect regulation and the maternal neural circuit. They also suggest that these PPD-related neural differences are present beyond the peak of symptom severity/time of diagnosis as data was collected at 15-18 months postpartum and with many participants reporting subclinical depressive symptoms.

In addition to studies that investigated fMRI-brain response to sensory stimuli, some studies investigated the fMRI-brain response at rest. During these paradigms, participants are instructed to lay in the MRI scanner and to not think about anything in particular while staring at a fixation cross. These studies evaluate resting-state functional connectivity (RSFC) comparing mothers with and without PPD. Overall, such studies have found *decreased* RSFC between fronto-limbic regions in PPD compared to Non-PPD. Deligiannidis and colleagues (2013) investigated RSFC in mothers with and without PPD at 2 months postpartum or less. They that compared to non-depressed mothers, mothers with PPD showed a decreased RSFC between the bilateral amygdalae and the ACC as well as between the bilateral amygdalae the dorsolateral prefrontal cortex (DLPFC)—an area that is implicated in the circuitry underlying MDD and important for emotional regulation. This inverse pattern of activity between the amygdala and DLPFC is consistent with what has been observed in depression outside the postpartum period (Disner, Beevers, Haigh, & Beck, 2011; Moreno-Ortega et al., 2019; Seminowicz et al., 2004). Similarly, Chase and colleagues (2014) investigated RSFC in mothers with and without PPD at 3 months postpartum or less. Curiously, they found that mothers with PPD showed a decreased RSFC between the right amygdala and the posterior cingulate cortex (PCC). The PCC is part of the default mode network (DMN)—an intrinsic functional network that has been shown to be active (i.e., increased metabolic activity) at rest (Raichle et al., 2001). This inverse amygdala to PCC RSFC pattern is not typically observed in depression occurring outside the postpartum period (reviewed by Wang, Hermens, Hickie, & Lagopoulos, 2012) and so this may be pathognomonic of PPD.

1.5 Amygdala: a brain region implicated in both the maternal and depression neural networks

1.5.1 Overview. The amygdala is an almond-shaped collection of subcortical nuclei located in the medial temporal lobe. There are two amygdalae—located in the right and left cerebral hemispheres (Blumenfeld, 2010). Broadly, the human amygdala can be divided into three nuclei each with its own afferent and efferent connections: the basolateral, centromedial and superficial amygdala (Amunts et al., 2005). Classically, the amygdala is well known as a brain region that is central to the neural circuitry underlying the conditioned fear response. This is well-established as evident from experimental studies in non-human mammals, studies in patients with brain lesions, as well as fMRI studies in humans (Davis, 1992; LeDoux, 1992; Phelps & LeDoux, 2005; Rogan, Staubli, & LeDoux, 1997). However, the amygdala's role in emotional processing is not limited to the fear response; the amygdala has been shown to be responsive to a wide range of affective stimuli including affectively positive and rewarding stimuli such as in response to winning (Zalla et al., 2000), listening to positively valenced words (Hamann & Mao, 2002), and viewing smiling faces (Breiter et al., 1996; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002; Hamann, Ely, Hoffman, & Kilts, 2002; Lane, Reiman, Ahern, Schwartz, & Davidson, 1997; Liberzon, Phan, Decker, & Taylor, 2003). More recent evidence points to amygdala's sensitivity to stimuli that are socially, emotionally, and motivationally relevant and thus salient to the individual (Adolphs, 2003; Cunningham & Brosch, 2012; Pessoa, 2010; Sander, Grafman, & Zalla, 2003). Given that infants are socially, emotionally, and motivationally relevant to mothers in particular, and women in general (Kringelbach et al., 2016; Thompson-Booth et al., 2014), it not surprising that the amygdala is a brain region implicated in the neurobiology underlying maternal behaviour (Lonstein et al., 2015). Furthermore, given that a depressed state involves a shift in what an individual finds emotionally and motivationally salient, it is also not surprising that the amygdala is implicated in neural networks underlying affective/emotional regulation (Jaworska et al., 2015; Price & Drevets, 2010).

1.5.2 Healthy Mothers. Experimental studies in rodents have shown that the amygdala is central to the expression of maternal behaviour/mothering (Fleming, Miceli, & Moretto, 1983; Fleming, Vaccarino, & Luebke, 1980; Numan, Numan, & English, 1993). The amygdala's role is conceptualized as regulatory for the final and crucial common neural pathway for the expression of mothering to occur. The pathway includes cells from the hypothalamic medial preoptic area (MPOA) and the adjacent basal forebrain's bed nucleus of the stria terminalis (BNST). While the *medial* amygdala plays an inhibitory role, the *basolateral* amygdala plays an excitatory role in the expression of maternal behaviour. For instance, inactivation of the *medial* amygdala by chemical or physical lesions in virgin nulliparous female rats—typically neophobic and respond to pups with either avoidance or aggression—results in lack of aggression, approach-related behaviours and eventual maternal behaviour towards the pups (Fleming et al., 1983, 1980; Lonstein et al., 2015; Numan et al., 1993). This inactivation of the *medial* amygdala in nulliparous female rats results in the disinhibition of downstream circuits (i.e., the MPOA and BNST) and thus the expression of maternal behaviour. Further, electrical stimulation of the same region (i.e., medial amygdala) in rat dams (i.e., mothers) has been shown to result in the inhibition of mothering (Morgan, Watchus, Milgram, & Fleming, 1999). In contrast, inactivation of the *basolateral* amygdala in rat dams has been shown to impair maternal behaviour (Lee, Li, Watchus, & Fleming, 1999; Lee, Clancy, & Fleming, 1999; reviewed by Lonstein et al., 2015; Martel, Nishi, & Shumyatsky, 2008; Numan et al., 2010).

In humans, amygdala volume may also be an important area undergoing structural changes across the postpartum period. Although the neuroplasticity of the human maternal brain is not well understood and is limited to a few studies showing mixed results (Duarte-guterman, Leuner, & Galea, 2019), a prospective longitudinal study found increased gray matter volume in the amygdala at 4 months postpartum compared to 1 month postpartum (Kim et al., 2010). Functionally, infant-related amygdala response is greater to own infant cues compared to unfamiliar infant cues of various sensory modalities. For instance, a human mother's amygdala has been shown to be preferentially responsive to: own vs unfamiliar infant distress auditory cues (i.e., cries) (Hipwell, Guo, Phillips, Swain, & Moses-Kolko, 2015; Kim et al., 2011; Olsavsky, Stoddard, Erhart, Tribble, & Kim, 2021b; Swain et al., 2008), to own vs unfamiliar positive infant pictures (e.g., smiling faces) (Barrett et al., 2012; Leibenluft et al., 2004; Strathearn et al., 2008), to own vs unfamiliar negative infant pictures (e.g., crying faces) (Strathearn & Kim, 2013), and to videos of own vs unfamiliar infant (Ranote et al., 2004). Further, research by our group found that infant-related amygdala activity is positively related to greater reported maternal attachment towards the infant, and is negatively associated with parental distress and subclinical anxiety levels in a community sample of healthy mothers (Barrett et al., 2012). Regarding functional neuroplasticity, some fMRI studies showed a maternal-experience-dependent brain response to infant vocal cues (vs adult vocal cues) in mothers. For instance, Seifritz and colleagues (2003) found an interaction between maternal status and the valence of an infant's auditory cues. Compared to non-mothers, mothers had a greater amygdala response to infant cries, but a lower amygdala response to infant laughter (Seifritz et al., 2003). Parsons and colleagues (2017) investigated the association between the duration of motherhood and brain response to infant vocal cues compared to adult vocal cues in primiparous mothers. They found an experience-dependent response in several brain region. Specifically, greater maternal experience (assessed via age of infant) was associated with a greater blood oxygen level-dependent (BOLD) response in the left OFC and left amygdala in response to infant vocal cues (Parsons et al., 2017). Taken together, these findings suggest that the amygdala is an important brain region associated with maternal mood, the quality of mothering, individual differences in the motivation to mother, and the duration of motherhood.

1.5.3 Depression. Neuroimaging studies of MDD (outside the peripartum period) show aberrant structural and functional measures of the amygdala in depressed participants compared to healthy controls. Structurally, meta-analyses of voxel-based morphometry studies consistently show reduced gray matter volumes in unmedicated depressed patients relative to healthy controls (Gray, Müller, Eickhoff, & Fox, 2020; Hamilton, Siemer, & Gotlib, 2008). This has been shown to be reversed after treatment with a selective serotonin reuptake inhibitor (SSRI) antidepressant (Hamilton et al., 2008). This suggests that changes in amygdala volume are important in the pathophysiology underlying depression. Functionally, the amygdala consistently shows hyperactivity to emotionally negative stimuli in MDD relative to controls (e.g., Suslow et al., 2010; Victor et al., 2012). This hyperactivity has also been shown to be normalized after treatment with either an SSRI or cognitive behavioural therapy (CBT) (reviewed by Jaworska et al., 2015). In contrast to amygdala hyperresponsivity to emotionally negative stimuli in MDD, mothers with PPD show hypo-responsivity to emotionally negative stimuli (Moses-Kolko et al., 2010; Silverman et al., 2011, 2007). This suggests that amygdala hypo-responsivity may be pathognomonic of PPD. More recently, there has been a shift in the understanding of the neurobiology underlying mood disorders from a focus on single brain regions to understanding brain networks. Evidence points towards disruptions in fronto-limbic-striatal pathways in emotion regulation (Mayberg et al., 1999; Seminowicz et al., 2004). For example, women with MDD showed decreased functional connectivity between the amygdala and ACC while viewing emotional positive faces (Thomas et al., 2011; Almeida et al., 2011). Further, as previously mentioned (see subsection: In search of a neural signature for PPD), studies found decreased RSFC between the amygdala and other frontal brain regions in PPD compared to mothers without PPD (Chase et al., 2014; Deligiannidis et al., 2013).

Taken together, these findings demonstrate the role of the amygdala response and connectivity in depression both within and outside the postpartum period.

Study 1 (Chapter 2) Specific aims. To examine using fMRI: 1) the amygdala response to affectively positive infant pictures of varying familiarity and to positive non-infant pictures; 2) functional connectivity using the amygdalae as seeds of interest during the viewing of positive infant and positive non-infant pictures comparing mothers with and without clinically determined postpartum depression (PPD). **Hypotheses and predictions.** Given the amygdala's role in processing emotionally, socially, and motivationally salient stimuli, we predict that mothers' amygdala responds preferentially to positive pictures of their own infant compared to unfamiliar infant and positive non-infant pictures. Given the generally hyporesponsive amygdala in PPD, we predict a blunted amygdala response to positive infant and non-infant pictures in the PPD compared to the Non-PPD group. We expect a differential pattern of task-modulated functional connectivity along the cortico-limbic pathway while viewing pictures of infant and non-infants comparing mothers with and without PPD.

Study 2 (Chapter 3) Specific Aims. To examine the neural amygdala response (using fMRI) and the subjective affective response to positive infant and non-infant pictures (scenery) as a function of maternal status and depression status in a 2x2 design. This is the first direct fMRI investigation comparing depressed mothers and non-mothers (PPD vs MDD). **Hypotheses and predictions.** In line with the salience hypothesis, we predicted that compared to non-mothers, mothers will have a greater amygdala and subjective affective response to positive pictures of an unfamiliar infant. It is not clear whether comparing depressed mothers and non-mothers (PPD vs MDD) would result in a similar pattern of amygdala response as this is the first study to directly compare those two groups. Given the established negativity bias in depressed populations, we predict that decreased subjective affective positivity ratings across conditions when comparing depressed to non-depressed participants.

1.6 Infant cuteness

Human infants are biologically, socially, emotionally, and motivationally salient (i.e., relevant) stimuli to their own mother and to adult humans in general (Kringelbach et al., 2016). Compared to adult faces, infant faces are perceived as cute (Brosch, Sander, & Scherer, 2007; Parsons, Young, Kumari, Stein, & Kringelbach,

2011) and elicit fast brain responses (Kringelbach et al., 2008, 2016; Parsons et al., 2013). Ethologists such as Konrad Lorenz were the first to describe a set of infantile features shared by the majority of young mammals (and some birds) that are perceived as cute. Lorenz used the term "kindchenschema" or baby schema to refer to these infantile features which include a round head, protruding forehead, large eyes that are set relatively low in the face, and round protruding cheeks. Lorenz also posited that baby schema/cuteness is evolutionarily advantageous as it elicits caregiving behaviour by increasing approach-related and nurturant behaviours while also suppressing avoidance-related and/or aggressive behaviours from an adult (Lorenz, 1943). Therefore, infant cuteness has been described as a 'potent protective mechanism' that greatly aids the infant's chances of survival (Kringelbach et al., 2016). Recent empirical studies demonstrate that the attentional bias to baby schema/cuteness generalizes beyond human infants to include adults with neotenous features (Zebrowitz, 2003; Zebrowitz, Luevano, Bronstad, & Aharon, 2009), other animals (Lehmann, Huis in't Veld, & Vingerhoets, 2013) including pets such as cats and dogs (Borgi & Cirulli, 2016; Golle, Probst, Mast, & Lobmaier, 2015; Parsons, Young, Parsons, et al., 2011), and inanimate objects such as cartoon characters (e.g., Mickey Mouse as described by Gould, 1979), plush toys (e.g., Teddy Bear as described by Morris, Reddy, & Bunting, 1995), and other products (Miesler, Leder, & Herrmann, 2011). Also, while perceptions of adult attractiveness are influenced by the ethnicity of the rater and ratee (i.e., adult faces), perceptions of infant cuteness are agnostic to the ethnicity of both rater and the ratee (i.e., infant faces) (Esposito et al., 2014; Golle et al., 2015). Cuteness, therefore, is universal and transcends ethnic/cultural boundaries (Kringelbach et al., 2016).

Infants vary on the cuteness dimension. In line with ethological observations and ideas, recent behavioural studies show that cuter (vs less cute infants) are attentionally and motivationally salient. For instance, adults favor looking at cuter infants (vs less cute infants) (Glocker, Langleben, Ruparel, Loughead, Gur, et al., 2009; Hildebrandt & Fitzgerald, 1978) regardless of their parental status (Senese et al., 2013). Similar to adults, infants and children also favor looking at cuter infants and rate them as more attractive (Borgi & Cirulli, 2016; Van Duuren, Kendell-Scott, & Stark, 2003). Adding on, cuteness elicits action. For example, participants were more likely to give toys and adopt cuter infants (vs less cute infants) in a contrived task (Golle et al., 2015), and were more likely to key-press in order to maintain looking at cuter infants for a longer duration (Parsons, Young, Kumari, et al., 2011). Harlow (1971) argued that the bias for baby schema would be more pronounced in females compared to males. Nonetheless, the evidence to support this claim is mixed. Most studies investigating sex differences in response to cuteness show no sex differences in autonomic (unconscious) response (Parsons, Young, Kumari, et al., 2011; Sprengelmeyer et al., 2009; Reiner Sprengelmeyer, Lewis, Hahn, & Perrett, 2013). The sex differences are most strongly detected when using measures of self-report (conscious) (e.g., Parsons, Young, Kumari, et al., 2011). Further, both adult men and women show motivational/incentive salience in experiments that require repeatedly pressing a key and thus work to maintain the viewing of a cute infant's picture (Parsons, Young, Kumari, et al., 2011).

Cute infants also elicit a fast brain response in brain regions involved in reward and socioemotional processing (e.g., the orbitofrontal cortex (OFC) and the nucleus accumbens (NAc)). Several studies, using magnetoencephalography (MEG) to investigate neural response to infant faces, found that cute infant faces elicited a fast (~130 ms) response from the OFC (Kringelbach et al., 2008; Parsons et al., 2013). This response was exclusive to cute infant faces and was absent (Kringelbach et al., 2008) or diminished in response to adult faces (Parsons et al., 2013). Further, this fast response in the OFC did not occur in response to infant faces with a cleft-palate (Parsons et al., 2013). A cleft-palate or cleft lip is a minor facial congenital abnormality that is relatively common. In addition to disrupting the fast brain response in the OFC, this minor structural facial abnormality to a small component of the face (upper lip) is enough to disrupt the infant's perceived cuteness (Parsons, Young, Parsons, et al., 2011; Rayson et al., 2017). Using fMRI, Glocker and colleagues (2009) investigated brain response to infant cuteness in a sample of young nulliparous women. Each infant picture was digitally manipulated to produce super cute and low cute versions of the infant's face. They found that the super cute (vs low cute) infant pictures elicited a response in the NAc—part of the reward network.

Study 3 (Chapter 4): Rationale. While valuable, previous attempts to quantify infant cuteness are limited by line measurements of a few facial features. They were also limited to black and white pictures and line drawings of infants (Alley, 1981; Hildebrandt & Fitzgerald, 1979; Sternglanz, Gray, & Murakami, 1977). Pictures taken in colour were manipulated to create a super cute infant (Glocker, Langleben, Ruparel, Loughead, Valdez, et al., 2009). In this study, we use modern face morphing software and colored pictures of infants to investigate the morphological correlates of infant cuteness at a higher resolution. **Specific Aims.** To explore: 1) the facial features important for the perception of infant cuteness using a novel data-driven approach; 2) for the first time, the relationship between the level of infant cuteness and affective (emotional) response to positive pictures of infant faces. **Hypotheses and predictions**. In line with ethological description of infant cuteness, we hypothesized that the following morphological facial features are associated with infant cuteness: a rounder face shape, larger eyes and pupils, larger forehead compared to a smaller chin, as well as larger round cheeks. Also, in line with ethological observations about infant cuteness, we hypothesized more positive and less negative affective ratings of highly cute pictures of infant faces compared to pictures of infants that are low on the cuteness dimension.

1.7 Attitudes about children: pet ownership, sex differences, and previous caregiving experience

1.7.1 Overview. Young nulliparous couples (i.e., couples without children) are increasingly opting to own and care for a pet (i.e., an animal that is considered a companion) prior to having their first child (Owens & Grauerholz, 2019; Walsh, 2009). Pets—particularly dogs and cats—share physical and behavioural similarities with human infants (i.e., infantile/neotenous features perceived as cute) (Borgi & Cirulli, 2016). Further, there are similarities between the attachment parents feel towards their child and the attachment pet owners feel towards their pets (Archer, 1997; Borgi & Cirulli, 2016; Feldman, 2017; Hines, 2003; Sable, 1995; Serpell, 2015). One measure of attachment that is associated with the degree of affiliation is behavioural synchrony (Borgi & Cirulli, 2016; Feldman, 2017). Similar to mothers interacting with their infants and children, pet owners exhibit synchronous eye gaze with their pets (Koyasu et al., 2022; Koyasu, Kikusui, Takagi, & Nagasawa, 2020; Nagasawa, Kikusui, Onaka, & Ohta, 2009), decreased heart rate (Handlin et al., 2011) and increased oxytocin (Handlin et al., 2011; Odendaal & Meintjes, 2003; Petersson et al., 2017) when interacting with their pets. Also, using fMRI, one study found that pet owners showed an increased BOLD response to their own dog in brain regions that are responsive to their own child (e.g., amygdala, hippocampus, and OFC) (Stoeckel, Palley, Gollub, Niemi, & Evins, 2014). Taken together, this suggests that the biobehavioural mechanisms underlying parent-child and owner-pet attachment styles are similar. It is therefore not surprising that, colloquially, people refer to their pets as ‘fur babies’ (Greenebaum, 2004) and address their dogs in vocal intonations and inflections (i.e., ‘doggerel’) similar to mother-infant vocal communication (i.e., motherese) (Burnham, Kitamura, & Vollmer-Conna, 2002; Prato-Previde, Fallani, & Valsecchi, 2006; Hirsh-Pasek & Treiman, 1982; Jeannin, Gilbert, & Leboucher, 2017; Mitchell, 2001). Given the psychobiobehavioural similarities in attachment between parents-children and owner-pets, some researchers have proposed that pets are preparatory for parenthood (Borgi & Cirulli, 2016; Nast, 2006; Shell, 1986). However, this idea has not been empirically investigated. Here, I present a brief literature review on the benefits of pet ownership, sex differences in attitudes about children, and the role of caregiving experiences in moderating these sex differences. In study 4—presented in chapter 5—we investigated whether pet ownership and lifetime experiences of care for pets moderated the relationship between sex and attitudes about children and childcare in non-parents. Although this study does not investigate whether pet ownership is preparatory for parenthood, it provides an initial step in that direction setting the stage for future studies.

1.7.2 Pet ownership. Pet ownership is ubiquitous in modern life. In 2018, demographic studies showed that 58% of Canadian households (Canadian Animal Health Institute, 2021) and 57% of American households (American Veterinary Medical Association, 2018) have at least one pet—mostly dogs and/or cats. Given the widespread integration of pets in human life, it is not surprising that an emerging field of study is dedicated to understanding the human-pet relationship. The majority of the evidence shows that pet ownership confers benefits to people's wellbeing including physical and psychological health. Evidence supporting this stems from cross-sectional correlational studies as well as longitudinal and experimental studies. Compared to non-pet owners, pet owners have better cardiovascular health, recover better after surgical procedures, and had a longer lifespan compared to non-pet owners after a heart attack (reviewed by Amiot & Bastian, 2015; Friedmann & Thomas, 1995). Relatedly, a national longitudinal survey of German and Australian populations showed that people who always have pets were the healthiest group and that people who once had but currently do not have pets were the least healthy (Headey & Grabka, 2007). Further, an experimental study found that participants assigned to a pet condition (vs no-pet condition) showed attenuated blood pressure following a stressful task (Allen, Shykoff, & Izzo, 2001). Also compared to non-pet owners, pet owners showed better psychological health including greater self-esteem and well-being (McConnell, Brown, Shoda, Stayton, & Martin, 2011). Similarly, compared to children without pets, children who grew up with a pet showed more self-confidence and autonomy (Van Houtte & Jarvis, 1995). Adding on, a longitudinal study found significant reductions in depressions scores two months after adopting a pet (McConnell, Lloyd, & Buchanan, 2017). Although many studies found pet ownership to be beneficial, it is important to note that some studies found negative associations and others found no associations between pet ownership and health outcomes (Amiot & Bastian, 2015; Herzog, 2011; Parslow, Jorm, Christensen, Rodgers, & Jacomb, 2005).

Experimental studies show that the benefits of pet ownership are partly due to the enhanced social support and/or perceived social support experienced by pet owners relative to non-pet owners (e.g., Allen et al., 2001; Brown, Hengy, & McConnell, 2016; McConnell et al., 2011, 2017). Especially since compared to non-pet owners, pet owners were found to more likely seek closeness with other humans (Joubert, 1987; McConnell et al., 2011). Beyond health outcomes, recent studies shows evidence for the notion that people’s attitudes about their human-pet relationships are similar to their attitudes about their human-human relationships (Bastian, Costello, Loughnan, & Hodson, 2012; Costello & Hodson, 2010; Guthrie, Marshall, Hendrick, Hendrick, & Logue, 2018; McConnell et al., 2011; McConnell, Paige Lloyd, & Humphrey, 2019). Relatedly, pet ownership was associated with enhanced attitudes about romantic partners (Bonas, McNicholas, & Collis, 2000; Cloutier & Peetz, 2016; Guthrie et al., 2018; McConnell et al., 2019). Beyond human-human relationships, pet ownership was also associated with enhanced attitudes about other non-human animals (Bowd & Santrock, 1984) and associated with more environmentally conscious attitudes (Muldoon, Williams, & Lawrence, 2015; Torkar, Fabijan, & Bogner, 2020). Therefore, viewing animals, including pets, in a more favorable manner is indicative of more prosocial outcomes. However, the relationship between pet ownership and attitudes about children has not been investigated. The study presented in chapter 5 adds to this literature by investigating the association between owning and caring for a pet (human-pet relationship) and attitudes about children and childcare (human-human relationship).

1.7.3 Sex differences and caregiving experience. There are clear sex differences in people's attitudes about infants and children. This sex effect is most robust when attitudes are measured by self-report. Compared to men, women report more positive feelings about- and interest in infants and children (Berman, 1980; Kringelbach et al., 2016; Maestripieri & Pelka, 2002). For instance, Maestripieri and Pelka (2002) investigated sex differences in people's interest in infants. Multiple measures were used to assess interest in infants. Measures included self-reported willingness and motivation to be near infants as well as to engage in caretaking activities. Measures also included a preference task in which participants were asked to choose whether they preferred a picture of an infant or an adult. Pictures included human and non-human animals (silhouettes and pictures in colours). Across all age groups (children, adolescents, young adults, and older adults), Maestripieri and Pelka (2002) found that compared to males, females are more interested in infants across all measures. In contrast to the clear sex differences in people's attitudes about infants and children, physiological responses to child-related cues are not as clear and show mixed results (Berman, 1980). Nonetheless, some studies have found sex differences in the physiological response to infant-related cues. For example, compared to males, females demonstrate increased pupil dilation in response to pictures of infants (Hess, 1975) and decreased latency to judge infant emotion (Babchuck et al., 1985). Also, mothers are able to identify their own child's odor a few hours after birth while fathers cannot (Russel, Mendelson & Peeke, 1983). In a sample of undergraduate students who are non-parents, males had a significantly elevated heart rate when prompted to imagine the costs of parental investment compared to females (Geher et al., 2007). These findings are consistent with the 'primary caretaker hypothesis' which states that the sex that is most involved in caretaking across evolution will have the most developed skills to care for the young (Babchuk, Hames, & Thompson, 1985). This hypothesis draws on the theory of parental investment from evolutionary psychology. Across the majority of mammalian species, females expend a greater cost of parental investment compared to males starting at the level of gametes (anisogamy). Therefore, there is a clear sex difference in parental investment including caregiving. In humans, this is also the case across cultures; males invest less time and energy in caretaking activities (Babchuk et al., 1985).

Despite these sex differences in parental investment and conscious self-reported (i.e., overt) attitudes about children in humans, the literature on unconscious (i.e., covert) responses to human infants and children is mixed. Further, the cultural definition of fatherhood is changing across cultures and more prominently in the western world as fathers are investing more time and energy into caregiving (Feldman, Braun, & Champagne, 2019; Hernandez & Brandon, 2012). Evidence from recent studies shows that sex differences in biobehavioural measures of attachment were not present if men and women are similarly involved in caregiving (Abraham et al., 2014; Feldman, 2017). This is illustrated in findings from a study by Abraham and colleagues (2014) that investigated parental brain response to videos of the parents interacting with their infant by comparing three groups of parents: heterosexual mothers who were primary caregivers, heterosexual fathers who were secondary caregivers, and homosexual fathers who were primary caregivers raising the child without maternal influence. They found that similar to mothers who were primary caregivers, fathers who were primary caregivers showed similar levels of parent-infant synchrony (a measure of the quality of parental behaviour) as well as similar activation in brain regions associated with emotional processing such as the amygdala. Also similar to fathers who were secondary caregivers, fathers who were primary caregivers showed activation in brain regions associated with social comprehension such as the Superior Temporal Sulcus (STS). Further, across all fathers, amygdala-STS functional connectivity was associated with the extent of caregiving experience that fathers are involved in; greater experiences of caregiving with their infant (quantified as time spent alone with the infant) was associated with increased amygdala-STS connectivity while viewing their own interactions with the infant.

Beyond parents (mothers and fathers), there is evidence that extends this notion to include the importance of caregiving experience on caregiving behaviour in non-parents (men and women) who care for infants and children. For instance, among professionals, van Polanen et al. (2017) found no sex differences in responsiveness to children and in caregiving behaviour if men and women had the same level of experience caring for children.

1.7.4 Response to infants: prior experiences of caregiving and parity.

Evidence from non-human mammals point to the importance of prior caregiving experiences on the neuroplasticity underlying high quality maternal behaviour. This is strikingly evident by the sensitization process by which nulliparous virgin female rats—normally avoidant or aggressive towards pups—exhibit maternal behaviour that is not distinguishable from parturient females after repeated experiential exposure to pups and pup-related stimuli (Fleming & Rosenblatt, 1974; Jakubowski & Terkel, 1985; reviewed by Lonstein et al., 2015). This has also been observed in primates. For instance, female juveniles of Old-World monkeys (e.g., baboons and macaques) and apes are the most interested to handle infants (Maestripieri, 1994). In turn, females with more prior experiences of infant handling (caregiving) exhibit greater quality of caregiving with their own infants (Fairbanks, 1990).

In humans, the influence of prior caregiving experience on autonomic, hedonic, and attitudinal responsiveness to infant cues and the quality of maternal behaviour has been demonstrated as a function of maternal status (comparing mothers vs non-mothers), parity (experienced multiparous mothers vs first time primiparous mothers), as well as alloparental care experiences with infants (i.e., prior experiences of caring for non-own infants) such as experiences babysitting or caring for siblings and/or other relatives (Bleichfeld & Moely, 1984; Numan et al., 2006). For instance, compared to nulliparous women, new mothers reported increased sympathy and alertness in response to infant cries (Stallings, Fleming, & Corter, 2001). Further, compared to primiparous mothers, multiparous mothers reported greater attraction to infant odors and greater positive maternal attitudes (Fleming, Steiner, & Corter, 1997) as well as a greater difference in sympathy levels to pain compared to hunger cries (Stallings et al., 2001). Also, prior caregiving experience (e.g., babysitting) was associated with more favorable attitudes among primiparous teen mothers such that more prior experience with infants was associated with greater self-confidence and more attachment to- and positive feelings about their infants (Krpan, Coombs, Zinga, Steiner, & Fleming, 2005).

Given the similarities in attachment between parent-child and pet-owner relationships, it is plausible that experiences of care for a pet—a member of another species—may be related with more favorable attitudes about the young of the same species, i.e. young conspecifics. This begs the question of whether the experience caring for a pet would generalize to confer benefits towards caring for a child. In study 4—presented in chapter 5—we investigated whether pet ownership and/or lifetime experiences of care moderated the relationship between sex and attitudes about children and childcare.

Study 4 (Chapter 5): Specific Aims. To investigate whether sex differences in attitudes about children and childcare are moderated by current pet ownership and/or lifetime experiences of car for pets in a sample of non-parents. **Novelty statement.** This is the first investigation of the relationship between pet ownership and attitudes about children and childcare. **Hypothesis and predictions.** Given that findings from previous studies converge on females reporting more positive ratings of- and response to children compared to males, males are the least child-centric group. Therefore, we hypothesize that the moderating effects of current pet ownership and/or lifetime experiences of care for pets on attitudes about children would be the greatest for non-parent males.

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Chapter 2

Study 1: Postpartum depression and brain response to infants: differential amygdala response and connectivity.

2.1 OVERVIEW

Rationale. Despite the prevalence and widespread impact of postpartum depression (PPD), there is a dearth of studies investigating the neural circuitry underlying PPD. Most fMRI studies of PPD use negatively valenced non-infant stimuli. We chose to investigate the neural response to positive infant faces. This is because PPD typically involves anhedonia (i.e., the inability to feel pleasure) and occurs within the context of the mother-infant dyad, it is important to understand brain response to rewarding (positive) and infant-related stimuli. Positive appraisal of the infant may be disrupted in PPD. **Amygdala.** We chose to investigate the amygdala because it is a subcortical brain region that is implicated in both the maternal neural circuitry as well as the affective neural circuitry. Further, several fMRI studies have shown greater amygdala responsiveness to own compared to unfamiliar infant stimuli in community samples of mothers. This amygdala responsiveness to own-unfamiliar positive infant pictures was negatively associated with trait anxiety and parental distress; but positively associated with mothers' positive feelings and attachment to their infant (Barrett et al., 2012). This suggests that infant-related amygdala activity may be an important factor in maternal mood, quality of mothering and/or in the motivation to mother. **PPD.** The few studies investigating the fMRI responsiveness in PPD have mostly been conducted using negatively valenced stimuli (such as negative words or adult faces). These studies found decreased amygdala responsiveness to negative stimuli in PPD compared to Non-PPD mothers. This is in contrast to the predominantly elevated amygdala response in MDD. These results suggest that compared to MDD, a hypo-responsive amygdala may be pathognomonic to PPD. **Specific aims.** To examine the following in mothers with and without PPD: 1) the amygdala response to own and unfamiliar positive infant pictures as well as non-infant pictures; 2) functional connectivity using amygdala as the seed region of interest, during the viewing of positive infant and non-infant pictures; 3) the subjective affective response to positive own infant, unfamiliar infant, and non-infant pictures as a function of depression status. **Methods.** Mothers with (n=28) and without (n=17) clinically determined postpartum depression (PPD) underwent an fMRI scanning while completing an affect rating task (ART) at 2-5 months postpartum. During the ART, mothers viewed positively valenced pictures for 4 seconds and were then asked to rate 'How does this picture make you feel?' on a 9-point likert scale for another 4 seconds. The pictures belonged to one three conditions: own infant, an unfamiliar infant, and non-infant pictures (includes: scenery, food, and mammals). Outside of the scanner mothers completed questionnaires on mood and demographic information. **Results: *ROI.*** We found that both PPD and Non-PPD mothers show greater right-amygdala

responsiveness to own compared to unfamiliar infant pictures. Uniquely for Non-PPD, we also found greater left-amygdala response to own compared to unfamiliar pictures. These results are in-line with previous studies. Compared to Non-PPD mothers, PPD mothers showed greater right-amygdala response to unfamiliar infant. Thus, the unique amygdala response to positive pictures of one's own infant is blunted in PPD compared to Non-PPD mothers. Further across all mothers, right-amygdala responsiveness to unfamiliar infant was positively correlated with trait anxiety scores (measured by the State-Trait Anxiety Inventory-Trait version (STAI-T) (Spielberger, 1996; Spielberger, Gorsuch, & Lushene, 1970)) and right-amygdala responsiveness to non-infant pictures was positively correlated with scores of depression severity (measured by EPDS). ***Connectivity.*** For Non-PPD mothers, we found increased functional connectivity between the bilateral amygdalae with the right insular cortex (IC) while viewing own compared to an unfamiliar infant. In contrast for mothers with PPD, we found decreased functional connectivity between the bilateral amygdalae and the right insular cortex while viewing the same contrast (own-unfamiliar infant). This parameter estimate (bilateral amygdalae to right insular cortex connectivity) was negatively correlated with depression severity (measured by EPDS) and trait anxiety scores (measured by STAI-T); higher depression and anxiety scores were associated with decreased connectivity between bilateral amygdalae and the right insular cortex during the own-unfamiliar infant contrast.

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Postpartum depression and brain response to infants: Differential amygdala response and connectivity

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ABSTRACT
Recent evidence suggests that postpartum depression is associated with reduced amygdala (AMY) response to negative stimuli. However, given the anhedonic features of PPD, it is important to consider mothers' brain response specifically to positive infant and to other positive stimuli. Mothers with (*n* = 28) and without (*n* = 17) clinically determined PPD (*n* = 28) viewed smiling pictures of infants (Own and Other), and positive non-infant stimuli (Non-Infant). First, we examined group differences in AMY response across conditions. Next, psychophysiological interaction was used to examine group differences in AMY connectivity across conditions. Connectivity estimates were then correlated with measures of maternal mood and anxiety. PPD mothers, compared to non-PPD mothers, showed overall increased AMY response across conditions in the right AMY. Despite this, PPD mothers demonstrated decreased bilateral AMY–right insular cortex (IC) connectivity as compared to non-PPD mothers when they view Own–Other infants. Furthermore, decreasing AMY–IC connectivity was associated with increasing symptoms of depression and anxiety. These differences were evident only for infant stimuli and did not apply to all positively valenced stimuli. Thus, PPD mothers show altered brain response and connectivity in regions strongly implicated in the processing of socially and emotionally relevant stimuli, as well as interoception and the evaluation of subjective emotional experience.

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Postpartum depression (PPD) is the most common maternal birth complication (Ross, Dennis, Blackmore, & Stewart, 2005). For approximately 15% of mothers, this time period is accompanied by severe mood disturbance that meets the criteria for depression and includes symptoms such as irritability, uncontrollable crying, extreme sadness/hopelessness, and sometimes thoughts of harm to self and to the baby (American Psychiatric Association, 2000; Beck, 2001; Cox, Murray, & Chapman, 1993; Dennis, Heaman, & Vigod, 2012; Halbreich & Karkun, 2006; O'Hara & Swain, 1996). Despite its prevalence and pervasive impact on the developing infant (Halligan, Murray, Martins, & Cooper, 2007; Murray, 1992; Pawlby, Sharp, Hay, & O'Keane, 2008), our understanding of the neural bases of PPD relies on only a few recent studies (Moses-Kolko et al., 2010, 2011; Silverman et al., 2007, 2011; Moses-Kolko et al., 2012; Chase, Moses-Kolko, Zevallos, Wisner, & Phillips, 2013; Laurent & Ablow, 2013, 2012; see Barrett & Fleming, 2011; Swain et al., 2014; Moses-Kolko, Horner, Phillips, Hipwell, & Swain, 2014; for reviews). These studies have identified an inverse relation between PPD symptom severity and amygdala (AMY) response (Moses-Kolko et al., 2010; Silverman et al., 2011), and suggest that this AMY hyporesponsiveness may be pathognomonic for PPD.

With a known role in the processing of motivationally, emotionally, and socially relevant stimuli (Adolphs, 2003; Adolphs, Baron-Cohen, & Tranel, 2002; Cunningham & Brosch, 2012; Pessoa, 2010), it is not surprising that the AMY may play an important role in PPD and mothering, in general. Previous work in women *without* clinical depression has found that the AMY responds preferentially, or selectively, when mothers view their own compared to an unfamiliar infant (Barrett et al., 2012; Leibenluft, Gobbini, Harrison, & Haxby, 2004; Ranote et al., 2004; Seifritz et al., 2003; Strathearn & Kim, 2013). As such, it appears that healthy mothers have an AMY that responds selectively to their own baby. Thus, we predict that an AMY response that deviates from this pattern of response, especially to images of infants, may be problematic for

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childrearing. In fact, work with other mammals suggests that species-typical maternal behavior is dependent upon normative AMY functioning (Fleming, Vaccarino, & Luebke, 1980; Numan, Numan, & English, 1993). Furthermore, work from our lab (Barrett et al., 2012) has demonstrated that infant-related AMY function is related to maternal anxiety, levels of distress during parenting, and individual differences in attitudes toward mothering. The current study will characterize whether and how infant-related AMY functioning differs in human mothers with PPD as compared to nondepressed mothers, and whether in PPD mothers, the AMY is differentially engaged with other brain regions during the processing of infant cues.

To date, negative non-infant stimuli have primarily been used to examine the neural correlates of PPD (e.g., Moses-Kolko et al., 2011, 2010; Silverman et al., 2011, 2007). Laurent and Ablow (2012) used negative *infant* stimuli for the first time, choosing to examine the brain response in mothers with depressive symptomology in the late postpartum stage (15–18 months) to infant cries. Although this work provides important first insights, for most mothers, infants represent motivationally relevant, positive stimuli. Relatedly, PPD is characterized by an altered emotional, cognitive, and behavioral response toward a stimulus that is typically interpreted as rewarding (e.g., one's own infant). The impact that this disorder has on mothering abilities highlights the need to understand the neural response of mothers with PPD to *positive* infant stimuli, specifically in comparison to other positive non-infant stimuli. It is also important to understand whether the pattern of brain response is specific to their own, or generalizable to all infants. Examining this may have implications for the treatment of PPD.

One recent study (Laurent & Ablow, 2013) examined the brain response in mothers with late postpartum stage depression (15–18 months) to positive pictures of their own infant as compared to positive pictures of an unfamiliar infant. They identified no group differences (PPD vs. non-PPD). Numerous factors may explain these unexpected results. For example, PPD has a high rate of onset in the early postpartum period (Cox et al., 1993), and depressive symptoms tend to remain elevated throughout the first postpartum year (Dennis et al., 2012). It is possible that brain differences in mothers with PPD may change across the postpartum period and that the authors may have failed to capture these mothers at their most vulnerable stage. Furthermore, the authors used a whole-brain approach to data analysis rather than an a priori hypothesis-driven region-of-interest analysis. As much of the existing research indicates that there may be altered brain response in PPD in relatively small brain regions (e.g., the AMY), some of their results may have been masked due to the stringent corrections for multiple comparisons inherent to whole-brain analyses.

In contrast to the paucity of brain-related research on PPD, brain response differences in individuals with major depressive disorder (MDD) have been relatively well characterized. MDD is associated with negative biases in processing facial expressions and altered activity in emotion-related brain regions in response to emotional facial expressions (Anand et al., 2005; Arteche et al., 2011; Dannlowski et al., 2009; Gil, Teissèdre, Chambres, & Droit-Volet, 2011), especially in limbic structures. More specifically, there is greater AMY response to emotional faces in individuals with MDD, and this AMY hyperresponsiveness is primarily for negative stimuli (Hamilton et al., 2012; Suslow et al., 2010; Victor, Furey, Fromm, Öhman, & Drevets, 2010). Thus, although both MDD and PPD are classified as depression, there appears to be a stark contrast between the AMY *hyper*responsiveness to negative stimuli in studies of MDD and the *hypo*responsiveness to negative stimuli observed in existing studies of PPD (Moses-Kolko et al., 2010; Silverman et al., 2011). As of yet, we do not know whether this paradox in brain response to negative stimuli (e.g., decreased in PPD and increased in MDD) will carry over into research with positive stimuli (e.g., increased in PPD and decreased in MDD). Relative to MDD, our understanding of the neurobiology of PPD is still in its "infancy", and continued research into this contradictory AMY response is important given that the symptoms of the disorders overlap to such a large degree.

While previous work with nonclinical samples has suggested that the AMY may play a unique role in the processing of negative- or threat-related stimuli (see Phelps & LeDeoux, 2005), more recent work supports the notion that the AMY is also responsive to uncertainty (e.g., Whalen, 2007) and novelty (e.g., Balderston, Schultz, & Helmstetter, 2011), regardless of the emotional valence of the stimuli. Thus, the AMY may play a role in relevance detection (Sander, Grafman, & Zalla, 2003) based on the particular motivational state, goals, and/or needs of the observer (see also Cunningham & Brosch, 2012). Throughout pregnancy, the postpartum period, and continued motherhood, women are placed in a particularly unique motivational state to which infants and children serve as stimuli worthy of detection, sine qua non. Thus, we believe this proposed role for the AMY forms a particularly relevant foundation for reconciling the growing literature examining the brain response to various stimuli, infant and non-infant, positive and negative, in mothers with and without mood changes.

In addition to differences in mean-level AMY responsivity, it is becoming increasingly clear that brain networks underlie many cognitive processes, and differential connectivity is associated with many forms of psychopathology. For instance, resting-state connectivity between the prefrontal cortex and AMY is reduced in depression (Chase et al., 2013; Tang et al., 2013; Zhang et al., 2014). Only one study has examined task-dependent (during viewing of negative adult faces) functional connectivity of mothers with PPD in the immediate postpartum period (Moses-Kolko et al., 2010). This study found decreased top-down dorsomedial prefrontal cortex-AMY effective connectivity in mothers with PPD. Although functional connectivity has been examined with mothers who vary in maternal responsiveness (Atzil, Hendler, & Feldman, 2011), we do not yet understand, however, how task-dependent functional brain networks that covary with the AMY (Mayberg, 2003; Shafi, Westover, Fox, & Pascual-Leone, 2012) may be altered in mothers with PPD when they are viewing infant faces.

To address the above concerns, through fMRI, the current study will examine (1) AMY response to positively valenced infant stimuli of varying familiarity, and to positively valenced non-infant stimuli; (2) functional connectivity using the AMY as a seed of interest, during the viewing of infant and non-infant stimuli, in mothers with and without clinically determined PPD. First, in line with recent views that the normative functional role of the AMY includes assisting with both the identification of a salient stimulus and the convening of necessary resources for an adaptive response to said stimulus (Cunningham & Brosch, 2012), we predict that we will replicate the existing work that shows that non-PPD mothers show a preferential blood-oxygen-level dependent (BOLD) response in the AMY for their own, as opposed to another infant (Barrett et al., 2012; Leibenluft et al., 2004; Ranote et al., 2004; Seifritz et al., 2003; Strathearn & Kim, 2013). Second, we predict that this preferential BOLD response for one's own baby in the AMY in non-PPD mothers will be blunted in mothers with PPD. Third, we expect to see an altered pattern of task-based cortico-limbic connectivity in PPD compared to non-PPD mothers between the AMY and other brain regions important in affective processing or reward. As work with other species demonstrates that parity or maternal experience is known to influence many aspects of mothering, including brain response (Anderson, Grattan, Van Den Ancker, & Bridges, 2006; Featherstone, Fleming, & Ivy, 2000; Love et al., 2005; Scanlan, Byrnes, & Bridges, 2006), we will include this as a predictor in our analyses. We expect that multiparity, as compared to primiparity, will be associated with decreased AMY response (due to its proposed role in uncertainty detection), but overall enhanced connectivity between the AMY and other brain regions known to be important in affective or reward processing during the viewing of infant cues, as these connections may be strengthened with greater maternal experience.

Methods and materials

There were three phases in the study: (1) Diagnostic Interview and Photography Session, (2) fMRI Session, and (3) Home Visit. Of interest for the current study are Phases 1 and 2. A similar paradigm has been used successfully in previous work in our lab (Barrett et al., 2012). This study was approved by the Research Ethics Boards of St. Joseph's Healthcare (SJH), Hamilton, ON, Canada, and the University of Toronto at Mississauga (UTM), Mississauga, ON, Canada. Informed written consent was obtained from all participants.

Subjects

All participants were right-handed, English-speaking women, 20–40 years of age, with singleton, full-term babies. They presented with no contraindications to fMRI (e.g., metallic implants) and had corrected or normal vision. According to structured clinical interview (Composite International Diagnostic Interview-Venus (CIDI-V)(Martini, Wittchen, Soares, Rieder, & Steiner, 2009), all participants reported no serious medical or neurological condition, no substance dependence in the past year (except caffeine or nicotine), and no current or history of psychotic or bipolar disorder, according to Diagnostic and Statistical Manual fourth edition text revision (DSM-IV TR (American Psychiatric Association, 2000) criteria. Additionally, the Children's Aid Society was not involved in the care of the baby, and mothers did not present with suicidal, homicidal, or infanticidal risk. Mothers with no history of or current psychiatric illness (non-PPD, $n = 23$) were recruited from the maternity ward at SJH. Mothers who met DSM-IV TR criteria for major depressive episode, with perinatal onset (PPD, $n = 31$) were recruited from the Women's Health Concerns Clinic (WHCC) at SJH. A principal investigator (MS) provided clinical care to these participants. Since PPD mothers were recruited from an outpatient psychiatric clinic, some were receiving treatment in the form of selective serotonin reuptake inhibitors (SSRI use $n = 13$; no medication $n = 18$). Although these women were recruited based on a diagnosis of PPD at the time of their intake at the WHCC, they also completed a diagnostic interview (CIDI-V) administered by a trained graduate student or research assistant approximately 1 week prior to the fMRI scan. To ensure a representative sample, these mothers were not excluded from the study and medication status was considered in all analyses. Symptom type and severity after the initial clinical diagnosis was assessed 1 week after diagnosis (and at the time of the scan) using the Edinburgh Postnatal Depression Scale (EPDS), a self-report measure of PPD severity and the State-Trait Anxiety Inventory, Trait version (STAI-T). These measures of mood reflect moment-to-moment changes in affect and are not necessarily consistent with the clinical diagnosis based on DSM-IV for major depressive episode with perinatal onset.

Mothers participated at 2–5 months postpartum. This range was chosen as this was the minimum age, based on our previous work (Barrett et al., 2012), at which positive (i.e., smiling) facial expressions were produced by infants in a relatively consistent manner. However, due to the often time-limited nature of PPD, keeping the time period under 5 months was ideal (Cox et al., 1993). Prior to the fMRI, mother–baby pairs attended a laboratory session at SJH, where a minimum of 50 positive infant facial expressions were photographed (by the first (KEW) and second (CBM) authors). Five observers then rated these images on a 9-point scale (1 = "not at all positive" and 9 = "extremely positive"). Twenty of the most positive infant face pictures (average rating of 5 or higher) were chosen for use in the fMRI protocol. The images were standardized for overall brightness, and framed and masked to present just the facial area. Own baby stimuli were matched by randomly choosing another baby from our stimulus set. For their participation, mothers were provided with $100 remuneration plus the cost of parking.

fMRI

Affect rating task

PPD and non-PPD mothers completed an affect rating task (ART) during an fMRI session at the Imaging Research Centre at SJH. The ART was presented using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA, USA), and timing was synchronized with the acquisition of functional images. During each ART run, three conditions were presented four times using a block-design: (1) smiling own infant face (Own); (2) smiling other infant face (Other); (3) positive non-infant stimuli (e.g., scenes, animals, food; Non-Infant). Prior to each condition-block, a 1.5 s visual cue was presented (Set A, Set B, Set C) followed by a 4 s fixation cross. Cue to condition-block assignment was randomized across participants. For each 40 s condition-block, five unique picture stimuli were presented randomly for 4 s. After this, mothers had 4 s to make a subjective rating of their emotional response to each stimulus ("How does this picture make you feel?"), made on a 9-point scale (1 = "not at all positive" and 9 = "extremely positive"). Each condition-block was followed by a jittered 8–10 s interstimulus fixation cross (see Figure 1). PPD mothers may interpret infant faces more negatively than non-PPD mothers (Arteche

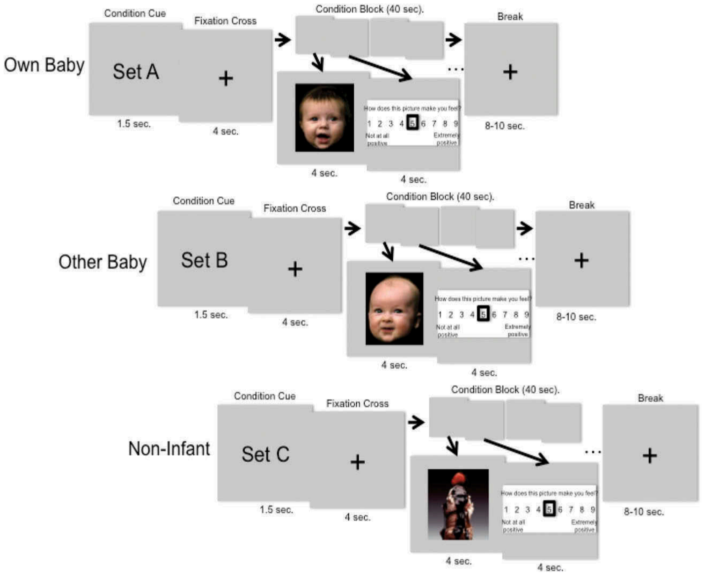

Figure 1. fMRI affect rating task (ART) design.

et al., 2011). Thus, prior to the onset of the task, mothers were verbally instructed to rate the infant faces for the degree of emotional intensity *they* felt internally when viewing them, rather than on the emotional intensity conveyed by the facial expressions. It is also possible that PPD mothers would display an altered response to all emotional stimuli. Consequently, each mother also viewed 20 Non-Infant, control images from the International Affective Picture System based on pre-chosen emotional subset categories defined by Mikels et al. (2005): amusement, contentment, and undifferentiated positive. Of note, all mothers practiced the same task outside of the scanner immediately prior to their scan, in which all of the babies were unfamiliar or "Other", in order to familiarize them with the task.

Acquisition

MRI scanning was conducted using a General Electric 3-T short-bore scanner with 32 parallel-receiver channels (General Electric, Milwaukee, WI, USA). BOLD response to infant faces was acquired using T2 weighted interleaved echo-planar imaging (EPI). A total of 256 volumes were obtained from each participant, consisting of 42 axial slices of 3 mm thickness (repetition time = 2.7 ms, echo time = 35 ms, flip angle = 90°, resolution = 64 × 64 over 24 cm field of view).

Preprocessing

The fMRI data processing was carried out using fMRI Expert Analysis Tool (FEAT Version 6.00), part of FMRIB's Software Library (FSL, www.fmrib.ox.ac.uk/fsl). Pre-statistic processing included: motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002); brain extraction using Brain Extraction Tool (Smith, 2002); spatial smoothing using a full width at half maximum 5 mm Gaussian kernel; grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor; highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 75.0 s). Participants were excluded from further analysis if they exhibited greater than 2 mm movement. The first four images were discarded to ensure the scanner had achieved steady state during image acquisition. Warped functional images were combined to create a mean study-specific template for coregistration with individual functional data. Registration to this template was carried out using FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001). Time-series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich). In the following description, "Own" refers to own baby pictures, "Other" refers to other baby pictures and "Non-Infant" refers to all positive nonbaby pictures. Ten experimental conditions were included as regressors: OwnSet (instructions for mothers), OwnView, OwnRate, OtherSet, OtherView, OtherRate, NonInfantSet, NonInfantView, NonInfantRate, and ThankYou (end of task message). BOLD response when the mothers were viewing infant faces (View = passive viewing of the faces) was modeled separately from the time they were making a subjective rating of the infant faces (Rate = rating scale on screen; mothers making response), as AMY activation can be inhibited by cognitive activity (Drevets & Raichle, 1998; Phan, Wager, Taylor, & Liberzon, 2002).

Region of interest analysis

An AMY region of interest (ROI) (Gil et al., 2011) was anatomically defined using the Harvard-Oxford anatomical atlas, at 70% probability threshold. We recognize that the human AMY is comprised of distinct subregions, each with their own afferents and efferents (Amunts et al., 2005; Ball et al., 2007; McDonald, 2003; Price, 2003). Subregions are also differentially involved in the processing of emotional face stimuli, especially in anxious individuals (Etkin et al., 2004; Etkin, Prater, Schatzberg, Menon, & Greicius, 2009). We chose to examine the AMY as a whole for comparison with the extensive work that uses this approach to examine the functional significance of the AMY in MDD. We examined the View conditions rather than the conditions during which mothers were actively using the response box to respond to the pictures (Rate). The mean time series of AMY ROI voxels was generated for OwnView, OtherView, and NonInfantView conditions in the right and left AMY (defined using the abovementioned anatomical mask). In order to examine both familiarity- and specificity-related differences, we examined AMY response to the following contrasts: OwnView–OtherView (familiarity) and OtherView–NonInfantView (specificity). To replicate our previous work (own positive–other positive contrast from Barrett et al., 2012), we first examined these contrasts in non-PPD and PPD mothers, separately. Next, we conducted group-level analyses in FSL, masked for the bilateral AMY, where Z-statistic images (Gaussianized T/F) were cluster thresholded ($z > 2.3$), and a cluster significance threshold of $p = 0.05$ was applied (Worsley, 2001). This represents a more sensitive alternative to voxel-based thresholding, where a Z-statistic is used to define contiguous clusters with an estimated significance level (from GRF-theory), which is then compared with the cluster probability threshold. For group-level analyses, we examined both contrast-level (OwnView–OtherView and OtherView–NonInfantView) and condition-level (e.g., OwnView, OtherView, and NonInfantView) effects, as well as the overall BOLD response across conditions (e.g., in

OwnView, OtherView, and NonInfantView, combined). To examine PPD and anxiety symptom severity, EPDS and STAI-T scores were entered into SPSS-21 for analyses with AMY mean signal change across contrast conditions. Medication status was used as a covariate in the group-level model.

Psychophysiological interaction

Again, in order to examine both familiarity and infant-related connectivity differences, separate psychophysiological interaction (PPI) models were conducted for OwnView–OtherView and OtherView–NonInfantView, respectively. Mean deconvolved time course was extracted from seed regions in the left and right AMY to serve as the psychophysiological variable. We restricted our bilateral AMY seed regions to those voxels within the anatomical ROI defined above that showed an overall enhanced BOLD response relative to baseline in all three of our conditions combined (OwnView, OtherView, and NonInfantView). PPI interaction terms were calculated as the cross product of the physiological variable and the task regressor. In each task model, separate analyses were computed for the right and left AMY with three regressors: task condition (OwnView–OtherView or OtherView–NonInfantView), PPI interaction term, and left or right AMY time course. Although not specifically of interest, all other task conditions were also included as regressors. The PPI interaction term was then brought to a second-level group analysis (non-PPD, PPD), with medication status entered as a covariate. *Z*-statistic(Gaussianized T/F) images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = 0.05$ (Worsley, 2001). For any cluster of voxels identified as significantly connected with the AMY in non-PPD or PPD mothers, mean time series data was extracted and entered into SPSS-21 for analysis with covariates of interest using one-way ANOVA.

Analysis of other demographic and clinical data

Demographic and clinical variables were analyzed with SPSS using one-way ANOVA or chi-square test, where appropriate. We used Spearman correlations to examine the relationship between ART, clinical variables (EPDS and STAI-T), and parity with our fMRI contrasts (OwnView–OtherView and OtherView–NonInfantView) and conditions of interest (OwnView, OtherView, and NonInfantView). As these tests were considered exploratory, alpha level for significance was set at .05.

Results

Subject characteristics

Fifty-four mothers completed the study; however, nine mothers were excluded from analyses due to high movement during the fMRI (>2 mm); the current results represent data from 17 non-PPD mothers and 28 PPD mothers. Maternal age and education, as well as delivery method, parity, and breastfeeding status were not significantly different across non-PPD and PPD mothers (see Table 1). Other than parity (discussed subsequently), these variables did not contribute to the models discussed below, and were thus excluded from analyses. From a multivariate ANOVA, PPD mothers reported significantly higher depressive symptomology (EPDS ($F(1,43) = 14.403$, $p = .001$) and trait anxiety (STAI-T ($F(1,43) = 45.952$, $p = .001$); Table 1). Although 11 PPD mothers were taking SSRI medication, EPDS and STAI-T scores for PPD mothers did not differ based on medication status (SSRI vs. no medication; EPDS $F(1,26) = 1.180$, $p = .287$ and STAI-T $F(1,26) = .758$, $p = .392$).

Table 1. Subject characteristics.

	Non-PPD mothers ($n = 17$)		PPD mothers ($n = 28$)		Statistical analysis	
	Mean	SEM	Mean	SEM	$F(1,43)$	p-value
Demographic measures						
Age (years)	29.18	1.19	30.64	0.93	1.02	.317
Education (% high school)	5.88%		14.29%		$\chi^2 = 0.76$	.384
Delivery method (vaginal:ccesarean)	70.59%		75.00%		$\chi^2 = 1.05$	.746
Parity (primiparous:multiparous)	70.59%		64.43%		$\chi^2 = 0.19$	.664
Feeding method (breast:bottle)	70.59%		57.14%		$\chi^2 = 0.81$	.367
Clinical measures						
Edinburgh Postnatal Depression Scale	3.12	1.07	8.29	0.84	14.40	.001*
State-Trait Anxiety Inventory (Trait version)	27.82	1.98	44.86	1.54	45.95	.001*

Chi-square test (df = 1); PPD=Postpartum Depression, *indicates significant group difference at $p < .05$.

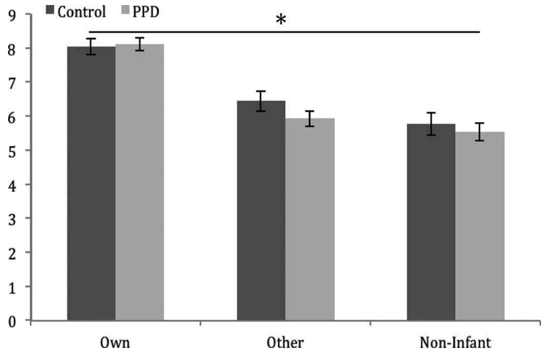

Figure 2. During the affect rating task (ART), all mothers reported feeling more positive when viewing their Own compared to Other infants or Non-Infant pictures ($F(1,43) = 75.405$, $p = .000$). There were no group differences in ratings across conditions ($F(1,43) = .733$, $p = .397$).

ART

During the ART, all mothers reported that they felt more positive when they viewed their own compared to other infants or non-infant pictures ($F(1,43) = 75.405$, $p = .001$). There were no group differences in this self-reported experience of positivity across conditions ($F(1,43) = .733$, $p = .397$; Figure 2); PPD mothers and non-PPD mothers all reported experiencing the same degree of positive affect when they viewed pictures of own, other, and non-infant stimuli.

ROI analysis

Non-PPD mothers

As shown in Figure 3a, average BOLD response in the bilateral AMY in mothers without PPD was greater for OwnView–OtherView (right AMY: 190 voxels, $p = 0.00473$, $z = 3.65$, peak $x = 24$, $y = -2$, $z = -14$; left AMY: 63 voxels, $p = 0.039$, $z = 3.12$, peak $x = -24$, $y = -4$, $z = -12$). There were no differences in AMY response to OtherView–NonInfantView.

PPD mothers

Average BOLD response in PPD mothers was greater for OwnView–OtherView only in the right AMY (87 voxels, $p = 0.0246$, $z = 3.76$, peak $x = 26$, $y = 0$, $z = -12$; see

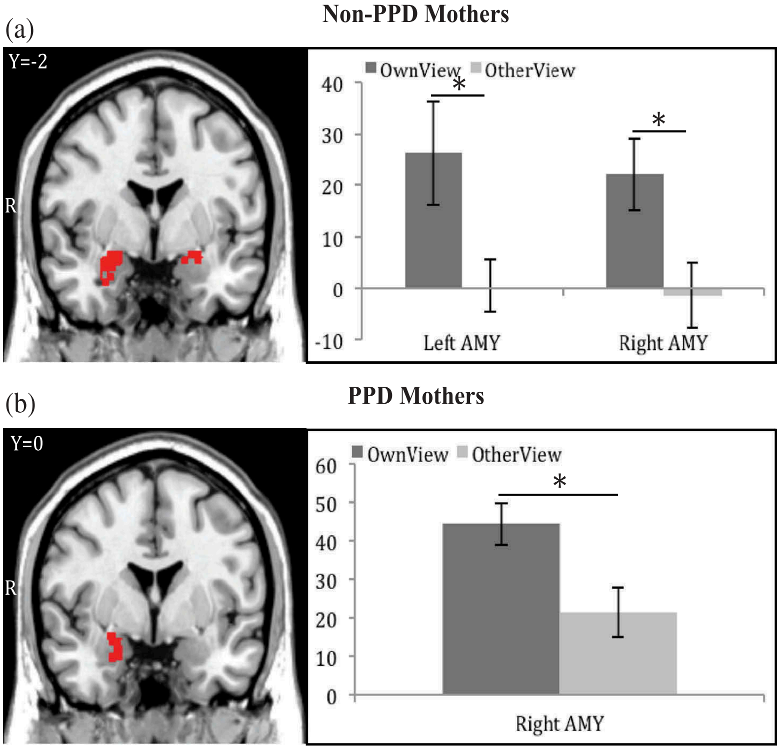

Figure 3. Average BOLD response in the amygdala (AMY) in non-PPD (3a) and PPD (3b) mothers. **3a**. Average BOLD response in the *bilateral* AMY was greater for OwnView compared to OtherView in non-PPD mothers (right AMY: 190 voxels, $p = 0.00473$, $z = 3.65$, peak $x = 24$, $y = -2$, $z = -14$; left AMY: 63 voxels, $p = 0.039$, $z = 3.12$, peak $x = -24$, $y = -4$, $z = -12$). There were no differences in AMY response to OtherView–NonInfantView. **3b**. Average BOLD response in the *right* AMY was greater for OwnView compared to OtherView in PPD mothers (87 voxels, $p = 0.0246$, $z = 3.76$, peak $x = 26$, $y = 0$, $z = -12$). There were no differences in *left* AMY response to OwnView–OtherView. There were also no differences in AMY response to OtherView–NonInfantView.

Figure 3b). There were no differences in AMY response to OtherView–NonInfantView.

Group-level

No group differences (e.g., both PPD > non-PPD and/or non-PPD > PPD) were observed for our contrasts of interest: OwnView–OtherView or OtherView–NonInfantView. With respect to condition-level differences, there were no group differences in average BOLD response for OwnView in non-PPD compared to PPD mothers. However, in comparison to non-PPD mothers, PPD mothers demonstrated *increased* BOLD response to OtherView (105 voxels, $p = 0.0173$, $z = 3.06$, peak $x = 24$, $y = -8$, $z = -18$; see Figure 4a) and to NonInfantView (54 voxels, $p = 0.0472$, $z = 3.24$, peak $x = 26$, $y = 0$, $z = -14$; see Figure 4b) in the right AMY. Thus, when BOLD response was collapsed across all conditions (OwnView, OtherView, and NonInfantView), PPD mothers showed an overall increased response in the right AMY (78 voxels, $p = 0.0291$, $z = 3.44$, peak $x = 28$, $y = -2$, $z = -12$; see Figure 4c). Medication status was used as a covariate in the model.

Parity

There was a marginal Parity × Group interaction for bilateral AMY response to OwnView (right AMY: $F(1,41) = 3.72$, $p = .061$; left AMY: $F(1,41) = 3.315$, $p = .076$; see Figure 5). While there was no group

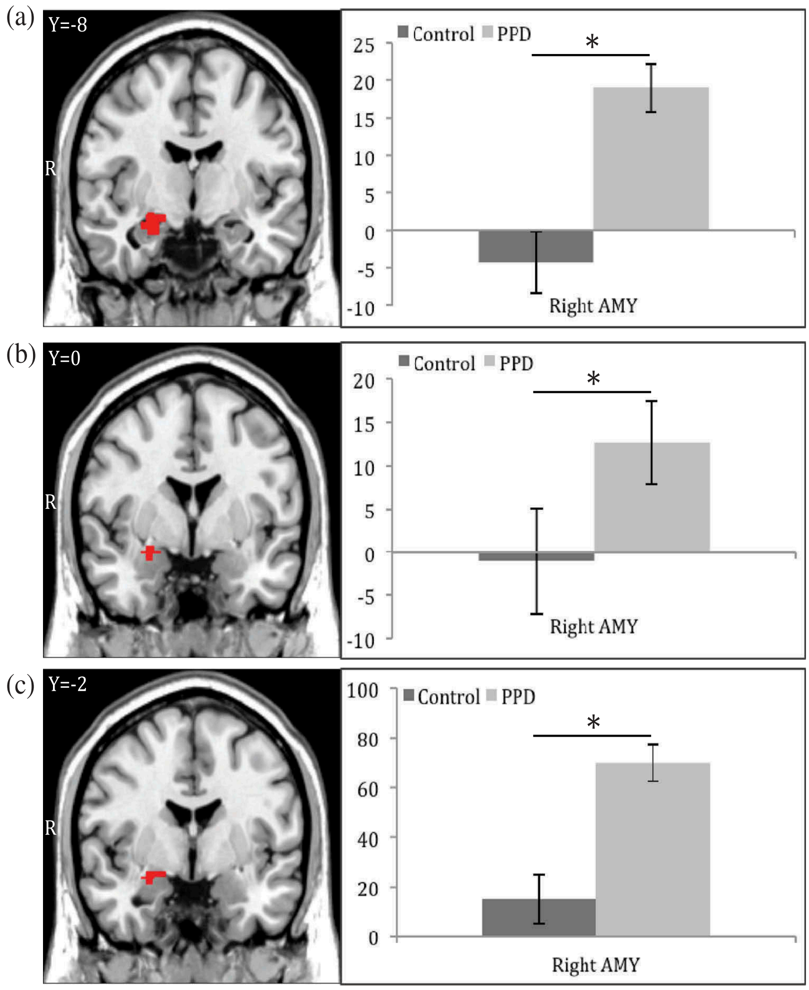

Figure 4. Group-level differences in average BOLD response in the amygdala (AMY) in non-PPD as compared to PPD mothers. **4a**. In comparison to non-PPD mothers, PPD mothers demonstrate increased BOLD response to OtherView in the right AMY (105 voxels, $p = 0.0173$, $z = 3.06$, peak $x = 24$, $y = -8$, $z = -18$). **4b**. In comparison to non-PPD mothers, PPD mothers demonstrate increased BOLD response to Non-InfantView in the right AMY (54 voxels, $p = 0.0472$, $z = 3.24$, peak $x = 26$, $y = 0$, $z = -14$). **4c**. Average BOLD response in the right AMY across all conditions is greater in PPD compared to non-PPD mothers (78 voxels, $p = 0.0291$, $z = 3.44$, peak $x = 28$, $y = -2$, $z = -12$).

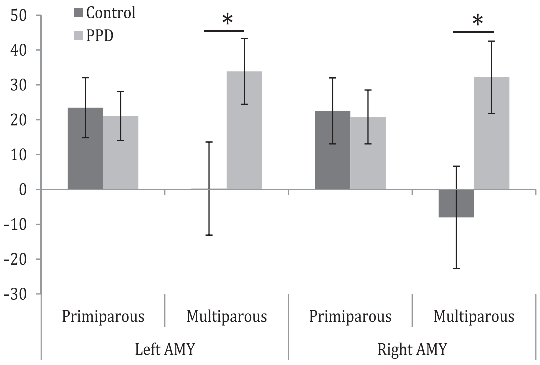

Figure 5. Marginal Parity × Group interaction for bilateral amygdala (AMY) response to OwnView (right AMY: *F* (1,41) = 3.72, *p* = .061; left AMY: *F*(1,41) = 3.315, *p* = .076). While there was no group difference in AMY response in primiparous mothers, multiparous PPD mothers had greater bilateral AMY response than non-PPD multiparous mothers; AMY response appears to decrease with experience in non-PPD mothers, but increase with experience in PPD mothers. There were no group differences in AMY response to OtherView or NonInfantView by maternal experience.

difference in AMY response in primiparous mothers, multiparous PPD mothers had greater bilateral AMY response than non-PPD multiparous mothers. In other words, AMY response appears to decrease with experience in non-PPD mothers, but increase with experience in PPD mothers. There were no group differences in AMY response to OtherView or NonInfantView by maternal experience. These findings should be considered exploratory, as they are derived from a small sample of multiparous (non-PPD *n* = 5, PPD *n* = 10) relative to primiparous (non-PPD *n* = 12, PPD *n* = 18) women, in the non-PPD sample, in particular.

Connectivity analysis

Group level

Although we observed group-level ROI differences in the right AMY, but not the left AMY, BOLD response differences do not always predict connectivity differences. Furthermore, our a priori hypothesis did not predict this laterality effect. As such, we proceeded to examine both right and left AMY connectivity differences with PPI. During OwnView–OtherView, at cluster-corrected $p < .05$ ($z = 2.3$), controlling for medication status, non-PPD mothers showed *increased* connectivity between the bilateral AMY and the right insular cortex (IC), whereas PPD mothers showed *decreased* AMY–IC connectivity (right AMY–right IC: 933 voxels, $p = 0.000244$, $z = 3.83$, peak $x = 54$, $y = -10$, $z = 4$; left AMY–right IC: 534 voxels, $p = 0.0239$, $z = 3.29$, peak $x = 34$, $y = 8$, $z = 14$; see

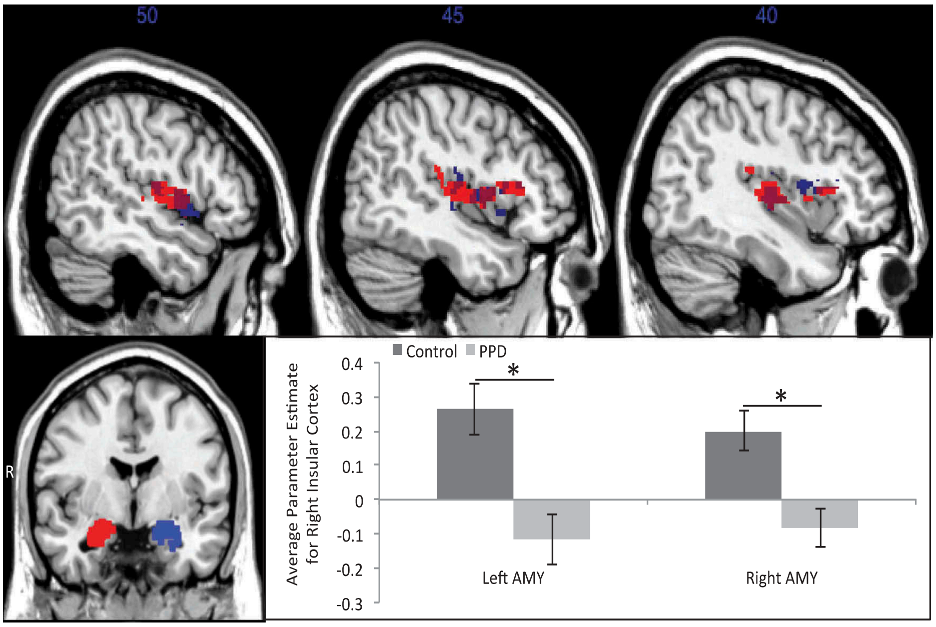

Figure 6. During OwnView–OtherView, *non-PPD mothers* showed *increased* connectivity between bilateral amygdala (AMY) and the right insular cortex (IC), whereas *PPD mothers* showed *decreased* AMY–right IC connectivity (right AMY–right IC: 933 voxels, $p = 0.000244$, $z = 3.83$, peak $x = 54$, $y = -10$, $z = 4$; left AMY–right IC: 534 voxels, $p = 0.0239$, $z = 3.29$, peak $x = 34$, $y = 8$, $z = 14$). Blue = left AMY–right IC connectivity, Red = right AMY–right IC connectivity. There were no group differences in connectivity with the left or right AMY during OtherView–NonInfantView.

Figure 6). There were no group differences in connectivity with the left or right AMY during OtherView–NonInfantView.

Parity

From a repeated measures ANOVA with group (non-PPD vs. PPD) and parity (primiparous vs. multiparous) as between-subjects factors and bilateral AMY to IC connectivity as within-subject factor, an interaction between group and parity was observed ($F(1,41) = 5.617$, $p = 0.023$). Although AMY–IC connectivity was low in PPD mothers, regardless of the amount of parenting experience they had (e.g., low in both primiparous and multiparous mothers), in non-PPD mothers, AMY–IC connectivity increased with maternal experience (e.g., multiparous > primiparous; see Figure 7). These findings should be considered exploratory, as they are derived from a small sample of multiparous (non-PD $n = 5$, PPD $n = 10$) relative to primiparous (non-PPD $n = 12$, PPD $n = 18$) women, in the Non-PPD sample, in particular.

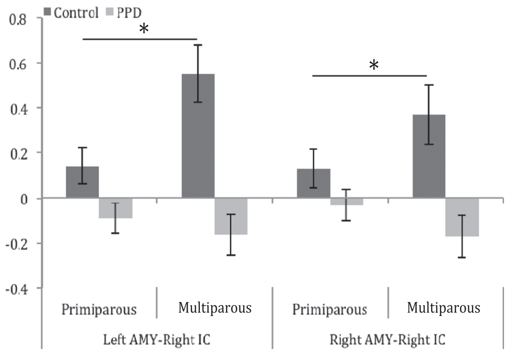

Figure 7. In non-PPD mothers, AMY–right IC connectivity increases with experience (e.g., multiparous > primiparous). However, in PPD mothers, AMY–right IC connectivity is low in both primiparous as well as multiparous mothers. Interaction between group and parity: $F(1,41) = 5.617$, $p = 0.023$.

Correlations

Non-PPD mothers

As can be seen in Table 2, EPDS scores were negatively correlated with left AMY response to OtherView–NonInfantView ($r = -.59$, $p = .013$) and positively correlated with left AMY response to NonInfantView ($r = .71$, $p = .001$). STAI-T scores were also negatively correlated with left AMY response to OtherView–NonInfantView ($r = -.59$, $p = .013$). In other words, more anxious mothers within the non-PPD group tended to show reduced Other Infant–NonInfant differences in BOLD response in left AMY. We also observed a negative correlation between STAI-Trait and left AMY response for OwnView ($r = -.54$, $p = .026$) and OtherView ($r = -.50$, $p = .039$). Hence, greater trait anxiety was associated with reduced left AMY response to babies (both own and other) in non-PPD mothers. There were no significant correlations between right AMY response to our conditions of interest and EPDS or STAI-T.

ART ratings made by non-PPD mothers during the fMRI for their own infant were not significantly correlated with bilateral AMY response to OwnView or OwnView–OtherView. However, ART ratings for other infants were positively related to bilateral AMY response for the contrast OwnView–OtherView ($r = .49$, $p = .046$). This suggests that mothers who showed a larger differential AMY response to their own infant (e.g., greater own-other difference in the AMY) reported higher positivity ratings for "other" infants.

PPD mothers

As shown in Table 2, EPDS scores were positively correlated with left AMY response to NonInfantView ($r = .39$,

Table 2. Significant correlations between amygdala ROI conditions of interest and clinical variables. Note, if there were no significant correlations between clinical and fMRI measures, they are not represented in this table.

	All mothers ($n = 45$)		Non-PPD mothers ($n = 17$)		PPD mothers ($n = 28$)	
	r-value	*p*-value	*r*-value	*p*-value	*r*-value	*p*-value
Left AMY						
OwnView (STAI-T)			−.54	.026[a]		
OtherView (STAI-T)			−.50	.039[a]		
NonInfantView (EPDS)	.49	.001[a]	.71	.001[a]	.39	.043[a]
OwnView–OtherView (ART Other Infant)	.49	.046[a]				
OtherView–NonInfantView (STAI-T)			−.60	.010[a]		
OtherView–NonInfantView (EPDS)			−.59	.013[a]		
Right AMY						
OtherView (STAI-T)	.30	.045[a]				
NonInfantView (EPDS)	.45	.002[a]				

[a] indicates significant correlation ($p < .05$).

p = .043). There were no other significant correlations between EPDS or STAI-T and bilateral AMY response to our contrasts or conditions of interest. There were no significant correlations between ART ratings of Own or Other infants and AMY response in mothers with PPD.

All mothers

EPDS scores were positively correlated with right AMY (r = .45, p = .002) and left AMY (r = .49, p = .001) response to NonInfantView. We also observed a positive correlation between STAI-T scores and right AMY response to OtherView (r = .3, p = .045). There were no significant correlations between ART ratings of Own or Other infants and AMY response in mothers with PPD.

Connectivity analysis

AMY–right IC connectivity parameters were negatively correlated with both EPDS (right AMY–right IC: r = –.339, p = .023; left AMY–right IC: r = –.411, p = .005; Figure 8) and STAI-T (right AMY–right IC: r = –.501, p = .001; left AMY–right IC: STAI-T r = –.548, p = .001; Figure 8); increasing depressive symptomology and trait anxiety were related to decreasing AMY–right IC connectivity. AMY–right IC connectivity was not correlated with ART scores.

Discussion

The first goal of the current study was to replicate our and others' previous work showing preferential AMY responsiveness to one's own as compared to another infant's face (Barrett et al., 2012; Leibenluft et al., 2004; Ranote et al., 2004; Seifritz et al., 2003; Strathearn & Kim, 2013). Indeed, we identified enhanced bilateral AMY response when non-PPD mothers view their own versus other infants. This effect has been replicated in similar studies that demonstrate enhanced AMY response to personally relevant faces (e.g., partner faces (Taylor et al., 2009)). The AMY is a brain region known to play a critical role in socioemotional processing (Adolphs, 2003; Adolphs et al., 2002; Pessoa, 2010) and maternal behavior (Barrett & Fleming, 2011; Fleming et al., 1980). Recently, Cunningham and Brosch (2012) have conceptualized the AMY as an early part of an affective system responsible for identifying important environmental stimuli and facilitating appropriate responding to said stimuli. One's own infant represents a particularly salient environmental stimulus for the recently postpartum mother. This saliency appears to be manifest at the neural level through enhanced AMY response.

Next, we sought to examine whether this specificity effect was conserved in mothers with PPD. For the first time, we found that PPD mothers did, in fact, show a preferential response in the right AMY to their own as compared to an unfamiliar infant. As such, all mothers, regardless of depression status, showed greater BOLD response in the AMY for their own infant compared to an unfamiliar infant. This increased BOLD response for one's own infant in the AMY is interesting in the context of findings by Kim et al. (2010), which identified increased AMY volume across the early postpartum period as associated with enhanced positive perception of one's baby. Although these findings may appear contrary to existing fMRI studies that find blunted activation in the AMY in PPD mothers (Moses-Kolko et al., 2010; Silverman et al., 2011), the current study differs in a notable way. Rather than using negative stimuli (e.g., words, adult faces), we utilized stimuli that are positively salient and specific to the motivational state for the observer: positive

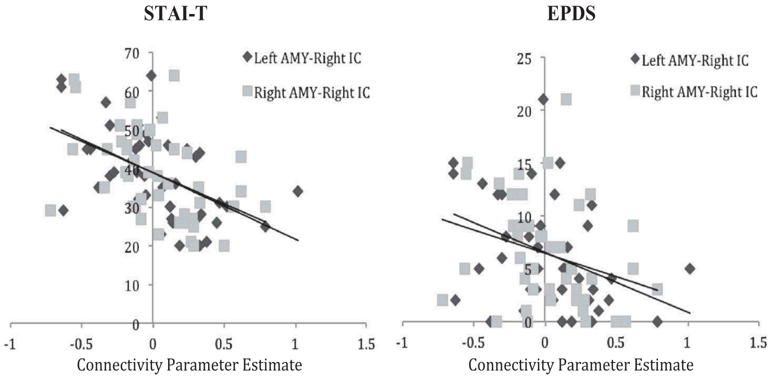

Figure 8. AMY–IC connectivity was not correlated with ART scores; however, AMY–IC connectivity was significantly correlated with both clinical measures: EPDS (right AMY–right IC: r = –.339, p = .023; left AMY–right IC: r = –.411, p = .005) and STAI-T (right AMY–right IC: r = –.501, p = .000; left AMY–right IC: r = –.548, p = .000).

pictures of babies—specifically, one's own baby. Facial expressions are a primary means of communicating emotion for a developing infant, and they are known to elicit infant-directed gaze from the mother (Colonnesi, Zijlstra, Van Der Zande, & Bögels, 2012; Klaus, Trause, & Kennell, 1975; Yale, Messinger, Cobo-Lewis, & Delgado, 2003). This relationship indicates that infant visual stimuli elicit maternal arousal and may reflect maternal motivation. In line with recent theories of AMY functioning as being involved in novelty (Balderston et al., 2011), uncertainty (Whalen, 2007), and relevance detection based on the particular motivational state, goals and/or needs of the observer (Cunningham & Brosch, 2012), it is possible then, that negative stimuli are not motivationally salient enough to engage the AMY in a PPD population.

Interestingly, from group analyses, while we observed no differences between PPD and non-PPD mothers in their AMY BOLD response to their own infant, we did see an overall enhanced response to both other as well as non-infant stimuli in the right AMY in PPD mothers. In other words, while the unique response to own infant was preserved in mothers with PPD, they showed a ramping up of AMY response to all other positive stimuli, both infant and non-infant. It is possible that the enhanced right AMY response we observed in mothers with PPD to all stimuli represents a generally enhanced or even dysregulated arousal/vigilance for salient stimuli. Although this study was designed to examine differences between clinical and nonclinical depression, anxiety is also a prominent feature of PPD. Importantly, in addition to depressive symptomology, the mothers in our PPD group also reported elevated trait anxiety, as compared to non-PPD mothers. Future studies should seek to tease apart the degree to which these findings may be related to symptoms of depression, anxiety, or both.

During the fMRI, mothers in the current study were instructed to think about and rate how they felt when viewing pictures of infants and other positive stimuli. All mothers, regardless of depression status, reported feeling most positive when viewing their own infant. Thus, the increased AMY we observed in the current study occurred in the absence of self-reported differences during the rating task. Notably, BOLD response does not necessarily map onto behavioral response; we cannot assume that increased signal in a particular brain region will be associated with behavioral changes. In fact, from our ART results, we did not observe a correlation between ratings in the scanner and BOLD response in the AMY. Rather, we observed the opposite in non-PPD mothers: the more positive they rated pictures of *other* babies, the more preferential their BOLD response was for their *own* baby in the left AMY. Thus, in non-PPD mothers, the specificity of the response (high for own baby, low for other baby), rather than the average activation, appears to relate to self-reported positive affectivity when viewing the pictures. This relationship was absent in PPD mothers. Further studies should seek to clarify whether the increased BOLD response to all positively salient stimuli in PPD mothers is reflected in other behavioral measures, such as those obtained from mother–infant interactions. Knowing how a depressed mother's brain responds to infant stimuli is critical, as the symptoms of PPD impact the mother–infant dyad and often involve excessive worry or guilt surrounding parenting abilities (Ross et al., 2005). Relatedly, mothers with PPD typically display an altered pattern of behavioral interaction with their infants (e.g., more intrusive and irritated and less sensitive and contingent (Murray, Fiori-Cowley, Hooper, & Cooper, 1996; Cohn, Campbell, Matias, & Hopkins, 1990; Stanley, Murray, & Stein, 2004; Fleming, Ruble, Flett, & Shaul, 1988)). Knowing this, it will be important for future studies to investigate how these differences relate to brain response to infants in mothers with and without PPD.

The second major goal of the current study was to investigate whether the pattern of connectivity between the AMY and other brain regions was altered in mothers with PPD. Using task-based AMY connectivity in PPD and non-PPD mothers, we found that AMY–right IC functional connectivity, brain regions with strong reciprocal anatomical connections, was enhanced when no-PPD mothers are viewing their own compared to another infant, but decreased in PPD mothers. Furthermore, this connectivity pattern was positively correlated with both depressive symptomology and trait anxiety. The dorsal posterior IC has been conceptualized as the primary interoceptive cortex, responsible for representing the physiological sense of one's body (Craig, 2002). The right anterior IC is important for representing one's internal state (Craig, 2009) and is activated in tasks that measure subjective emotional awareness, in particular, studies that assess recall of sadness (Mayberg et al., 1999), anger (Damasio et al., 2000), anxiety (Benkelfat et al., 1995), pain (Ploghaus et al., 1999), disgust (Phillips et al., 1997), and other aspects of emotional awareness (see Craig, 2002 for summary). Researchers have proposed that the representation of the physiological condition of the body in the IC serves as the neural substrate for these subjective feelings and emotions (Craig, 2002, 2009). This role of the IC is of particular relevance to PPD, as self-perceived maternal health was recently identified as the strongest risk factor for persistent PPD (Dennis et al., 2012), and anxiety and parenting stress are common postpartum (Miller, Pallant, & Negri, 2006). It is also interesting in the context of the current study instructions ("think about how you feel when viewing these pictures"). Non-postpartum mood disorders have been associated with decreased anterior IC volume (Takahashi et al., 2010), decreased IC activity during interoception (Avery et al., 2014), and altered IC BOLD response following a variety of treatments (see McGrath et al., 2013). Additionally, altered connectivity between the IC and limbic structures, important for fast processing of emotional stimuli, such as the AMY (Manoliu et al., 2014; Ramasubbu et al., 2014), and more prefrontal regions thought to be important in guiding motivated actions, such as the anterior cingulate cortex (Connolly et al., 2013), has been identified in individuals with MDD (see Drevets, Price, & Furey, 2008 for review).

The IC has been proposed as a brain region involved in the physiological pathway underlying the negative or overly catastrophic evaluations of the sensations in one's body, often observed in anxiety disorders (Paulus & Stein, 2006). More specifically, Paulus and Stein (2006) propose that there may be a mismatch between observed and expected body states in individuals with anxiety disorders, which can result in cognitive and behavioral compensatory mechanisms (e.g., worrying and avoidance, respectively), and that this process may be related to IC functioning. As aforementioned, while the goal of this study was to examine clinical depression, anxiety is also common in the postpartum period and is a prominent feature of PPD. Furthermore, the PPD and no-PPD mothers in this study reported significant differences in levels of trait anxiety. Preliminary analyses (Wonch et al., in prep) indicate that a similar pattern of findings are observed if individual differences in anxiety are used to predict connectivity, rather than PPD diagnostic grouping. Given the striking differences in AMY–right IC connectivity observed here in the context of increased self-reported trait anxiety, future studies should seek to clarify the unique influence of both depression as well as anxiety.

Interestingly, we also found that AMY–right IC connectivity increased with maternal experience in non-PPD mothers, a pattern that was not observed in PPD mothers. Although this finding was not anticipated, it is consistent with our conceptualization of AMY–IC functionality. If the AMY is thought to play a role in rallying together appropriate recourses to respond to emotionally salient or intense environmental stimuli (Cunningham & Brosch, 2012), one could hypothesize that increasing connectivity between this brain region and the IC, important for representing the physiological state of the body to guide subjective emotional experience (Craig, 2002), would increase with parental experience. Interestingly, we observed this in the context of a marginal difference based on parity in overall BOLD response in the AMY; while there was no group difference in AMY response in first-time mothers, multiparous PPD mothers had marginally greater bilateral AMY response as compared to multiparous non-PPD mothers. In other words, despite increased overall BOLD response in the AMY in multiparous PPD mothers, they did not show increased AMY–right IC connectivity. To our knowledge, this is the first report of altered response and functional connectivity in mothers as a function of their parity status. However, it is important to note that the current study was not designed to test this hypothesis directly. Further studies should continue to investigate the role of the AMY in maternal experience in mothers with and without PPD. For example, by examining unique contributions of AMY subregions (see, for example, with anxiety (Etkin et al., 2009)).

As research with MDD indicates that AMY hyperresponsivity to negative stimuli may be a trait-like characteristic of the disorder (Price & Drevets, 2010), studies with PPD postulate that AMY hyporesponsiveness to negative stimuli may be pathognomonic of PPD (Silverman et al., 2011). Although this is the first study to examine AMY response to positive stimuli in PPD, recent studies with MDD suggest that AMY response is decreased in response to positive stimuli (Stuhrmann et al., 2013). It is interesting, then, that we again found the opposite pattern of AMY responsivity in PPD (increased to positive stimuli in the right AMY rather than decreased, similar to what is seen with MDD). The present findings add to the literature examining the brain response of PPD mothers to emotional stimuli. They also support the notion that PPD may be phenotypically distinct from MDD. Future research should seek to compare directly how the AMY and other brain regions important in monitoring affective stimuli (e.g., the salience network and/or affective network (Menon & Uddin, 2010; Price & Drevets, 2010), respond to both positive as well as negative stimuli, infant and non-infant, in mothers with PPD.

There are a few potential limitations that cannot be addressed by the current study. For example, disturbances to the sleep-wake cycle are hallmark symptoms of MDD (American Psychiatric Association, 2000). However, under normal circumstances, the postpartum period is characterized by disrupted sleep and in some cases, extreme sleep disturbances, leading some researchers to postulate that disrupted circadian rhythms, which we did not measure, may be part of the pathogenesis of PPD in vulnerable women (Park, Meltzer-Brody, & Stickgold, 2013; Ross et al., 2005). Additionally, PPD is a heterogeneous condition with wide variations in time of onset (e.g., pregnancy (which trimester?) vs. postpartum) and previous history of MDD or PPD. Some suggest that there may be phenotypic variation in uniquely "postnatal" depression, rather than antenatal (Cooper & Murray, 1995; Phillips, Sharpe, Matthey, & Charles, 2010). Although there are benefits to having strict inclusion criteria, the wide variations in symptomology, onset, history, and course of PPD are often not captured by such rigidity. Our study did not attempt to impose such criteria, thereby enhancing the ecological validity and generalizability of our findings to the greater population of women with PPD. A variety of other factors may influence how the brains of new mothers respond to their infants. For example, an association was identified between BDNF Met66 carrier status and development of PPD symptoms, only when mothers delivered during autumn/winter (Comasco et al., 2011). Ideally, future studies should adopt a multidimensional approach when assessing maternal behavior in relation to brain response in PPD mothers.

Despite neuroimaging evidence that brain regions showing decreased activation in individuals with MDD show increased activation following treatment with SSRIs, and vice versa (Fitzgerald, Laird, Maller, & Daskalakis, 2008; Price & Drevets, 2010), as noted, we did not see differences in AMY response with SSRI use in PPD mothers. It is possible that with stronger controls (e.g., specific type of SSRI, duration of use, dose, etc.) and a study designed specifically to target this relationship, we may see an association between brain response in PPD mothers and medication use. Future studies should do this, as controversy surrounding medication use during pregnancy and during breastfeeding still exists (Nulman et al., 2012; Steiner, 2012; Weissman et al., 2004).

In our study, the average EPDS scores for the mothers in our PPD group were not above the widely cited cutoff score of 12 at the time of the scan (Cox, Holden, & Sagovsky, 1987). While we recognize that this is below standard clinical cutoffs on this measure, due to both the repeat nature of our testing (e.g., clinical interview conducted approximately 1 week before fMRI scan) and the potentially fluctuating nature of PPD symptomology, we are not surprised that scores on this measure varied within mothers; it is possible that some women may have begun to compensate for their depressive symptomology by the time of the scan. Interestingly, a recent meta-analysis identified wide variation in the sensitivity and specificity of the EPDS as a screening measure for PPD (Gibson, McKenzie-McHarg, Shakespeare, Price, & Gray, 2009). In another study, using EPDS cutoff scores to classify mothers with or without a history of PPD failed to identify a relationship between child outcomes at 11 years and PPD, yet when they examined group differences based on diagnostic criteria from a standardized clinical interview, they identified significant differences (Pawlby et al., 2008). This indicates that EPDS may not adequately distinguish mothers with and without PPD, when compared to a diagnostic interview. Thus, the design of our current study is preferred, where mothers were grouped by diagnostic criteria rather than scores on a nondiagnostic mood measure.

As mentioned throughout, depression is not the only mental health concern faced by mothers during pregnancy and/or the postpartum period; many mothers also experience clinically relevant symptoms of anxiety, substance abuse, and/or trauma (see Moses-Kolko et al., 2014 for review). Studies that examine the pattern of brain activity in mothers with other forms of maternal psychopathology have also identified altered AMY responsivity. For example, Kim, Fonagy, Allen, and Strathearn (2014) identified decreased AMY response to infant distress cues in mothers with unresolved trauma. Important future insights may come from studies that measure overlapping symptomology of these disorders and examine how these relate to brain function in regions known to be important for regulating affect, reward, and even memory.

As previously mentioned, top-down effective connectivity between the prefrontal cortex and AMY during the viewing of negative adult faces has been shown to be decreased in PPD mothers (Moses-Kolko et al., 2010). Thus, it is interesting that we also observed decreased functional connectivity between the IC, a region so strongly implicated in interoception and subjective emotional awareness (Craig, 2002), and the AMY, specifically when PPD mothers view pictures of their own infant. Given this, together with previous reports of decreased AMY response to threatening words (Silverman et al., 2007), future research should examine how the brains of mothers with PPD process both threatening and rewarding infant and non-infant stimuli, and relate this to actual mothering behavior. Future studies should also seek to clarify whether the decreased AMY–IC connectivity observed here in PPD mothers reflects increased or dysregulated bottom-up influence of the AMY on the IC. The frequency with which PPD occurs as well as the potential for negative consequences for the developing infant underscore the need for continued research into its neurobiological substrates.

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Chapter 3

Study 2: Amygdala and affective responses to infant pictures: Comparing depressed and non-depressed mothers and non-mothers.

3.1 OVERVIEW

Rationale. The few studies investigating the fMRI responsiveness in PPD have mostly been conducted using negatively valenced stimuli (such as negative words or adult faces). These studies found decreased amygdala responsiveness to negative stimuli in PPD compared to Non-PPD mothers. This is in contrast to the predominantly elevated amygdala response in MDD. These results suggest that compared to MDD, a hypo-responsive amygdala may be pathognomonic to PPD. **Specific aims.** To investigate the neural (amygdalae) and subjective affective response to positive smiling infant pictures compared to pictures of scenery as a function of depression status and maternal status. **Methods.** The data presented in this study overlaps with data presented in Chapter 2. Mothers with (PPD, n=32) and without (Non-PPD, n=25) clinically determined PPD and non-mothers with (MDD, n=15) and without (Non-MDD, n=29) depression (depression status for non-mothers was determined using a computer assisted diagnostic interview (CIDI-V)) underwent the same fMRI paradigm (i.e., ART) discussed in study 1 (Chapter 2). **Main results & brief discussion.** ***Subjective Affective Response.*** We found a significant maternal status by condition interaction such that mothers rated pictures of Unfamiliar Infants more positively than Scenery whereas non-mother rated pictures of Scenery more positively than those of Unfamiliar Infants. This is consistent with the salient hypothesis from the animal literature which shows that virgin female rats choose food (non-infant stimuli) over pups (infant stimuli) whereas rat dams choose pups over food. We also found a main effect of depression such that depressed groups, regardless of maternal status, had lower ratings compared to non-depressed groups to pictures of both Infants and Scenery. This is consistent with the well-established negativity bias and anhedonia observed as a function of depression. ***ROI.*** *Unfamiliar infant-scenery condition.* We found a depression by maternal status interaction in right amygdala response during the unfamiliar-scenery condition, indicating a greater right-amygdala response in PPD compared to Non-PPD mothers, but no difference between MDD and Non-MDD group. *Condition-level.* We found a different pattern of response to each condition (infant, scenery) between depressed and non-depressed groups given their maternal status. The PPD group has the greatest response to unfamiliar infant compared to both Non-PPD and MDD groups. In other words, compared to PPD group, the MDD group showed a decreased amygdala response to positive unfamiliar infant pictures. We did not find group differences in response to infant nor scenery when comparing the MDD and Non-MDD groups.

Differences in analytic choices between studies 1 & 2. In terms of the sample of participants, we increased statistical power by adding data from more mothers (PPD +4, n=32; Non-PPD +9, n=26). To investigate questions related to maternal status, we added data from depressed (MDD, n=15) and non-depressed (Non-MDD, n=29) non-mothers. We used different software and a slightly different modelling strategy in chapter 2 and 3 for preprocessing of fMRI data as well as for statistical analyses. In chapter 2 we used FSL, while in chapter 3 we used SPM and Marsbar. Also, while the View and Rate conditions were modelled together in chapter 3, they were modeled as separate conditions/regressor in chapter 2. Critically, in chapter 3 we used a specific (homogenous) subset (scenery) of the broader pool of non-infant pictures used in chapter 2. The larger pool of non-infant pictures contained multiple categories of pictures including mammals (dolphins, horses, etc), pets (dogs, cats, rabbits), and scenery. In chapter 3, we chose to focus on the category of scenery alone. Finally, while chapter 2 included functional connectivity analyses, chapter 3 did not. Despite differences, the main effects were maintained in both studies.

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ORIGINAL ARTICLE

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Amygdala and affective responses to infant pictures: Comparing depressed and non-depressed mothers and non-mothers

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Abstract

In many mammalian species, new mothers show heightened positive responsiveness to infants and their cues when they give birth. As is evident from non-human and human studies, the amygdala is a brain region implicated in both the maternal and affective neural circuitry, and is involved in processing socioemotionally salient stimuli. In humans, infants are socially salient stimuli to women, and mothers in particular. Neuroimaging studies investigating the maternal response to infant cues have identified infant-related amygdala function as an important factor in maternal anxiety/depression, in the quality of mothering and in individual differences in the motivation to mother. The present study investigated the effects of maternal status and depression on the subjective affective response and amygdala responsiveness to unfamiliar infants using functional magnetic resonance imaging. Smiling infant pictures were used in a 2 × 2 design comparing four groups of women: mothers and non-mothers, with and without depression (total of 101 women: postpartum depression [PPD] = 32, non-PPD = 25, major depression [MDD] = 15, non-MDD = 29). We undertook an anatomically defined region of interest analysis of the amygdala response for a priori defined group comparisons. We found that mothers rated infants more positively than non-mothers and non-mothers rated non-infant stimuli (scenery) more positively than mothers. In the amygdala, we found that depression elevated response to smiling unfamiliar infants in mothers but had no effect in non-mothers. Within the depressed groups, mothers (PPD) showed an elevated amygdala response to unfamiliar smiling infants compared to depressed non-mothers. Hence, our results indicate that women with PPD show an enhanced amygdala response to affectively positive infant pictures but not to affectively positive (but non-salient) pictures of scenery. Women with depression outside of the postpartum period show no change in amygdala responsiveness to either stimulus categories.

KEYWORDS
amygdala, depression, infant pictures, maternal status

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1 | INTRODUCTION

In many mammalian species, new mothers show heightened positive responsiveness to infants and their cues when they give birth.[1] Indeed, virgin female rats will attack, cannibalise or withdraw from young pups, whereas new mothers respond by retrieving, licking and crouching over their young. These differences in maternal responsiveness are associated with parity-related changes in other behavioural systems that contribute to responses to young conspecifics, including differences in mother's affect, salience of infant cues and cognitive function.[2] Also associated with such behavioural differences are differences between new mothers and virgin female rats in their hormonal and neurochemical profiles, as well as brain function, especially in the hypothalamic-amygdala-striatal systems.[1,3] Using the animal model as our guide, over the years, our group has explored these factors in the regulation of human mothering and identified a very similar set of behaviour-physiology-brain relations in new mothers.[2,4] In a first of a series of studies from our group Wonch et al[12] investigated differences between amygdala responsiveness to infant pictures in depressed and non-depressed mothers. The current study builds on the results reported by Wonch et al[12] and adds to the literature by comparing non-mothers with mothers as a function of depression status. The rationales for our focus on the amygdala and depression are outlined below.

1.1 | Amygdala

The amygdala is a brain region that plays a role in processing socially and emotionally motivational stimuli[5,6] and is implicated in both the maternal[7,8] and affective[9,10] neural networks in both human and non-human mammals.[1] In a recent study, Barrett et al[11] found that new non-depressed mothers show an elevated amygdala response to viewing an image of their own infant in contrast to viewing another unfamiliar infant. In addition, own-infant amygdala engagement was associated with elevated feelings of attachment.[5] Furthermore, the amygdala response was inversely related to maternal distress and anxiety.[11] In depressed mothers, Wonch et al[12] found that the unique amygdala response to positive pictures of one's own infant was blunted in comparison to non-depressed mothers. These findings are in line with work from a number of other laboratories[7,13-17] and suggest that, for human mothers, infant-related amygdala engagement may be an important factor in maternal anxiety/depression,[18-21] quality of mothering[22] and/or in individual differences in the motivation to mother.[23,24]

Animal work in rodents has identified that the amygdala plays a differential role in response to pups based on maternal status. Lesioning the amygdala of virgin females who are neophobic and react with avoidance or aggression towards pups results in the disinhibition of the maternal circuitry and the expression of approach-related behaviours towards pups.[25] Similar lesioning in the new mother rat, which is normally maternal, does not produce a comparable disinhibition.[1,26] However, the effects of human maternal status on amygdala responsiveness to infant cues are not clear as the evidence is limited to a few neuroimaging studies reporting mixed results.[15,27-29] To begin with, Seifritz et al[15] found that mothers and non-mothers showed a different pattern of amygdala responsiveness to infant vocalisations based on their emotional valence. Compared to non-mothers, mothers showed an elevated amygdala response to baby cries. Alternately, non-mothers, compared to mothers, showed an elevated amygdala response to infant laughter.[15] By contrast, region of interest analyses by Rupp et al[30] found that mothers showed a decreased amygdala responsiveness to negative (non-infant) images relative to non-mothers. Interestingly, other studies did not find differences in amygdala responsiveness to infant cries between mothers and non-mothers,[27,29] nor between parents and non-parents.[28]

1.2 | Depression status

Postpartum depression (PPD) is the most common maternal birth complication[31] because it affects 15%-20% of new mothers.[32] It is characterised by similar symptomology to major depression (MDD), although it is differentiated by timing of onset during the peripartum period (ie, late pregnancy and a few months postpartum) and it involves excessive worry and guilt surrounding parenting abilities.[32-36] Furthermore, depressed mothers show lower maternal sensitivity towards the infant compared to non-depressed mothers[37-40] and, as a result, this can have a pervasive impact on the developing infant.[41] However, the neural mechanisms underlying PPD are not well understood. What we do know about the neural underpinning of the condition/disorder is a result of a few recent functional magnetic resonance imaging (fMRI) studies.[17,42] These studies have identified an inverse relationship between amygdala responsiveness to negative stimuli (including infant faces in distress) and symptom severity in PPD.[43,44] Thus, in comparison to non-depressed mothers, depressed mothers show reduced amygdalar responses to negative infant-related stimuli.[43] By contrast, the more extensive fMRI literature on MDD[10] points to a hyper-responsive amygdala to negative stimuli.[9] This difference between PPD and MDD women suggests that amygdalar hypo-responsiveness to negative stimuli in PPD women may be unique and specific to the postpartum period. To delineate differences in the amygdalar response between PPD and MDD, the present study directly compared the effects of depression on amygdala responses in mothers and non-mothers.

As indicated above, the majority of studies to date have used negative infant stimuli in fMRI studies of PPD. However, depression is characterised by altered emotional, cognitive and behavioural responses towards a stimulus that is typically interpreted as rewarding.[45,46] Infants are perceived as socially and motivationally positive and salient for women in general,[47,48] and for mothers in particular.[49] As such, we chose to investigate the effects of depression and maternal status on responsiveness to positive smiling infant pictures.

In the present study, we extend these findings by applying a 2 × 2 design to assess the effects of maternal status and depression status by directly comparing the response (amygdala and affective) of four groups of women (mothers: depressed, not; non-mothers: depressed, not) to smiling infant pictures. In line with the salience hypothesis showing that young conspecifics, including human infants, are more salient to mothers than to non-mothers,[1,47,48] we hypothesise a greater amygdala and subjective affective responsiveness to smiling infant pictures in mothers compared to non-mothers. Whether a similar pattern of amygdala responsiveness is maintained as a function of maternal status among women who are depressed (PPD vs MDD) is not clear and constitutes the second objective of the present study. Finally, given the tendency of depressed individuals to rate positive stimuli less positively,[45,50] we predict dampened positivity ratings to positive infant pictures as a function of depression in both groups of depressed women.

2 | MATERIALS AND METHODS

2.1 | Overview

As described above, this is the second in a series of studies by our group. Given our focus on the effects of maternal status on the amygdala response to infant pictures, we re-analysed data originally reported on in our earlier publication[12] from 54 mothers (both depressed, n = 31, and not, n = 23) and added six newly recruited mothers (depressed, n = 3, and not, n = 3) and 44 non-mothers (depressed, n = 15 and not, n = 29) to them. Mothers completed three phases in the study each 1 week apart: (i) a diagnostic assessment and photography Session; (ii) a fMRI session; and (ii) a home visit. Non-mothers completed the first two phases only. Data collection began on 28 April 2011 (upon receiving consent from the first participant) and ended on 27 August 2013 (upon final participant's exit). The study was approved by the Research Ethics Boards of St Joseph's Healthcare (SJH), Hamilton, ON, Canada, and the University of Toronto at Mississauga (UTM), Mississauga, ON, Canada. Informed written consent was obtained from all participants. This section is an abridged version of the methods; a more detailed description is provided in Wonch et al.[12]

2.2 | Participants

All participants were right-handed, English-speaking women, 20-40 years of age. They presented with no contraindications to fMRI (eg, metallic implants) and had corrected or normal vision.

2.2.1 | Mothers

Mothers participated at 2-5 months postpartum, with singleton, full-term babies. Mothers who were not depressed (non-PPD, n = 26) were recruited from the maternity ward at SJH. Mothers who met Diagnostic and Statistical Manual fourth edition text revision (DSM-IV TR)[33] criteria for major depressive episode, with peripartum onset (PPD, n = 34), were recruited from the Women's Health Concerns Clinic (WHCC) at SJH. This was determined by a clinician (MST) at the WHCC. Because mothers with PPD were recruited from an outpatient psychiatric clinic, some were receiving treatment in the form of selective serotonin reuptake inhibitors (37.5%) or other forms of treatment such as psychotherapy. As a result, some women's symptoms had stabilised or become subclinical at the time of the diagnostic interview (visit 1) and/or at the time of the scan (visit 2). To ensure an ecologically valid and representative sample, these mothers were not excluded from the study and medication status was considered in all analyses. Therefore, all women in the PPD group had had at least one major depressive episode at some point throughout their most recent peripartum period. For their participation, mothers were provided with $100 remuneration plus the cost of parking.

2.2.2 | Non-mothers

All non-mothers (MDD, n = 15; non-MDD, n = 29) were recruited by online advertisement via kijiji.com localised to the Hamilton region. Non-mothers received $50 remuneration plus the cost of parking.

2.3 | Phase 1: Diagnostic assessment

2.3.1 | Diagnostic assessment

Depression status was determined by a structured clinical interview (Composite International Diagnostic Interview-Venus; CIDI-V[51]) consistent with the DSM-IV TR[33] criteria administered by a trained graduate student or research assistant. For the PPD group, the CIDI-V confirmed the clinician diagnosis at the WHCC; all women in the PPD group had at least one major depressive episode during their most recent peripartum period. Women in the non-PPD and the non-MDD groups had no history of a major depressive episode as determined by CIDI-V. According to the clinical interview (CIDI-V) and DSM-IV TR criteria, all participants reported no serious medical or neurological conditions, no substance dependence in the past year (except caffeine or nicotine) and no current or history of psychotic or bipolar disorder. Additionally, child protective services were not involved in the care of the baby, and participants did not present with suicidal, homicidal or infanticidal risk.

2.3.2 | Assessment of symptom severity

Symptom type and severity were assessed at two time points: during phase 1 (at the time of the diagnostic interview) and 1 week after during phase 2 (at the time of the fMRI scan). This was conducted using the Edinburgh Postnatal Depression Scale (EPDS),[52] a self-report measure of PPD severity, and the State-Trait Anxiety Inventory, Trait version (STAI-T).[53] These measures of mood reflect moment-to-moment changes in affect and are not necessarily consistent with the clinical diagnosis based on DSM-IV for major depressive episode with perinatal onset. Both mothers and non-mothers also completed the Montgomery and Asberg Depression Rating Scale (MADRS)[54] to assess symptom severity outside the perinatal period.

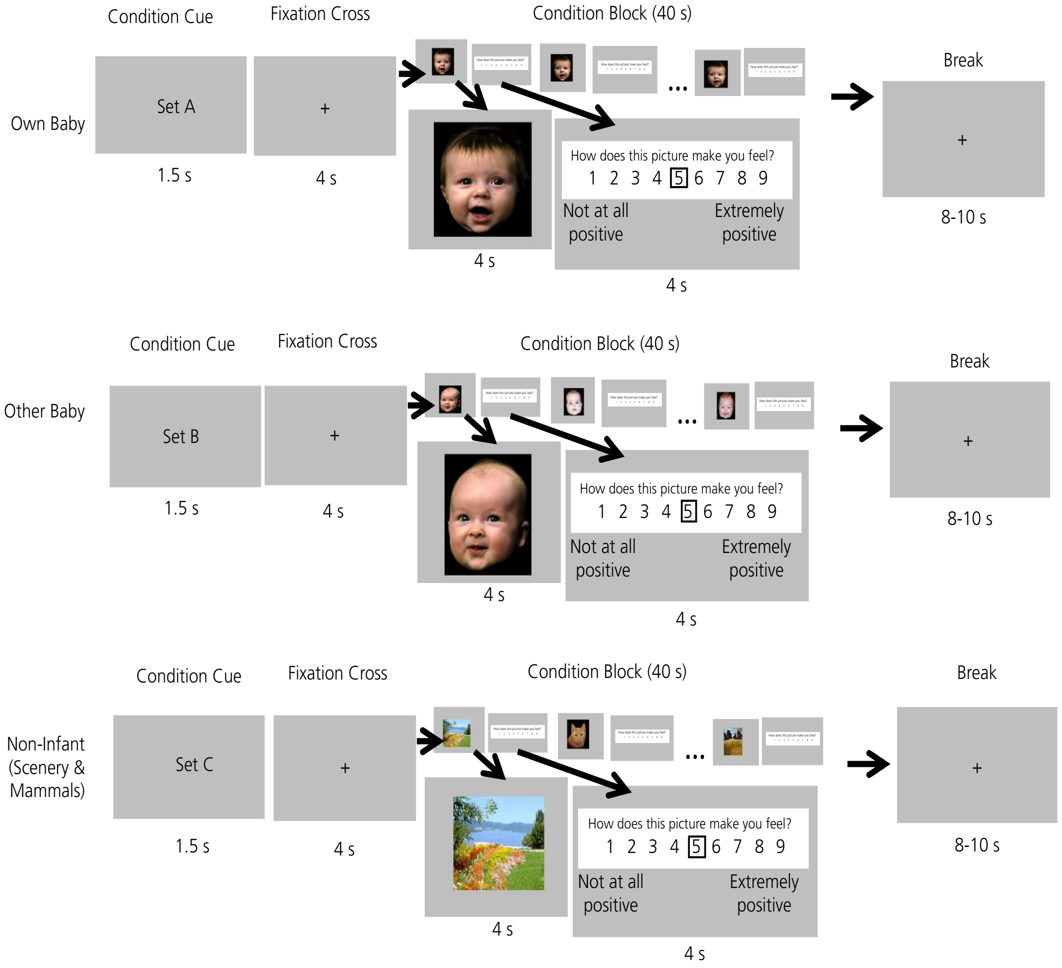

FIGURE 1 The design of the affect-rating task (ART) presented during functional magnetic resonance imaging.

2.4 | Phase 2: fMRI

2.4.1 | Paradigm: Affect rating task

All women completed an affect rating task (ART) during an fMRI session at the Imaging Research Centre at SJH. The ART was presented using E-PRIME, version 2.0 (Psychology Software Tools, Pittsburgh, PA, USA) and the onset of the task and image acquisition were synchronised. During each ART run, three conditions were presented four times using a block-design: (i) smiling own infant face (Own); (ii) smiling unfamiliar infant face (Unfamiliar); and (iii) positive non-infant stimuli (Non-Infant: scenery, n = 9, and mammals, n = 11). Each block consists of: a 1.5 seconds visual cue was presented (Set A, Set B, Set C), followed by a 4 second fixation cross, then a 40 second condition-block. Cue to condition-block assignment and the order of condition presentation was randomised across participants. To randomise the order of condition presentation, we used five different versions of the task differing in the order of condition presentation. The condition block consists of five unique picture stimuli each presented for 4 seconds followed by 4 seconds of rating ('How does this picture make you feel?') on a nine-point scale (1 = 'not at all positive' and 9 = 'extremely positive'). Each condition-block was followed by a jittered 8-10 second interstimulus fixation cross (Figure 1).

2.4.2 | Stimuli acquisition

MRI scanning was conducted at the Imaging Research Centre of SJH. All images were acquired on a 3 Tesla GE short-bore scanner using a multichannel receiver head coil (GE Healthcare, Chicago, IL, USA). Following localisation, a 3D T1-weighted structural image was acquired (magnetisation-prepared gradient echo; axial orientation; 1.6 mm thick slices; FOV = 240 × 240 mm^2; phase FOV = 0.7; matrix size = 256 × 256; TR = 7.2 ms, TE = 2.1 ms; TI = 450 ms; flip angle = 12°; ASSET acceleration with R = 2). fMRI images were acquired during response to infant and non-infant pictures using T2-weighted single-shot interleaved echo-planar imaging. A total of 256 whole-brain volumes were obtained from each participant, consisting of 42 contiguous axial slices with 3 mm thickness (FOV = 240 × 240; matrix size = 64 × 64; TR = 2.7 seconds; TE = 35 ms; flip angle = 90°; imaging time 11.5 minutes).

2.4.3 | fMRI preprocessing

Dicom images were converted to 3D NIfTI format and the first four volumes were discarded before preprocessing in SPM, version 12 (http://www.fil.ion.ucl.ac.uk/spm) running under MATLAB (R2012a; MathWorks Inc., Natick, MA, USA). The functional images underwent slice time correction, realignment and co-registration to the anatomical data. Functional data were also smoothed (Full width at half maximum (FWHM) = 5 mm). Finally, anatomical and functional images were transformed into MNI152 standard-space. Participants with over 2 mm of total displacement as a result of motion in any direction were excluded from further analyses (n = 3 removed: 1 non-PPD; 2 PPD).

fMRI data were analysed using a general linear model specifying a block-design, random effects analysis in SPM. Coefficients (beta-weights) were estimated for eight conditions of interest: OwnView, OwnRate, UnfamiliarView, UnfamiliarRate, SceneryView, SceneryRate, MammalsView and MammalsRate. Six motion correction parameters and a constant were included in the model as regressors of no interest. Processing also included a 128 second high pass filter and used the canonical haemodynamic response function. Although viewing and rating conditions were modelled separately, the design was not meant to tease apart the relationship between viewing pictures and rating them. Hence, the block design results reflect a blending of both task components by combining the View and Rate conditions to generate the following one-sided contrasts of interest: Own, Unfamiliar and Scenery. The main goal of the study was to compare mothers and non-mothers, and it is not possible, nor intended, to test group differences using the Own condition. The Unfamiliar-Scenery contrast was used to assess the specificity of the neural response to infants. Given that the Mammals condition consisted of mammalian animal pictures, we chose to contrast the Unfamiliar infant condition with inanimate, non-face stimuli constituting the Scenery condition.

2.4.4 | Region of interest (ROI) analysis

Amygdala ROI was anatomically defined at 70% probability threshold using the Harvard-Oxford subcortical anatomical atlas,[55] distributed with FSL (www.fmrib.ox.ac.uk/fsl). We recognise that the human amygdala is comprised of distinct subregions, each with their own afferents and efferents.[56-59] Subregions are also differentially involved in the processing of emotional face stimuli, especially in anxious individuals.[60,61] We chose to examine the amygdala as a whole for comparison with the extensive work that uses this approach to examine the functional significance of the amygdala in MDD. Mean beta-weights were extracted as parameter estimates[62] from each region of interest (right and left amygdala) for each contrast and condition using the SPM *Marsbar* toolbox[63] and entered into SPSS, version 20 (IBM Corp., Armonk, NY, USA) for statistical analyses.[21,30,64]

2.4.5 | Defining the BOLD response

The term BOLD response throughout the paper refers to a differential response as measured by the extracted beta-weights for amygdala responsiveness to the Unfamiliar infant and Scenery conditions. It is important to note that beta-weights refer to the slope of the line in the GLM model, indicating the strength and direction of the relation between the BOLD signal and the expected signal for the condition of interest. The further away a beta-weight is from zero, the greater the strength of the relationship between the BOLD signal and condition of interest.[65]

2.5 | Analysis strategy

ANOVAs were computed to investigate the effects of maternal and depression status on the amygdala BOLD response to the scan conditions separately at the contrast- (Unfamiliar-Scenery) and condition-level (Unfamiliar infant, Scenery). By contrast to the study by Wonch et al[12], the analyses in the present paper focused on responses by non-mothers in comparison to mothers and on unfamiliar infant stimuli in comparison to Scenery. Because of the non-mother status of the non-mother groups, Own infant analyses were obviously not undertaken. Separate analyses were performed for the right (R-AMY) and left amygdala (L-AMY). Participant age and medication status were entered as covariates in all ROI-related ANOVAs.

To examine depression and anxiety symptom severity, EPDS, MADRS and STAI-T scores were entered into SPSS, version 20 (IBM Corp.) for analyses with extracted mean beta-weights across contrast conditions. Alpha level for significance was set at 0.05. Partial eta squared (η^2) were reported and indicate the effect size. Cohen[66] categorises the effect size as small, medium, and large if the η^2 values are 0.01, 0.059 and 0.138, respectively.

3 | RESULTS

3.1 | Subject characteristics

Demographic characteristics are summarised in Table 1.

3.1.1 | Maternal status

Regardless of depression status, mothers and non-mothers differed on age t_{99} = 2.82, $P < 0.01$, such that non-mothers were younger than mothers. There were no significant differences, between mothers and non-mothers, in their level of education. Within the depressed groups, mothers and non-mothers did not differ on any demographic dimension. However, the non-depressed groups significantly differed on age (t_{52} = 2.96, $P < 0.05$), employment status (χ^2 = 14.67, df = 7, $P < 0.05$), marital status (χ^2 = 19.85, df = 1, $P < 0.001$) and household income (χ^2 = 12.98, df = 3, $P < 0.01$) such that non-depressed non-mothers were younger, less were married or living with

TABLE 1 Subject characteristics

	Mother		Non-mother	
Demographic	**Non-PPD (n = 25)**	**PPD (n = 32)**	**Non-MDD (n = 29)**	**MDD (n = 15)**
Age of participant (years), mean ± SD^{**,1,2,3,4}	29.44 ± 4.20	30.13 ± 5.04	26.59 ± 2.57**	29.27 ± 3.73
Highest education level (%)				
Some high school	0.00	3.10	0.00	0.00
High school graduate	4.00	9.40	3.40	6.70
Some college or technical training	16.00	12.50	10.30	0.00
Technical training complete	4.00	9.40	0.00	6.70
College/university graduate	52.00	50.00	51.70	53.30
Some graduate school	4.00	9.40	13.80	6.70
Graduate degree	20.00	6.30	20.70	26.70
Employment status (%)^{*,b,**,a}				
Full time	44.00	43.80	35.70	33.30
Part time	12.00	6.30	25.00	33.30
Full time in home	4.00	12.5	3.60	6.70
Part time in home	4.00	0.00	0.00	0.00
Full time parent	24.00	25.00	–	–
Self-employed	0.00	0.00	3.60	0.00
Student	0.00	0.00	17.90	0.00
No occupation	12.00	9.40	14.30	13.30
Marital status (%)^{***,a,b}				
Single	4.00	18.80	62.10	46.70
Cohabitate	96.00	81.30	37.90	53.30
Household income (%)^{**,a,b}				
$ 0-28 000	12.00	25.00	46.40	64.30
$ 29 000-50 000	16.00	18.80	21.40	7.10
$> 50 000	36.00	43.80	28.60	14.30
$> 100 000	36.00	12.50	3.60	14.30
Want to have children (%)				
Yes	–	–	79.30	53.80
No	–	–	20.70	46.20
Parity (%)				
Primiparous	68.00	65.60	–	–
Multiparous	32.0	34.40	–	–
Delivery method (%)				
Vaginal	72.00	78.10	–	–
Caesarean section	28.00	21.90	–	–
Feeding method (%)				
Exclusively breastfeeding	60.00	34.40	–	–
Bottle, or combination of breast and bottle	40.00	65.60	–	–
Infant gender (boys:girls)	1.40	.940	–	–

Note: For participant age, *t* tests were conducted. We found group differences: (1) between mothers and non-mothers; (2) between non-depressed women (non-PPD vs non-MDD); (3) between depressed and non-depressed women; and (4) between non-mothers (MDD vs non-MDD).
Chi-squared analyses were conducted for categorical measures, we found group differences: (a) between mothers and non-mothers and (b) between non-depressed mothers and non-depressed non-mothers (non-PPD vs non-MDD).
Abbreviations: MDD, depressed non-mothers; non-MDD, non-depressed non-mothers; non-PPD, non-depressed mothers; PPD, depressed mothers.
$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

TABLE 2 Clinical measures

Clinical Measures (mean ± SD)	Mother		Non-mother	
	Non-PPD	PPD	Non-MDD	MDD
EPDS				
Visit 1^{***,1,2,3}	3.12 (2.26)	7.66 (5.77)	3.55 (2.65)	8.54 (3.10)
Visit 2^{**,3,***,1,2}	2.60 (2.27)	7.38 (5.27)	3.72 (2.39)	7.38 (4.91)
MADRS				
Visit 1^{***,1,2,3}	1.92 (1.98)	9.81 (7.99)	1.89 (2.70)	9.00 (7.42)
Visit 2^{*,3,***,1,2}	1.46 (1.91)	10.51 (6.74)	1.69 (1.91)	7.00 (9.45)
State-Trait Anxiety Inventory (Trait version)				
Visit 1^{***,1,2,3}	28.36 (5.18)	41.87 (11.90)	32.07 (6.82)	48.87 (11.06)
Visit 2^{*,3,***,1,2}	27.75 (5.10)	42.48 (11.09)	30.55 (7.03)	44.47 (12.12)
Medication Status (%Yes)	–	37.5	–	13.33

Note: Group comparisons based on *t* tests, differences were found: (1) between depressed and non-depressed women; (2) between mothers (PPD vs non-PPD); and (3) between non-mother (MDD vs non-MDD).

Visit 1 refers to the structured diagnostic interview consistent with the diagnostic criteria of the Diagnostic and Statistical Manual fourth edition text revision.[33] Visit 2 refers to the time of the functional magnetic resonnace imaging scan 1 week after visit 1.

Abbreviations: EPDS, Edinburgh Postnatal Depression Scale; MADRS, Montgomery and Asberg Depression Rating Scale; MDD, depressed non-mothers; non-MDD, non-depressed non-mothers; non-PPD, non-depressed mothers; PPD, depressed mothers.

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

a partner, and had lower household income (Table 1). Finally, a higher proportion of non-mothers compared to mothers were reported taking hormonal contraceptives ($\chi^2 = 8.189$, , $df = 1$, $P < 0.01$). As a result, we controlled for participant age and hormonal contraception status in subsequent analyses.

3.1.2 | Depression

Within mothers, there were no group differences between depressed and non-depressed on any demographic characteristics, nor any differences in parity, method of delivery, feeding methods and sex of their infants. Within non-mothers, we found group differences between depressed and non-depressed groups in age ($t_{42} = 2.80$, $P < 0.01$) because the non-depressed groups were younger. However, the two non-mother groups did not differ on any other demographic dimension. Furthermore, we did not find differences between groups in their reported desire to have children in the future (Table 1).

3.1.3 | Clinical measures

As indicated in Table 2, there were significant differences in depression severity between depressed and non-depressed groups. Within mothers, the PPD group had greater levels of depression severity (EPDS: $t_{55} = 4.61$, $P < 0.001$; MADRS: $t_{53} = 7.12$, $P < 0.001$) and trait-anxiety scores (STAI-trait version: $t_{53} = 6.554$, $P < 0.001$) than the non-PPD group. Similarly, within non-mothers, the MDD group had greater levels of symptom severity (EPDS $t_{36} = 2.54$, $P < 0.01$; MADRS: $t_{42} = 2.15$, $P < 0.05$; STAI-t: $t_{42} = 4.10$, $P < 0.01$) than the non-MDD group. Regardless of depression status, there were no differences between mothers and non-mothers on the severity of depression and anxiety levels. There were no differences between the depressed mothers (PPD) and depressed non-mothers (MDD), nor between non-depressed mothers (non-PPD) and non-depressed non-mothers (non-MDD) in depression severity scores (EPDS, MADRS) and anxiety scores (STAI-t) (Table 2). We found no relationship between symptom severity and medication status in the depressed groups.

3.2 | Subjective affective response

To determine the effects of maternal-status and depression on the subjective affective ratings to Unfamiliar infant and Scenery, we conducted a 2 (within: Unfamiliar infant, Scenery) × 2 (between: mother, non-mother) × 2 (between: depressed, non-depressed) mixed design ANOVA. We found a significant interaction between maternal status and condition ($F_{1,96} = 28.2$, $P < 0.001$), such that mothers rated the Unfamiliar infants more positively than Scenery, while non-mothers rated Scenery more positively than Unfamiliar infants (Figure 2A). We also found a main effect of depression ($F_{1,96} = 4.96$, $P = 0.028$), such that depressed groups, regardless of maternal status, had lower ratings than non-depressed groups to both Unfamiliar infant and Scenery (Figure 2B). The effects are maintained after including age as a covariate in the model.

We did not find a significant correlation between the subjective affective response and AMY BOLD response.

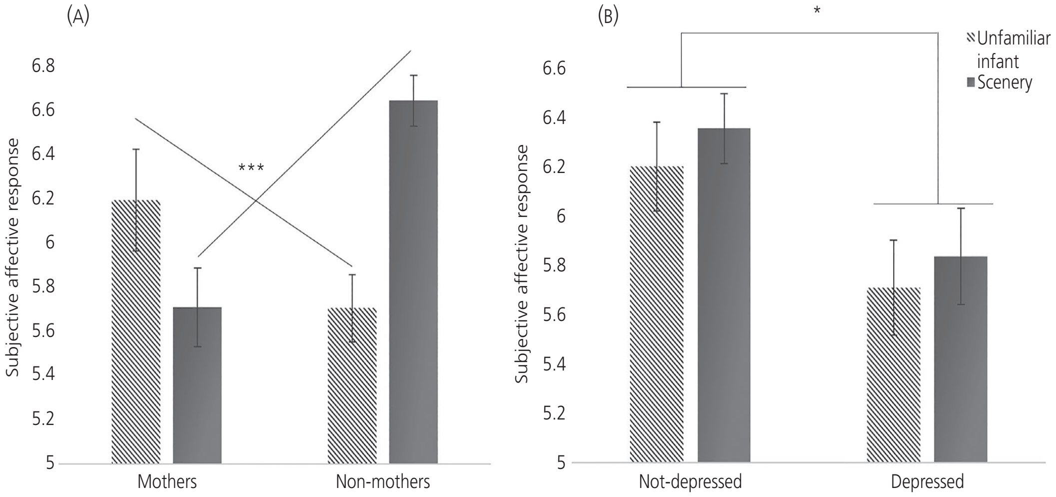

FIGURE 2 Subjective affective response. (A) Maternal status × stimulus-types interaction; collapsed across depression status, mothers rated the Unfamiliar infants more positively than non-mothers, and non-mothers rated Scenery more positively than non-mothers. (B) Main effect of depression; collapsed across maternal status, depressed women rated both Unfamiliar infant and Scenery less positively than non-depressed women. Error bars indicate the SEM. **P* < 0.05 ****P* < 0.001

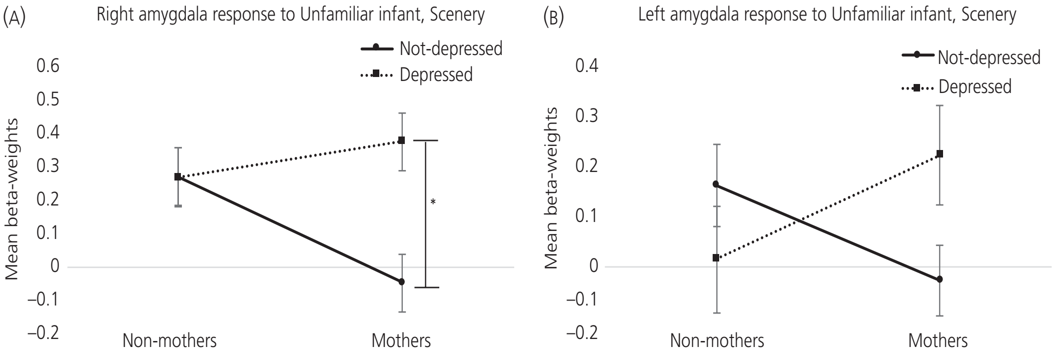

FIGURE 3 Contrast-level analyses. Amygdala response to the Unfamiliar-Scenery contrast as a function of maternal status and depression status in the right (A) and left (B) amygdala. A, Maternal status × depression status interaction in the right amygdala response to the Unfamiliar-Scenery contrast. Elevated right amygdala response in depressed mothers compared to non-depressed mothers but with no difference in amygdala response as a function of depression between the two non-mother groups. B, Similar pattern in left amygdala responsiveness but not statistically significant. Error bars indicate the SEM. **P* < 0.05

3.3 | ROI analysis

3.3.1 | Contrast-level (Unfamiliar-Scenery)

To determine the effects of depression and maternal status on amygdala responsiveness to the Unfamiliar-Scenery contrast, the extracted beta-weights were subjected to a 2 (mothers, non-mothers) × 2 (depressed, not depressed) one-way ANOVA. For the right amygdala (R-AMY), we found a significant interaction between maternal status and depression ($F_{1,95} = 5.048$, $P = 0.027$, $\eta^2 = 0.050$), indicating a greater amygdala response to the contrast in depressed compared to non-depressed mothers, although no difference between depressed and non-depressed non-mothers. In other words, we found a greater R-AMY response to the Unfamiliar-Scenery contrast in PPD compared to non-PPD but no difference in the R-AMY response between MDD compared to non-MDD (Figure 3A).

Although not statistically significant, we found a marginal interaction between depression and maternal status to L-AMY responsiveness to the Unfamiliar-Scenery contrast ($F_{1,95} = 3.277$, $P = 0.073$, $\eta^2 = 0.033$) showing the same patterns as the R-AMY (Figure 3B).

3.3.2 | Condition-level (Unfamiliar infant, Scenery)

It is important to consider that the Unfamiliar-scenery contrast is a difference score. Therefore, it is necessary to determine which stimulus condition is driving the aforementioned effects. To investigate the effects of depression and maternal status on the amygdala response to each condition, we computed a 2 (within ROI: Unfamiliar infant, Scenery) × 2 (between subjects: mothers, non-mothers) × 2 (between subjects: depressed, non-depressed) mixed design ANOVA. We found a main effect of maternal status, such that mothers' RAMY response was greater for both Infant and Scenery compared to non-mothers ($F_{1,95}$ = 6.005, P = 0.016, η^2 = 0.059), although the maternal status effect did not survive after controlling for parity. Within-subjects, we found a main effect of condition ($F_{1,95}$ = 5.355, P = 0.023, η^2 = 0.053), such that the mean response to Unfamiliar infant was greater than the mean response to Scenery. The differential response to Infant vs Scenery is greater in depressed compared to the non-depressed women, as indicated by the condition by depression interaction ($F_{1,95}$ = 6.307, P = 0.014, η^2 = 0.062). Finally, we found a three-way interaction between condition, depression and maternal-status ($F_{1,95}$ = 5.047, P = 0.027, η^2 = 0.050). This three-way interaction indicates a different pattern of response to each condition between mothers and non-mothers given their depression status and/or a different pattern of response to each condition between depressed and non-depressed given their maternal status (Figure 4). Post-hoc comparisons using Tukey's honestly significant difference test revealed that the right amygdala BOLD response for the Unfamiliar infant condition was significantly greater in depressed mothers (PPD) compared to non-depressed mothers (non-PPD). The two non-mother groups did not differ in their response to Infant, nor Scenery, but both groups of non-mothers showed differential response to condition such that the R-AMY responded more to Unfamiliar infant than Scenery. There were no group differences in the R-AMY response to the Scenery condition, suggesting that all four groups responded similarly to Scenery.

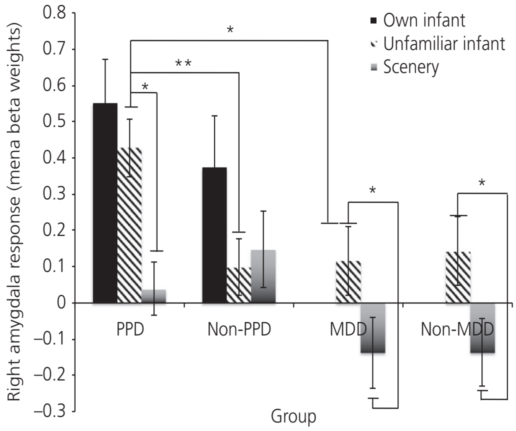

FIGURE 4 Condition-level analyses. Right amygdala response to three stimuli types (conditions) presented during the functional magnetic resonance imaging (fMRI) affect-rating task. With the exception of non-depressed mothers (non-PPD), all groups showed a greater right amygdala response to Unfamiliar infant compared to scenery. Maternal status × depression status × stimulus-type interaction (2 × 2 × 2 interaction). The depressed mothers (PPD) group showed elevated right amygdala response to Unfamiliar infant compared to non-PPD and compared to depressed non-mothers (MDD). Non-MDD, non-depressed non-mothers. Error bars indicate the SEM. Note that the present study does not include a response to own infant in any of the statistical analyses because these findings are detailed in our previous study.[12] The mother's response to own is included in this figure to present a more comprehensive illustration of the right amygdala response to all stimuli-types presented within the ART during the fMRI session. *P < 0.05 **P < 0.01

Although not statistically significant, we found a marginal three-way interaction between stimulus type, maternal status and depression in the left amygdala (L-AMY) BOLD response ($F_{1,95}$ = 3.28, P = 0.073, η^2 = 0.033), showing the same patterns of responsiveness as the R-AMY.

3.4 | Group-level comparisons

3.4.1 | Mothers vs non-mothers

Regardless of depression status, mothers' R-AMY was more responsive to both Unfamiliar infants and Scenery compared to non-mothers ($F_{1,95}$ = 6.005, P = 0.016, η^2 = 0.059). Within the non-depressed groups (non-PPD vs non-MDD), we found no group differences in their R-AMY response to Unfamiliar infant, although mothers showed a marginally greater response to Scenery compared to non-mothers (t_{52} = 2.007, P = 0.05). Within the depressed groups (PPD vs MDD), the PPD group showed a greater R-AMY response to Unfamiliar infant (t_{45} = 2.361, P = 0.023), although we found no group differences in R-AMY responsiveness to Scenery (Figure 4).

3.4.2 | Depressed vs non-depressed

Within mothers (PPD vs non-PPD), we found that the PPD group showed a greater R-AMY response to Unfamiliar infant compared to the non-PPD group (t_{55} = 2.921, P = 0.005), although there were no group differences in the R-AMY response to Scenery. Within non-mothers, we found no group differences in R-AMY response to either condition (Unfamiliar infant, Scenery) (Figure 4).

The ROI-BOLD effects described above were maintained after controlling for parity and hormonal contraception status by including them as covariates in the analyses models. These effects were also maintained when depression status was defined by EPDS scores (cut-off ≥ 7).

4 | DISCUSSION

This is the first study directly comparing the amygdala responsiveness to positive (smiling) pictures of infants in mothers and non-mothers, who are depressed or not depressed. This was achieved by employing a 2 × 2 experimental design. In terms of the subjective report, our predictions based on the salience hypothesis established from work on animals were confirmed.[1,67] Regardless of depression status, mothers rated infants more positively than did non-mothers and non-mothers rated scenery more positively than did mothers. In terms of depression effects on the subjective affective report, we found a main effect of depression, such that both groups of depressed women rated babies and scenery as less positively than non-depressed women, regardless of maternal status. This is consistent with studies showing that positive stimuli are perceived less positively by depressed and anxious individuals.[45,50]

Despite these clear results for stimulus effects on affective responses, the brain responses are less easy to interpret and affective responses are not predictive of how the brain interprets these same stimuli. We found that depression elevated amygdalar response to smiling unfamiliar infants in mothers but had no effect in non-mothers. This is consistent with our previous work[12] showing that, although PPD and non-PPD mothers did not show a differential amygdala response to their own infant's pictures, the PPD group in comparison to non-PPD group showed an elevated response to an unfamiliar infant's pictures. This elevated response to the own and unfamiliar infants in the PPD group but not the in the non-PPD group, indicated a blunted unique amygdala responsiveness to own infant in the PPD group.[12] These results are consistent with the literature showing that depression affects attention to salient events and stimuli[45,50,68] and is also consistent with the role of the amygdala in vigilance detection[6] and processing socioemotionally relevant stimuli.[5] By contrast, although we expected a depression effect in non-mothers, we did not find one. Compared to the non-MDD group, the MDD group did not show an elevated response to the unfamiliar infant. However, non-mothers were never presented with the contrast of their own infant, which has been established by various studies[7,8,11-14,16,17] as the source of an amygdala response unique to mothers. Furthermore, there is no clear consensus on the direction of amygdala responsiveness to positive stimuli in depressed individuals relative to non-depressed individuals with some studies showing no differences in amygdala responsiveness between depressed and non-depressed individuals.[9]

We also expected that non-mothers, compared to mothers, would show a reduced amygdala response to the unfamiliar infant because infants are considered less salient to non-mothers.[47,48] This did not occur. The two groups (non-PPD and non-MDD) showed similar amygdala responses to the infant stimulus condition. Our understanding of these surprising effects is again based on the fact that, in the design, mothers were exposed to both their own and another infant, whereas, by definition, non-mothers were only exposed to unfamiliar infants. This difference intrinsic to the subject populations could well result in the unfamiliar infant stimulus having a very different meaning as a function of the woman's maternal status. To directly assess the effects of familiarity and stimulus salience on amygdala responsiveness between mothers and non-mothers, it would be ideal to compare the amygdala response to a series of familiar and unfamiliar salient and nonsalient stimuli. However, this paradigm does offer a form of ecologically valid assessment of the neural response to infant stimuli. Specifically, because a non-mother's interactions with infants are by definition with infants that are not her own, and a new mother's interaction with unfamiliar infants are in the context of her own especially within the first 2-5 months postpartum--the selected postpartum duration assessed in this present study.

Although PPD and MDD share similar symptomology, they are differentiated by timing of onset, and PPD often involves excessive worry and/or guilt surrounding parenting abilities.[32-36] This may suggest that infants are more salient stimuli to PPD mothers in contrast to MDD non-mothers, and thus may be predictive of a greater amygdala response to infants in PPD relative to MDD. However, we were unable to predict the direction of amygdala responsiveness to *positive* infant stimuli between the two groups, given that this is the first direct comparison between PPD and MDD, and the predominant effects of depression on amygdala responsiveness have been generally assessed towards negative stimuli in PPD. PPD and MDD, assessed independently, show an amygdalar hypo-responsiveness[9] and hyper-responsiveness,[17] respectively, to negative stimuli. In addition, it is difficult to compare and interpret the neuroimaging literature on the neural responsiveness to infant stimuli as a result of the wide variability in methodologies such as stimulus modality (auditory, visual), standardisation of the stimuli, sample size, analysis methods and the postpartum stage of mothers.[17,42]

Our results clearly demonstrate that the PPD group's amygdala shows a hyper-responsiveness to positive infants both in comparisons with non-PPD mothers and MDD non-mothers. This elevated pattern of amygdala response in PPD mothers is also observed in response to their own infant's pictures,[12,21] as well as in response to infant cries when mothers were asked to imagine imagining themselves crying.[19] This is in contrast to the hypo-responsiveness previously demonstrated to negative stimuli including infants in distress.[43] This dissociation in amygdala engagement to positive and negative infant stimuli may suggest a dysregulation in the neural processing of infant cues as a function of affect (positive or negative facial expressions). Furthermore, this dysregulation may underlie the disruptions of normative parenting abilities observed in PPD. Compared to mothers without PPD, mothers with PPD respond less sensitively and contingently to their infants, and are more likely to display irritated and intrusive behaviours during mother-infant interactions.[37-40] PPD mothers also appear to engage in less affectionate[37,40] and less synchronous interactions[69] with their infants, relative to mothers without PPD. Kim et al.[70] demonstrated a correlation between maternal sensitivity and brain function in the amygdala and frontal cortex in a sample of breastfeeding and formula-feeding mothers. In addittion, recent studies have identified altered amygdala connectivity to downstream neuronal processes as a function of maternal depression[12,21] and anxiety[18] in response to infant cues. Furthermore, Guo et al[18] found that anxiety mediated the relationship between measures of maternal behaviour and amygdala connectivity. Taken together, these studies suggest that perturbations in amygdala connectivity to downstream processes as a function of maternal depression and anxiety may be inhibiting goal-directed behaviour[70] and contributing to decreases in sensitive and positive caregiving.

With respect to laterality effects, although we found a similar pattern of maternal and depression effects in both left and right amygdala responsiveness to infant pictures, the effects were statistically significant in the right amygdala only. This laterality of response to positive pictures is consistent with studies demonstrating a preferential right amygdala response to stimuli that is affectively positive,[71] pictorial in nature,[72-74] as well as with studies investigating differences in amygdala responsiveness to facial expressions and scenery.[75] Although the evidence remains inconclusive, there are a few suggested hypotheses on the differences between the functional specialisation of the left and right amygdalae. Markowitsch[74] proposed that the right amygdala may encode affective information in pictorial stimuli and would show greater engagement to fast processing of affect compared to the left amygdala, which may be more engaged to affective information presented through language or present in the fine-grained detail of a stimulus. Similarly, Phelps et al[76] hypothesised that laterality of amygdala activation may be related to the degree by which elaboration and interpretation is required of the affective stimulus to the individual subject, thus the greater right over left amygdala response is observed for stimuli that is visual and not ambiguous to the individual. In a meta-analysis, Wager et al[77] concluded a greater left amygdala engagement to emotional stimuli especially affectively negative stimuli. Similarly, Baas et al[72] found more studies reporting left amygdala engagement in a systematic review on the laterality of amygdala engagement in the neuroimaging studies of emotion.

Understanding that several brain regions are implicated in both the maternal[7,8] and depression[9,10] neural circuitry, we chose to focus on the amygdala. Thus, the present study is naturally limited to assessing the differential patterns of the whole amygdala response to infants, it does not extend the analysis to assess functional connectivity. Furthermore, the amygdala contains structurally and functionally heterogeneous subregions each with its own afferents and efferents.[56-59] Three subregions have been identified in humans: basolateral, centromedial and superficial amygdalae. From work on rodents, it is well established that the basolateral amygdala has an excitatory role in the expression of maternal behaviours through the nucleus accumbens within the ventral striatum, whereas the centromedial amygdala plays an inhibitory role.[1] Consistent with these findings, preliminary findings from our group (KE Wonch et al, unpublished data) show that non-PPD mothers had an increased basolateral amygdala connectivity to the ventral striatum which was not observed in the PPD group. The next steps include examining effects of maternal status and depression on the responsiveness and functional connectivity of each amygdala subregion to infant pictures.

A number of other limitations need to be considered. Depression status in the present study was established according to diagnostic criteria that are not always captured by the widely used EPDS cut-off of 12 for PPD.[52] PPD mothers received a diagnosis of at least one major depressive episode with peripartum onset by a clinician at the WHCC. However, some mothers were receiving treatment at the clinic. As such, for some PPD women, symptoms may have stabilised or become subclinical at the time of the scan. The mean EPDS score for PPD mothers was below an EPDS cut-off of 12. Nonetheless, the mean EPDS score of 7.66 for PPD mothers is within the range of published cut-offs for the postpartum period.[78,79] This could be for a variety of reasons in addition to the observation that some women were responsive to treatment at the clinic. For example, PPD symptoms are inherently variable in nature, and symptom heterogeneity is often observed in PPD samples.[80] Furthermore, a systematic review has demonstrated a wide range in the sensitivity and specificity of the EPDS metric across different experimental settings, and so a particular cut-off may not be sensitive to the wide range of symptoms associated with PPD.[81] The results of the present study may be best interpreted to reflect responsiveness to infant pictures by a sample of mothers who have had at least one major depressive episode during the perinatal period (during pregnancy and/or postpartum). With regard to the severity of depression among nulliparous women, MADRS scores are considered within the mild range[82] for most in the MDD group in the present study. Therefore, interpretation of the results of the study is limited to mildly depressed mothers (PPD) and non-mothers (MDD) at the time of study.

As discussed above, the present study assessed effects of depression and maternal status on amygdala responsiveness specifically to affectively positive stimuli (smiling infants). Given, the well-established/classic role of the amygdala in processing negative or threatening stimuli,[6] along with the heightened sensitivity to negative affect in late-pregnancy,[68] it would be ideal to assess group differences in responsiveness to infants across a range of affect. Furthermore, there is considerable evidence pointing to the effects of menstrual phase, and thus variations in oestrogen levels,[83] with respect to modulating the response of the amygdala to stressful and arousing stimuli as part of the stress and arousal neural circuitry.[83-85] The present study did not account for menstrual phase. Therefore, the neural and affective responsiveness to infant stimuli may have not been captured during the same menstrual phase for all women. This is a limitation of the present study, as well as other previous studies investigating neural responsiveness to infant stimuli.[18-23,27,64] Ideally, responsiveness to infant pictures should be captured during the same menstrual phase for all women in the study. Not doing so reduces the rigor of the study design and threatens the validity of the results because these may be confounded. As such, future studies are encouraged to collect responsiveness (neural and affective) to infant pictures during the same menstrual phase across participants, as well as to consider levels of gonadal steroids at the time of the data collection.

Finally, the present study provides some first insights into women's differential pattern of amygdala responsiveness to smiling infant pictures as a function of maternal status and depression, and demonstrates a clearly elevated right amygdala response in the PPD group. Considering that PPD is the most common maternal birth complication coupled with the condition's potential pervasive impact on the developing infant demonstrates the clear need for continued investigation into the neural underpinnings of PPD.

CONFLICT OF INTERESTS

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available as a result of privacy or ethical restrictions.

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Chapter 4

Study 3: Exploring the morphological and emotional correlates of infant cuteness.

4.1 OVERVIEW

Rationale. This study explores the morphological and emotional correlates of the infant pictures presented in chapters 2 and 3; therefore, providing a more in-depth examination of the stimuli. Ethologists postulated that mammalian infant's cuteness is a protective mechanism that ensures the young's survival by eliciting caregiving behaviour and decreasing negative emotional states such as aggression. Konrad Lorenz provided the first description of cuteness as a set of infantile features including a large head relative to the body, a large prominent forehead, and large eyes that are set relatively low in the head. Past efforts to quantify cuteness were restricted to line measurement techniques. Recent development of facial delineation software provides a tool that allows quantifying infant cuteness at a higher resolution. In this study, we developed a method to quantify infant cuteness to create an objective data-driven infant metric. To our knowledge, this is the first study to empirically investigate ethological claims regarding adults' emotional responses elicited by cuteness. **Specific Aims.** 1. To use a data-driven approach to quantify infant cuteness using morphological variations from positive infant pictures. 2. To investigate the emotional correlates of infant cuteness. **Methods.** We delineated facial elements of 72 infant pictures using the Psychomorph software by using 206 facial points forming 43 lines. Facial elements were entered into a principal component analysis, we retained components that explained 90% of the variance. Each infant picture therefore had a value corresponding to each component (components 0-14). To determine whether the components were associated with subjective perceptions of infant cuteness, 108 nulliparous females rated the pictures on cuteness and emotional dimensions (using the Emotional Response Scale (ERS)). Facial components that correlate with subjective cuteness ratings were then used to compute a data-driven infant cuteness metric (DDIcute). **Results.** In terms of morphological correlates of infant cuteness, we found that 5 facial components correlated with subjective ratings of infant cuteness (see Figure 2) including components characterized by a large and wide forehead relative to the narrower chin, a big smile, roundness of the face, as well as long asymmetrical features. Adult-like components such as a square jawline were negatively associated with subjective ratings of infant cuteness. The DDIcute metric is a sum of the centered (z-scored) measure of these components. In terms of emotional correlates of infant cuteness, the DDIcute metric was positively correlated to positive components of the ERS (positive affect, sympathy, calm, delighted, interested, and the need to respond) and negatively correlated to negative components of the ERS (distress, disturbed, alert, and irritated). Using a multiple linear regression, ERS scores significantly predicted the DDIcute measure when both negative and positive ERS components were entered together, but only the positive ERS factor predicted

DDIcute alone. **Conclusion.** We were able to successfully quantify infant cuteness into a single data driven metric. This is the first investigation into the relationship between infant cuteness (morphologically) and emotional responses.

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Full Length Article

Exploring the morphological and emotional correlates of infant cuteness

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ABSTRACT

Ethologists have observed that “baby schema” or infant cuteness is an adaptive protective mechanism ensuring the young’s survival. Past efforts to quantify cuteness have been restricted to line measurement techniques. We developed a novel data-driven approach to quantify infant cuteness into a single metric. Using the Psychomorph program, we delineated facial elements of 72 infant pictures using 206 facial points and identified the facial components that were significantly related to subjective cuteness perceptions of the faces. 108 nulliparous females rated the pictures on cuteness and emotional dimensions. We found that cuter infants have larger cephalic curvature compared to a smaller chin, a big smile, and round chubby features among others. We also investigated the relationship between cuteness and emotional responses. Our results show that a greater degree of cuteness elicits both increased positive emotional responses and decreased negative emotional responses. Cuter infants also elicited greater feelings of alertness, interest, and the need to respond. In fact, the participants’ emotional responses were predictive of both data-driven scores and subjective perceptions of cuteness.

1. Exploring the morphological and emotional correlates of infant cuteness

For most of us it would be near to impossible to keep a straight face while looking at a cute infant. According to ethologists, offspring cuteness is a “potent protective mechanism” as it elicits caregiving behavior and decreases aggression, thus ensuring infant survival (Eibl-Eibesfeldt, 1970; Hess & Polt, 1960; Kringelbach, Stark, Alexander, Bornstein, & Stein, 2016; Lorenz, 1943). Initial observations regarding infant cuteness were documented by ethologists like Lorenz (1943) who observed that for a variety of mammalian species, the young share a particular set of features—or “baby schema”—that distinguish them from adults and serve to elicit caretaking behaviours (Eibl-Eibesfeldt, 1970). Among others, these infantile features include: a large head in relation to the body; a large prominent forehead, with the eyes set relatively low in the head; round and protruding cheeks; plump, rounded body shape; short, thick extremities and soft body surfaces.

In general, mammalian infants are perceived as cuter than older conspecifics (Lorenz, 1943). This is also true across human

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cultures, both men and women respond more positively to an infant's face than to an adult's (Brosch, Sander, & Scherer, 2007; Parsons, Young, Kumari, Stein, & Kringelbach, 2011). Importantly, adults respond differentially to infants varying in the degree of cuteness; they are willing to repeatedly press a button to maintain looking at cuter infants (Hahn, Debruine, & Jones, 2015), and will preferentially adopt and donate toys to cuter infants in a contrived experimental task (Golle, Probst, Mast, & Lobmaier, 2015). Interestingly, compared to infants perceived as less cute, infants rated highly on the cuteness dimension capture attention (Senese et al., 2013) and engage attention-related brain regions such as the precuneus (Glocker, Langleben, Ruparel, Loughead, Valdez et al., 2009). Furthermore, pictures of cuter infants rapidly activate brain regions associated with the reward neural network such as the nucleus accumbens and the orbitofrontal cortex (Brosch et al., 2007; Glocker, Langleben, Ruparel, Loughead, Valdez et al., 2009; Kringelbach et al., 2016; Parsons et al., 2014). Kringelbach et al. (2016) hypothesized that this rapid neural activation could cascade to other brain regions important for caregiving.

The relationship between the degree of infant cuteness and the maternal care received is not well studied; however, one study by Langlois, Ritter, Casey, and Sawin, (1995) showed that more attractive infants received higher quality of maternal care. To extend this work it would be beneficial to have a single data-driven metric of infant cuteness. To do so, it is essential to examine the association between morphological face measurements and perceptions of cuteness. In addition, it is important to note that attractiveness and cuteness are separate constructs especially with reference to adult features (Kuraguchi, Taniguchi, & Ashida, 2015). However, infant cuteness and attractiveness are highly correlated (Stephan & Langlois, 1984) and these terms are often used interchangeably in the infant cuteness literature (Alley, 1981; Boukydis, 1981; Glocker, Langleben, Ruparel, Loughead, Valdez et al., 2009; Hahn & Perrett, 2014; Hildebrandt & Fitzgerald, 1978; Hildebrandt & Fitzgerald, 1979; Karraker, 1990; Lehmann, Huis in't Veld, & Vingerhoets, 2013; Little, 2012; Sternglanz, Gray, & Murakami, 1977).

Past efforts that have utilized morphological measurements to examine cuteness have been limited by the use of a small number of line measurements to capture differences across a select few facial features. Furthermore, it may be suggested that the stimuli in such work had reduced ecological validity resulting from the use of line drawings of infants (Alley, 1981; Sternglanz et al., 1977), black and white photographs of infants (Hildebrandt & Fitzgerald, 1978; Hildebrandt & Fitzgerald, 1979), or infant photographs in colour manipulated to create a "super cute baby" with unrealistic features (Glocker, Langleben, Ruparel, Loughead, Valdez et al., 2009; Hahn et al., 2015). Recent developments in facial delineation and recognition software can help address such limitations and provide the means to more clearly elucidate facial features important in the perception of infant cuteness. Building on past work it is expected that cuter babies will have a larger foreheads, small and narrow features below the eyes (Alley, 1981; Hildebrandt & Fitzgerald, 1979; Sternglanz et al., 1977), and large eyes and pupils (Hildebrandt & Fitzgerald, 1979).

In order to understand how such characteristics can lead to optimal caregiving, as proposed by ethologists, it would be important to understand how adults respond to infants varying in cuteness. To our knowledge, no studies have directly investigated ethological claims regarding the role of cuteness in eliciting emotional responses from adults. Cuteness is postulated to facilitate caregiving by eliciting positive emotions and reducing negative, and potentially dangerous, emotional states such as aggression, (Eibl-Eibesfeldt, 1970; Lorenz, 1943). We investigated two separate but related aims: 1. To explore the facial features important in the perception of infant cuteness using a data-driven approach to quantify cuteness based on variations in morphological features between infant photographs, 2. To examine the emotional responses to infant cuteness. We hypothesized that infant cuteness will be associated a rounder face shape, larger eyes and pupils, larger forehead compared to a smaller chin, as well as larger round cheeks. Moreover, we predicted that higher ratings of infant cuteness will be associated with stronger positive emotional responses (delight and calm), greater attention- and approach-related responses (alertness, interest and the need to respond); and lower negative emotional responses (disturbed, distressed and irritated) in line with the ethological observations on cuteness. These emotional responses were examined because of their association with various measures of maternal behavior (Giardino, Gonzalez, Steiner, & Fleming, 2008; Stallings, Fleming, & Corter, 2001). Beyond this paper, we are interested in understanding the relationship between cuteness and caregiving maternal behaviors. As such, we chose to focus on nulliparous female raters. Although our results are limited to female raters, there is considerable evidence supporting a strong universal agreement on what is considered cute across genders (Hahn et al., 2015; Hildebrandt & Fitzgerald, 1979; Schein & Langlois, 2015) as well as across different cultures (1995, Langlois et al., 2000).

2. Methods

2.1. Stimuli selection (Baby Pictures)

2.1.1. Stimuli

72 baby photographs were selected from a larger database (Wonch et al., 2016), which made use of a professional photographer and consisted of a minimum of 20 different positively valenced, i.e. not crying nor distressed, pictures of each baby. The photography sessions always took place in the same room and on the same chair, with standard lighting source and levels calibrated against a black background. During photography, babies were held on the lap of the mother and expressions were elicited by the experimenters (KEW and AD). Positive facial expressions were primarily elicited by the presentation of a new toy or by vocalizations and animated facial expressions produced by the experimenter.

We selected one picture per baby based on the following criteria—presented in order of importance—the most head-on picture for each baby as this is the most optimum position for the delineation of markers, the picture with a medium rating of cuteness (as rated by 6 participants on a 5-point cuteness dimension) compared to others of the same baby, and the overall image quality of the picture (e.g. not blurry).

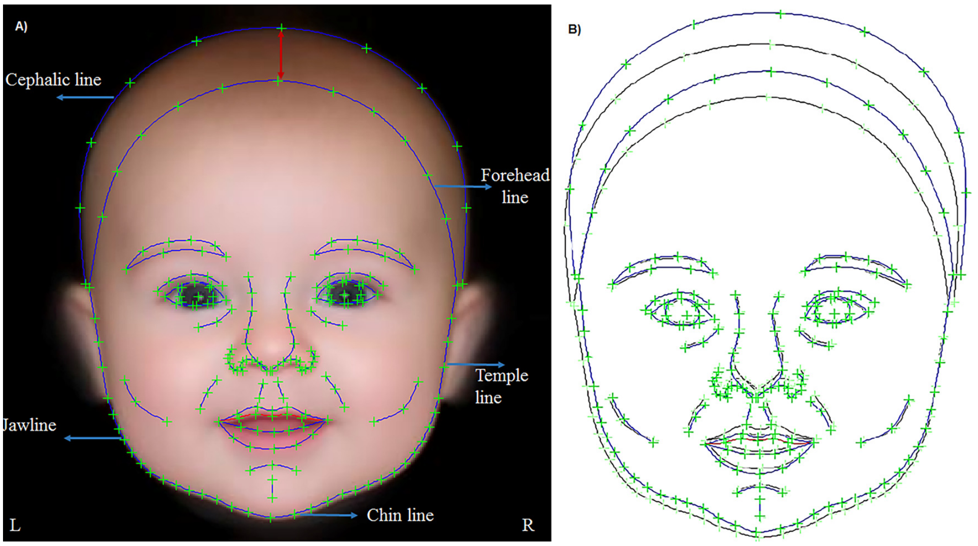


Fig. 1. A) Average image and template created with Psychomorph software (Tiddeman, 2011). 206 facial landmark points/fiducial markers (green points), which formed 43 lines (blue) defining the different parts of the face. The red arrow represents the "cephalic space", blue arrows label lines associated with cuteness: cephalic line, forehead line, jawline, temple line and chin line respectively. L = left, R = right. **B)** The superimposition of component 0 (blue line) to the average temple (gray line) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

2.1.2. Stimuli standardization

Following stimulus acquisition, photographs were cropped, re-sized (dimensions: 13.86 x 12.03 cm at a resolution of 28.35 pixel/cm), adjusted for brightness, and masked by a black background to present only the face according to a standard image format (see Fig. 1a).

2.1.3. Infant characteristics

Pictures of 41 boys and 31 girls were acquired when the infants were 2–5 months of age ($\mu = 3.96$, $\sigma = 0.99$). The sample was composed of 67 Caucasian infants and 5 of other ethnicities including Asian, African and South Asian. The sex of the infant stimuli did not corelate with the ratings of cuteness. All mothers provided signed informed consent permitting the researchers to show their baby's pictures to other research participants.

2.2. Subjective response (rating task)

2.2.1. Participants

108 first-year undergraduate nulliparous females were recruited from McMaster University in Hamilton, Ontario through an undergraduate on-line research recruitment program in the Psychology department. All participants were non-mothers, English-speaking, 18–22 ($\mu = 18.68$, $\sigma = 0.93$) years of age, and did not have a history of, nor current, mental health diagnoses. The majority of participants (92.52%) reported that they wish to have children in the future. The McMaster Research Ethics Board approved the study and written informed consent was obtained from each participant. Participants received academic credit for participating in the study.

2.2.2. Rating Procedure/Paradigm

Participants were divided into four rating sessions with roughly 25 participants per session. Infant pictures were displayed on a projector (BenQ MX812ST, Resolution: XGA 1024 × 768) in an auditorium, and participant responses were acquired using Google Forms' online survey platform via each participant's personal computer or smartphone. The stimuli were presented on standard 4:3 powerpoint slides, with a black background, in the horizontal orientation (Picture dimensions on screen: 1.4 m x 0.94 m). Participants were seated directly in front of the screen. The mean visual angle of presentation was calculated from the center of the room to the screen at 15.41° (range: 25.9° to 9.73°). Infant pictures were presented serially with a 5 s warning tone signaling the transition to the next infant picture. The order of infant pictures was counterbalanced across the four data collection sessions. Participants were given 60 s to rate each infant picture—which remained on the screen for the rating period–on 11 emotional dimensions presented in the following order:

Cuteness. "How cute is this baby?" on a 5 point Likert scale (1: NOT very cute, 5: VERY cute) (Glocker, Langleben, Ruparel, Loughead, Gur et al., 2009; Hildebrandt & Fitzgerald, 1979)
Positive Affect. "How does this picture make you feel?" 9 point Likert scale (1: not at all positive, 9: extremely positive) (Wonch et al., 2016)
The Emotional Response Scale. "Please rate how you feel when you look at this picture": Sympathetic, Alert, Distressed, Disturbed, Irritated, Calm, Delighted, Interested, Need to Respond 8 point Likert scale (1: not at all [adjective, e.g. Sympathetic], 8: extremely [adjective, e.g. Sympathetic]).

It is important to note that the Likert points were not identical across dimensions, as they were adapted from standard scales used in the field (Giardino et al., 2008; Glocker, Langleben, Ruparel, Loughead, Valdez et al., 2009; Hildebrandt & Fitzgerald, 1979; Stallings et al., 2001; Wonch et al., 2016).

Each session started with a practice trial to familiarize participants with the survey procedure and instructions. The task was relatively simple and all participants completed the task in its entirety. The total duration of a session was about 1 h and 15 min.

2.3. *Objective measure of infant cuteness*

Psychomorph software (Chen & Tiddeman, 2010; Tiddeman, 2011) was used to generate an objective measure of infant cuteness driven by the variance in facial dimensions that were related to subjective scores of cuteness. Briefly, each baby face was delineated by a set of markers at prescribed locations on the face, faces were averaged (Fig. 1), then a principal component analysis (PCA) was conducted to determine the main components contributing to the most variance. Re et al. (2013) used a similar approach to classify facial masculinity. These processes are described in detail below.

2.3.1. *Delineating facial characteristics*

Each of the 72 baby faces were delineated using a modified version of the standard face template provided by the developers of Psychomorph (Anonymous, 2013 "http://users.aber.ac.uk/bpt/jpsychomorph/," 2013; Tiddeman, 2011; Tiddeman, Burt, & Perrett, 2001). It was necessary to modify the standard template for better delineation of the baby faces, as the standard template was developed for adult faces. We added additional landmark points to the nose, cheeks and forehead, and removed points marking the ears as both ears were not fully visible in all infant pictures due to hair obstructions, or camera angle (see Fig. 1A for an example of the template). This resulted in 206 facial landmark points/fiducial markers, which formed 43 lines defining various facial elements (for a description of each line please see Table 1 in supplementary materials). These points formed a template and were positioned to match and overlaid onto the features of each baby face (Sutherland, 2015). Each point has x and y coordinates in the Euclidean space set by the program (Tiddeman et al., 2001). All other procedures were performed using the default settings of the program.

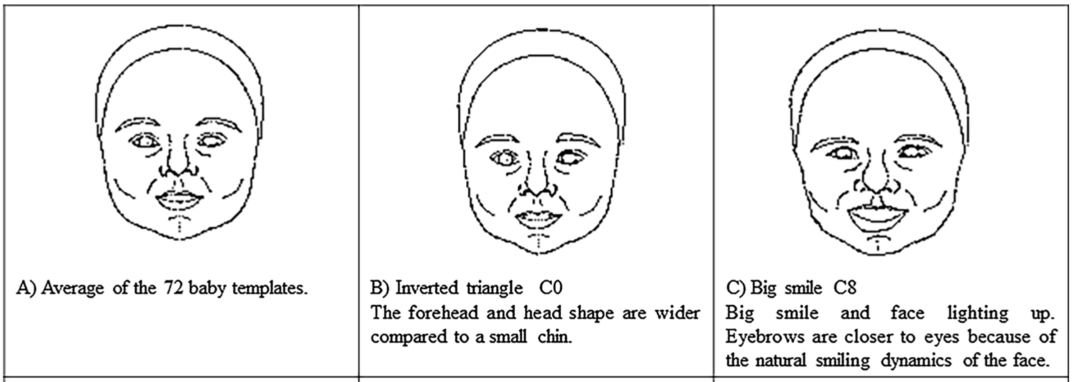
2.3.2. *Principal component analysis*

In order to run PCA the images were aligned, by centering on the two pupil points (0 & 1) (Sutherland, 2015), and combined to create an average template and image (Fig. 1A) (Re et al., 2013). The average infant face created for the PCA (Fig. 1a) was not presented to the participants for rating.

A PCA was conducted on the 72 templates with orthogonal rotation in Psychomorph. The analysis identified the components that explained the most variance in our sample of infant faces. For a more detailed explanation of this process refer to: Anonymous (2012) http://cherry.dcs.aber.ac.uk:8080/wiki/recipes/PCA/PCA (2012). PCA yielded 71 components (n-1 of the total stimuli). We used a standard method to reduce the dimensionality of the data, based on the cumulative percentage of total of variance (Cangelosi & Goriely, 2007; Joliffe, 2002). We retained the components that in combination explained 90% of the variance. This corresponded to components 0–14, n = 15, (Table 1). A bivariate correlation was used to determine the association between these components and

Table 1
Summary of eigenvalues and variance explained for each of the fifteen components after rotation.

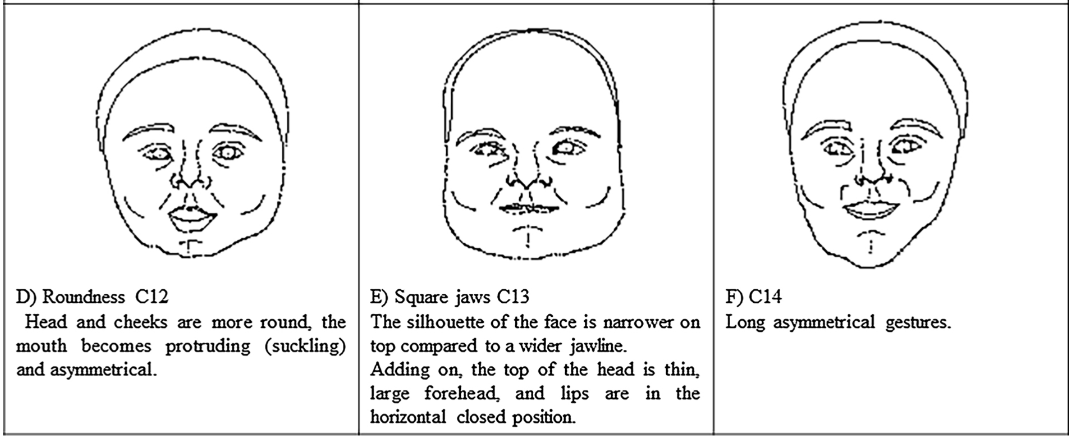
Eigenvector	Eigenvalue	Variance explained
0	4781.50	0.3062
1	2922.68	0.1872
2	1979.61	0.1268
3	745.64	0.0478
4	692.70	0.0444
5	613.85	0.0393
6	466.97	0.0300
7	376.09	0.0241
8	312.29	0.0200
9	266.88	0.0171
10	248.15	0.0158
11	207.15	0.0133
12	191.96	0.0123
13	172.02	0.0110
14	156.50	0.0100



A) Average of the 72 baby templates.

B) Inverted triangle C0
The forehead and head shape are wider compared to a small chin.

C) Big smile C8
Big smile and face lighting up. Eyebrows are closer to eyes because of the natural smiling dynamics of the face.



D) Roundness C12
Head and cheeks are more round, the mouth becomes protruding (suckling) and asymmetrical.

E) Square jaws C13
The silhouette of the face is narrower on top compared to a wider jawline.
Adding on, the top of the head is thin, large forehead, and lips are in the horizontal closed position.

F) C14
Long asymmetrical gestures.

Fig. 2. Description of the attributes that predominantly represent each component that correlated with rating cuteness. PCA analysis run with Psychomorph software (Tiddeman, 2011). (A) Average template, (B) C0, component 0, (C) C8. Component 8, (D) C12, component 12, (E) C13, component 13 (note this component was negatively correlated with perceptions of cuteness), and (F) C14, Component 14. For a visual and written description of the ten PCA components that were not related to cuteness please see Table 2 in the supplementary materials.

the subjective perceptions of cuteness. The objective “Data Driven Infant Cuteness” (DDIcute) metric was created by first identifying the components that were significantly correlated with the subjective perceptions of cuteness. Z-scores were then computed for the aforementioned components. Finally, the z-scored components were summed to create a single measure.

3. Results

3.1. Subjective perception of cuteness (ratings)

The inter-rater reliability for subjective perception of cuteness was high, Cronbach’s α = .97. This finding indicates that participants had very similar perceptions regarding baby cuteness. The cuteness rating data followed a normal distribution, such that the 72 infant pictures can be organized into three levels of cuteness, based on the subjective ratings, as they separated into the lowest 25 (range: 1.81–2.57 points, n = 18), mid 50 (range: 2.65–3.57 points, n = 36) and highest 25 (range: 3.60–4.07 points, n = 18) percentiles. Overall, most of the participants rated infants as “medium” in cuteness (mean = 3.05, SD = .05).

3.2. Principal component analysis of morphological measurements

Five components were significantly correlated with subjective perceptions of cuteness, such that components 0, 8, 12 and 14 were positively correlated, while component 13 was negatively correlated. To describe the attributes that predominantly represent each component we used both a visual inspection and a Euclidean distance analysis; examining the distance between pairs of points in Euclidean space. We found that the first PCA component 0 was characterized by a large forehead and small chin; Component 8 was defined by a big smile; Component 12 showed roundness of the face; Component 14 had long asymmetrical features (Fig. 2). The one component that was negatively correlated was Component 13 which showed a square jawline and appeared to have more adult-like

Table 2
Euclidian distance analysis of component 0. *Note:* Difference between the average template and the component 0. Changes per unit greater than 4 were considered significant.

Line	Face area	x –axis	y- axis
23	Left temple	(55.82 - 56.17) = 0.35	(188.94- 172.93)= -16.00
24	Right temple	(244.24- 246.42) = 2.18	(188.60- 175.13)= -13.47
25	Forehead	(150.98- 152.87) = 1.88	(89.56 - 76.18) = -13.38
26	Cephalic shape	(151.60 = 3.94- 155.54)	(78.16 - 60.25) = -17.91
51	Left jawline	(73.17 - 71.60) = -1.5	(244.64- 232.85)= -11.79
52	Chin	(149.20- 147.57)= -1.63	(274.28- 269.52)= -4.75
54	Right jawline	(226.63- 227.81) = 1.18	(244.49- 236.19)= -8.29

features.

3.2.1. Component 0: large forehead and small chin

Although each component was described by a Euclidean distance analysis, particular consideration should be given to the findings for component 0 as it explained 30% of the variance in our battery of infant stimuli. The Euclidean distance analysis allowed us to compute the magnitude by which each facial line deviated from the average template. Each line was defined as a series of fiducial points on the delineated pictures and carries information on the x and y values. These values were averaged for each line on both the component of interest and the average infant face. To carry out the Euclidian distance analysis we subtracted the average x and y values, independently, for each line of the average face from the corresponding lines in component zero. For example, we determined how line 23, which delineates the left temple, in component zero was different from the average infant face by taking the following steps: first, we averaged the x and y values of each point that creates line 23 on both component zero and the average face; second, we subtracted the resulting averages to arrive at the difference between the average face and component zero. The results of this subtraction, for all the lines, with greater than 4-unit change between components zero and average are shown in Table 2 and a graph of this analysis for all the lines on both axes is depicted in Fig. 3A, B. On the y-axis, lines that showed significant change were: the curvature of the cephalic shape, curvature of the forehead, left and right temples, jawline and chin (Fig. 3B). In contrast, changes on the x-axis were subtle (Fig. 3A). A visual inspection helped to further inform the information gained through the Euclidean distance analysis. We superimposed the template of component 0 onto the average template and observed that most of the changes for this component were along the y-axis in the vertical direction (Fig. 1B).

3.3. Creating & validating the single data driven infant cuteness metric (DDIcute)

In order to identify the changes in infant facial dimensions that relate to perceptions of cuteness, we calculated correlations using mean cuteness rating for each of 15 components. We found positive correlations between perceived subjective cuteness and component 0 r = .26, $p < .02$, component 8 r = .24, $p < .03$, component 12 r = .31, $p < .008$, and component 14 r = .26, $p < .02$. Finally, component 13 was negatively correlated with cuteness r = -.34, $p < .003$. These five components were used to create DDIcute metric, which was highly correlated with subjective perceptions of cuteness r = 0.63, $p < .0001$ and had the following characteristics: range of -7.07-4.32, a mean of zero and SD of 2.24. Fig. 4 shows the highest and lowest ranked baby templates according to the DDIcute variable, and Fig. 2 in the supplementary materials provides an exemplar of infant pictures averaged from each: low, medium and high scores on the DDIcute metric.

In addition, the DDIcute metric was highly positively correlated to the emotional response scales: positive affect, r = .61, sympathy r = .48, alertness r = .38, calm r = .56, delighted r = .57, interested r = .59 and need to respond r = .52, and negatively related to distress r = -.51, disturbed r= -.53 and irritated r= -.44, all ps < .0001. These results further validate the DDIcute metric.

3.4. Emotional response scores predict data driven infant cuteness metric (DDIcute) [regression analysis]

To further assess the validity of our measure DDIcute, we examined whether emotional response scores were predictive of an objective data-driven measure of cuteness. A bivariate correlation analysis revealed that all 10 ERS dimensions were strongly correlated to each other (see Table 3 and 4 in the supplementary material). As such, we controlled for the issue of multicollinearity between our predictive variables by combining some of the dimensions. This was done by first conducting an exploratory factor analysis on the 10 ERS dimensions. The analysis revealed the following: an examination of the Kaiser-Meyer-Olkin measure of sampling adequacy suggested that the sample (10 ERS dimensions) were factorable (KMO = .89). The analysis yielded a two factors solution. Six items load onto Factor 1 (affect, sympathy, calm, delighted interest and need to respond), this factor was labeled “positive ERS”. Four items load onto Factor 2 (alert, distress, disturbed and irritated), this factor was labeled “Negative ERS”.

The two factors— positive and negative emotion– were entered as predictors in a multiple linear regression model to calculate how well they predicted the DDIcute. This yielded a significant regression finding (F (2,69) = 20.86, $p < .0001$), with an R^2 of .38. The predicted DDIcute measure was equal to -10.74 + 2.42 (positive ERS) - .16 (negative ERS), where predictive factors were measured by units on a likert scale. For each unit of the positive ERS factor DDIcute increases by 2.42 units, and for each unit of the negative ERS factor DDIcute decreases by 0.16 units (see Fig. 5). Individually, only the positive ERS factor was a significant predictor

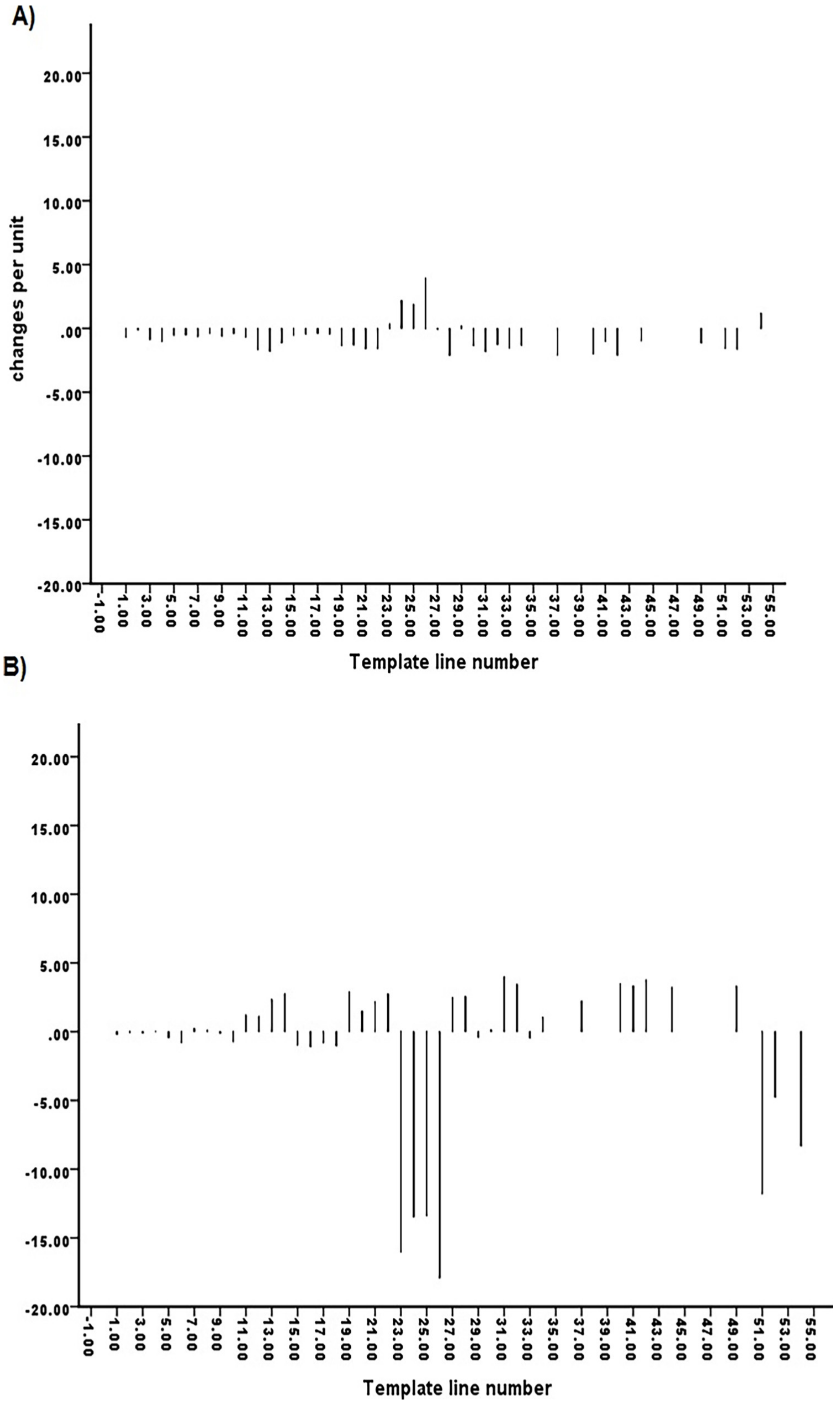
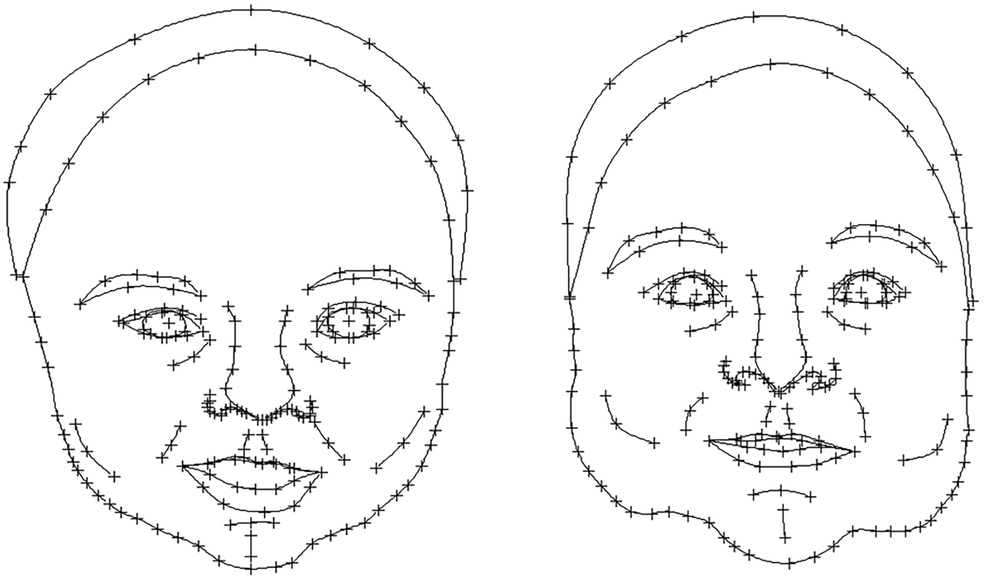


Fig. 3. Changes per unit of the different lines of the different face areas in component 0. (A) Changes in the x –axis, (B) Changes in the y-axis.

of DDIcute. Table 3 summarizes the relative influence of each factor, in a linear model, on the DDIcute metric.

4. Discussion

We were able to quantify infant cuteness into a single metric using a data driven approach that allowed insights into the facial elements associated with subjective perceptions of cuteness, or the Data-Driven Infant Cuteness (DDIcute) metric. Results from the PCA analysis revealed that the following facial elements are important to cuteness perception: compared to the average infant face a



A) Highest cute B) Lowest cute

Fig. 4. Highest and lowest ranked baby templates according to the Data Driven Infant. Cuteness (DDIcute) metric.

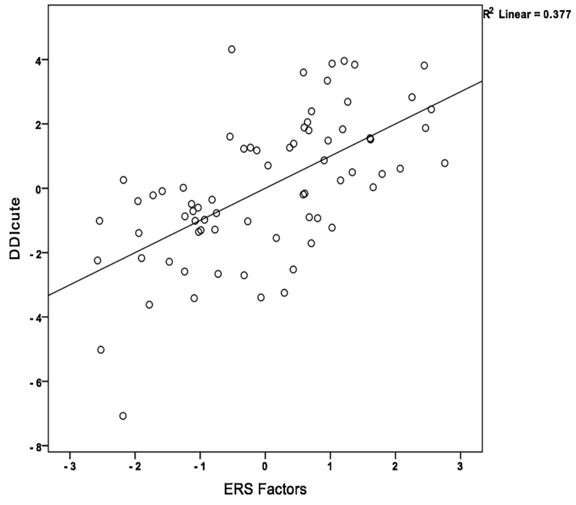


Fig. 5. Regression plot ERS (Positive and Negative ERS factors) with DDI cute. A scatter plot and the corresponding regression line for the model of the relationship between both positive and negative ERS factors, entered as predictors, and the Data Driven Infant cuteness metric (DDIcute), entered as the outcome.

cuter infant has a larger cephalic curvature, a smaller chin, a head outline shaped like a rounded inverted triangle, a big smile, round chubby features, full lips, and asymmetrical facial gestures. We also provide the first investigation into the relationship between cuteness and emotional responses, such that cuteness was directly related to the degree of negative or positive emotion being elicited by our nulliparous female participants. These results are consistent with the ethological idea that "baby schema" or cute features are rewarding stimuli that elicit positive emotions and decrease negative emotions, such as aggression, which ultimately aid in the infant's survival (Eibl-Eibesfeldt, 1970; Hess & Polt, 1960; Kringelbach et al., 2016; Lorenz, 1943).

Our results revealed that there is considerable agreement among participants in their perceptions of infant cuteness. Although our

Table 3
Linear model of ERS predictors of DDI cute.

	B	UC Std. Error	SC Beta	t	p
(Constant)	−10.74	04.92		− 2.18	.03
Positive ERS	02.42	0.50	0.60	14.86	.0001
ANegative ERS	− 0.16	01.26	-.016	− .127	.90

UC = Unstandardized Coefficients, SC = Standardized Coefficients.

results are based on nulliparous female participants, the same strong agreement has been observed in other studies on cuteness, both in men and women (Hahn et al., 2015; Hildebrandt & Fitzgerald, 1979; Schein & Langlois, 2015) and also across adults of different cultures (1995, Langlois et al., 2000). Taken together, this suggests that adult perceptions of cuteness are highly reliable and consistent. Our results thus support the idea that the ability to detect and perceive cuteness could be a biologically driven mechanism (Kringelbach et al., 2016; Lorenz, 1943).

According to ethologists like Lorenz, infants have a set of physical features or “baby schema” that are perceived as cute and elicit caretaking behavior from other individuals (Lorenz, 1943). Our PCA analysis revealed 5 components associated with the perception of cuteness. The component that explained the most variance was associated with the outer contour of the face that defined face roundness is an important factor in perceived cuteness. Also, an inverted triangle shape or “V” shape of the head was associated with cuter faces and was characterized by having a larger forehead and large round cephalic curvature relative to a narrower chin and temples. Conversely, an outer contour that conformed to a more triangular “A” shape was negatively associated with cuteness. This shape was characterized by smaller cephalic curvature and forehead line, and with wider chin and jawlines. Finally, cuter faces had a higher degree of roundness to the overall shape of the face. These results are consistent with the literature on cuteness both from ethological proposals on “baby schema” (Lorenz, 1943) and from experimental research. For example, Sternglanz et al. (1977) found that a small chin relative to a larger forehead are important elements for the perception of infant attractiveness. Hildebrandt and Fitzgerald (1979) also found that cuter infants have large foreheads, large eyes and small features. Glocker, Langleben, Ruparel, Loughead, Valdez et al. (2009) confirmed such findings when they manipulated infant photographs to increase the forehead space, among other dimensions, and produced a “super cute” infant.

Concerning facial features, we measured facial elements and identified a novel finding regarding the size of the area between the cephalic head line and the forehead line, or “cephalic space”, in cuteness perceptions (see labels on Fig. 1). Importantly, a large “cephalic space” is associated with greater infant cuteness. This has not been previously examined in the related literature, nor considered an important element of cuteness perception. However, “cephalic space” may be an important feature of infant cuteness if one considers the vantage point that characterizes parent-infant interactions. In fact, we found that infants are perceived as less cute if they have a small “cephalic space” presenting a triangular or “A” shaped face, which is more typical of adult than infant face shapes (Berry & McArthur, 1985). As such, infants with less neotenous features and more adult features are considered less cute. Following the ethological perspective, this is probably because an adult appearance elicits less necessity for protection (Eibl-Eibesfeldt, 1970; Hess & Polt, 1960; Lorenz, 1943).

Although the ethological theory suggests that large eyes are related to cuteness, our PCA analysis did not identify components related to changes in eye dimensions in our sample of baby photographs. Both Sternglanz et al. (1977) and Hildebrandt and Fitzgerald argue that eye size alone is poorly correlated with cuteness. However, when paired with other facial features the relationship between eye size and cuteness either increases or decreases in strength. Sternglanz also identified that increasing eye size beyond a certain point may increase perceptions of cuteness but could also result in a very unnatural shape, as can be seen by the eye size manipulation in the Glocker, Langleben, Ruparel, Loughead, Valdez et al., 2009 “super cute” baby. It is important to recognize that Glocker, Langleben, Ruparel, Loughead, Valdez et al. (2009) manipulated a variety of facial features, and not eye size exclusively, to produce a highly cute, albeit unnatural, infant picture. Since the nature of our analysis takes into account the relationship of various facial features, it is possible that it was not sensitive enough to detect a feature that is weakly related to cuteness. Furthermore, this study provides the first investigation of the relation between cheek shape and cuteness. Interestingly, we did not find significant differences in cheek shape when examining the component that explained the largest amount of the variance between infant faces (C0). However, component 12 was significantly related to perceptions of cuteness and was characterized by the general roundness of the face, including cheek lines that have a rounder shape compared to the average template.

Our analyses also revealed that some facial expressions are associated with perceptions of cuteness. A big smile and asymmetrical facial gestures were positively correlated with cuteness. It is well established that a smile is an important cue that facilitates the attachment between mother and infant (Bowlby, 1969). In turn, attachment ensures infant survival by prompting the caregiver to provide food, warmth and protection. Parsons et al. (2014) showed that infants with a happy temperament were perceived as cuter and adults looked at them longer. Thus, a big smile may suggest a happy temperament and lead to a higher cuteness rating. Although the PCA component of long asymmetrical features explains the least amount of variance in our sample, it visually captures an interesting infant gesture. Here, we observed that the long face of this component was a result of the mouth being open, as compared to the average infant template, the eyebrows were raised, and the eye gaze was not directed towards the camera but directed to the side with a pleasant expression. This component appeared to reflect a more playfully engaged face overall. Spontaneous asymmetrical infant movements have been documented in relation to a babbling and smiling which tend to be asymmetrically skewed to the right and left, respectively (Holowka & Petitto, 2002). These asymmetries in infant movements also occur when an infant is engaged in 'protoconversation' with adults and appear to play a role in imitating adult speech (Trevarthen, 1996). It is therefore interesting that such asymmetries in infant pictures were associated with cuteness, as they could reflect an adaptive mechanism by which infants elicit attention to engage with adults.

All of the components of infant cuteness identified through the DDIcute metric were associated with emotional responses from nulliparous females. We found that cuter babies elicit more positive affect, greater feelings of sympathy, delight, calm, greater feelings of alertness, interest and the need to respond. Pictures scoring highly on DDIcute were also negatively associated with negative emotional states such as feeling disturbed, distressed and irritated. Although both negative and positive ERS factors were highly correlated with the DDIcute metric, positive emotions alone were strongly predictive of the DDIcute. Studies on maternal behavior show that ERS scores are associated with maternal sensitivity, a well validated measure of caregiving quality (Fleming, Ruble, & Flett, 1988; Giardino et al., 2008; Stallings et al., 2001). In future research, it would be of interest to examine whether emotional responses mediate relationship between cuteness and quality of caregiving. There is evidence to suggest that after viewing infants rated as highly cute nulliparous women score higher on the maternal tendency questionnaire, a measure of the motivation to engage in caregiving behaviors (Hahn et al., 2015). Similarly, Langlois et al. (1995) found a direct relationship between an infant's attractiveness, as determined by non-mother raters, and the maternal attitudes and behaviors of the infant's own mother. Such findings along with findings from this paper–on the strong relationship between cuteness and positive emotional responses–beg the question of whether the association between perceived cuteness and emotional responses impacts on the quality of caregiving.

4.1. Limitations and future directions

It is important to recognize that particular facial elements are not the only factor that contribute to infant cuteness. Clearly perceiving cuteness draws on multimodal sensory information about the infant. Features of the infant's voice (crying or laughing), odor, whole body characteristics, and movements likely contribute to the perceived cuteness. Our cuteness scores are limited to the data from 72 infant pictures. While our pictures were not perfectly standardized due to variations in lighting and angle, they do provide greater ecological validity. In addition, it is important to note that some of the variance in our sample of infant pictures could have resulted from differences in camera angle such that certain angles of the face are viewed as cuter than others because they accentuate facial elements important for cuteness like the inverted triangle or "V" head shape outline. Furthermore, a fixed order of questions was used such that all raters first rated pictures on the level of cuteness. This could have affected subsequent ratings on the emotional dimensions and resulted in a halo effect (Feeley, 2002). Future work should safeguard against this limitation by randomizing question order.

It is well established that cuter infants are perceived as healthier than less cute infants (Golle et al., 2015). There is some evidence to suggest that infant facial features carry information about their health such as: having a cleft lip (Parsons et al., 2011; Rayson et al., 2017), down's syndrome (Yamamoto, Ariely, Chi, Langleben, & Elman, 2009), and fetal alcohol syndrome (Waller, Volk, & Quinsey, 2004). Other morphological features carry information about the infant's likelihood to survive such as body weight (McCormick, 1985; Volk, Lukjanczuk, & Quinsey, 2005; Volk, Lukjanczuk, & Quinsey, 2007). However, to our knowledge the relationship between infant head shape and infant health has not been investigated. Given that our findings show that the component relating to the "V"-shaped head outline explains the greatest percentage of variance and is strongly related to perceptions of cuteness, it would be interesting for future studies to investigate head shape it is related to infant health.

Taken together our results support the idea that cuteness perception is not exclusive to one facial element, but is rather a combination of head outline, facial features, as well as expressions and gestures. These observations are consistent with Lorenz's "baby schema" and the extant experimental literature and provide validity to the data driven cuteness metric. After having developed the DDIcute measure by investigating the morphological correlates of cuteness, our next aim is to investigate the neural correlates of infant cuteness to understand whether specific brain networks such as the reward, maternal, and affective neural networks are particularly responsive to cuteness.

5. Conclusion

We developed the DDIcute metric in response to a general need, expressed in the cuteness literature (Hildebrandt et al., 1978; Alley, 1981; Glocker, Langleben, Ruparel, Loughead, Valdez et al., 2009), for an "adequate method" to measure different curvatures of the face and improve on prior straight-line measurement methods. The DDIcute metric provides the first experimental measure of the facial features: curvature of forehead, curvature of chin, cheeks and shape of head. The results demonstrate that by utilizing a data-driven technique the curvature of the cephalic head shape, forehead and chin are identified as important in the perception of cuteness. Importantly, the DDIcute metric is not based on a singular measure but draws on the relationship between 206 points on the face (43 lines), which considerably increases the fidelity of the results compared to earlier techniques, as it takes into consideration the entire face. Although the DDI-cute metric methodology described here is time consuming, it supports a more substantive understanding of the morphological characteristics of infant cuteness.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.infbeh.2018.08.001.

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Chapter 5

Study 4: Interactions between sex and pet ownership on attitudes toward children

5.1 OVERVIEW

Background. Cuteness is not limited to human infants, and the same infantile features are observed in other mammals including pets like cats and dogs. Many people are attached to their pets, this attachment shares similar psychobiobehavioural characteristics with the parental attachment to children. Further, it is becoming increasingly common for young couples to own and care for a pet prior to having children. There is an established sex effect in attitudes about children (especially when measured via self-report); women compared to men report more positive attitudes about children. Parental experiences of care attenuate this sex difference. However, whether this sex difference is attenuated by owning and experiences of caregiving for pet(s) has not been investigated. **Methods.** In a sample of non-parents, we investigated whether the established main effect of sex on attitudes about children was moderated by pet ownership (using a 2x2 design; comparing males and females, pet owners and non-pet owners) and lifetime experiences caring for pets (using hierarchical multiple linear regression models). Attitudes about infants and experiences with pets was measured via online survey in a community sample (n=173). **Results.** We found that compared to females, males had more negative reactions to children and childcare (NRC). However, a significant sex by current pet ownership interaction revealed that current pet ownership eliminated the sex difference on NRC; males' NRC scores were similar to females in the current pet owner group. Further, regression analyses revealed that the relationship between sex and NRC was moderated by the extent of lifetime experiences caring for pets. Compared to males with low levels of lifetime experiences caring for pets, males with high levels of lifetime experiences caring for pets had less NRC; similar to attitudes of females. **Conclusion.** Taken together, these results provide the first reported evidence of the association between current pet ownership and lifetime experiences caring for pets with less NRC in non-parent males.

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Interactions Between Sex and Pet Ownership on Attitudes Toward Children

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Keywords: pets, pet ownership, attitudes about children, experience caring for pets, sex differences

Abstract **Background:** Many people are attached to their pets. This attachment shares characteristics with the parental attachment to children. Previous studies have established a sex difference in attitudes about children; women compared to men report more positive attitudes about children. However, whether this sex difference is attenuated by owning and caring for pet(s) has not been investigated. **Methods:** In a sample of non-parents, we investigated the following: (1) whether the established main effect of sex on attitudes about children was moderated by pet ownership using a 2 (male, female) x 2 (pet owner, non–pet owner) design; and (2) whether the established main effect of sex on attitudes about children was moderated by lifetime experiences caring for pets using hierarchical multiple linear regression models. Data was collected via online survey of a community sample ($n = 173$). **Results:** We found that compared to females, males had more negative reactions to children and childcare (NRC). However, a significant sex by current pet ownership interaction revealed that current pet ownership eliminated the sex difference on NRC; males' NRC scores were similar to females' scores exclusively among people who currently owned a pet. Further, regression analyses revealed that the relationship between sex and NRC was moderated by the extent of lifetime experiences caring for pets. This effect was driven by males but not females; compared to males with low levels of lifetime experiences caring for pets, males with high levels of lifetime experiences caring for pets had less NRC. **Conclusion:** Taken together, these results provide the first reported evidence of the positive association between current pet ownership/lifetime experiences caring for pets and more favorable attitudes about children and childcare in non-parent males, but not in non-parent females.

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IAHAIO International Association of Human-Animal Interaction Organizations

Many people become extremely attached to their pets. People care for their pets, get comfort from them, miss them when they are not around, and mourn for them when they die. The attachment and caregiving behaviors between owners and their companion animals share similarities to the relationship between human parents and their children. Young nulliparous couples often treat their pets as children (Owens & Grauerholz, 2019) and, colloquially, people refer to their pets as "fur babies" (Greenebaum, 2004). It has been observed that young couples often decide to get a pet prior to having their first child (Walsh, 2009). Further, it has been proposed that having a pet may be preparatory for parenthood (Borgi & Cirulli, 2016; Nast, 2006; Shell, 1986). However, to our knowledge, this proposal has not been empirically investigated. Given the similarities in parent–child and owner–pet attachment and the established sex difference in attitudes about infants, we investigated whether current ownership of a pet and lifetime experiences caring for a companion animal (pet) moderated the relationship between sex and attitudes about children and childcare in non-parents.

Sex Differences in Responsiveness to Infant Cues and Caregiving Experience

A clear sex difference has been demonstrated in responsiveness to infant cues when measured by subjective self-report. In general, compared to females, males consistently rate infants as less positive and less interesting (for a review see Berman, 1980; Kringelbach et al., 2016; also see Maestripieri & Pelka, 2002; Parsons et al., 2017). Maestripieri and Pelka (2002) investigated sex differences in interest and/or affection toward infants across the following age groups: children, adolescents, young adults, and older adults. They found that compared to males, females were significantly more interested in infants across all age groups (Maestripieri & Pelka, 2002). Empathy has also been shown to modulate responsiveness to infant cues (Hiraoka & Nomura, 2017; Lin & McFatter, 2012). A sex difference in empathy levels has also been well established using self-report; females report greater levels of empathy compared to males (Christov-Moore et al., 2014). Overall, males report less positive attitudes about infants compared to females.

There is evidence to suggest that previous experiences caring for children positively influence responsiveness to and attitudes about children. The extent of previous caregiving experience is predictive of the quality of maternal behavior in new mothers such that previous experience with infants and children is associated with increased positive responsiveness, attitudes, and feelings toward infants and children (Fleming et al., 1993, 1997, 2002). Given the inherent differences in the extent of caregiving experience between parents and non-parents, it is not surprising that parents respond more positively to infant stimuli compared to non-parents (Lehmann et al., 2013; Parsons et al., 2017). Also, differences between mothers and fathers appear to be diminished when both are involved in caregiving behaviors (for review see Feldman, 2017). Overall, parents report more positive attitudes about infants and children than non-parents. Taken together, non-parent males are the least child-centric group.

Caregiving can take many forms; observational studies have identified different aspects of caregiving behavior including instrumental care and affectionate care. Instrumental care includes grooming behavior and is not involved in warm and affectionate care and touch (Chico et al., 2014; Giardino et al., 2008; Krpan et al., 2005; Teberg et al., 1983). Earlier studies from our group examined attitudes about these different aspects of caregiving. For example, a cross-sectional study by Ruble et al. (1990) found decreases in attitudes about instrumental aspects of caregiving (i.e., negative attitudes about childcare) across the transition to motherhood but no differences in warm and affectionate attitudes about children (i.e., feelings about children) across the transition to motherhood. However, to our knowledge, sex differences in these particular self-reported measures of attitudes about children and childcare have not been investigated and are an objective of the current study. Critically, to our knowledge, the moderating effects of lifetime experiences caring for pets on sex differences in attitudes about children and childcare have not been investigated and constitute the primary objective of the current study.

Similarities between Parent-Infant and Owner-Pet Attachment

Attachment is of crucial importance to social animals, occurring within a variety of social relations beginning with mother–infant interactions (Rynearson, 1978). The human–animal relationship refers to a type of attachment developed reciprocally between pet owners and their companion animals (Fine & Beck, 2015; Hines, 2003; Serpell, 2016). Unlike animals raised for utilitarian purposes, pets have no financial or functional purposes other than for comfort and companionship (Cohen, 2002; Serpell, 2016; Serpell & Paul, 1994). The emotional attachment that people have for their pets involves strong psychological and emotional ties that can be similar to those observed in human–human bonds (Hines, 2003; Sable, 1995). For instance, some owners have refused to evacuate during natural disasters because they were not allowed to bring their pets to the rescue shelters (Rosenkoetter et al., 2007; Zottarelli, 2010). The concept of the human–animal bond was extrapolated from attachment theory as the human–animal bond shares characteristics with those observed in mother–infant interactions (Ainsworth, 1989; Barba, 1995; Beck & Katcher, 2003; Bowlby, 1969; Fine & Beck, 2015; Payne et al., 2015; Prato-Previde et al., 2003, 2006).

Human–pet interactions share similar biobehavioral synchrony to that observed in mother–infant attachments (Feldman, 2017; Fleming & Corter, 1988; Galbally et al., 2011). Similar to observations between the parent–child dyad, synchronous gaze behavior was observed between owners and their pets (Borgi & Cirulli, 2016; De Dreu et al., 2010; Nagasawa et al., 2009). Also similar to parental autonomic responsiveness during pleasurable and positive interaction with infants, pet owners' heart rate significantly decreased (Handlin et al., 2011) and oxytocin levels increased (Handlin et al., 2011; Odendaal & Meintjes, 2003; Petersson et al., 2017) in response to interactions with pets. Similarly, Stoeckel and colleagues (2014) demonstrated that the caregiving neural network—including brain regions involved in emotion, reward and affiliation—was engaged not only when mothers viewed pictures of their own baby but also when they viewed pictures of their own dog.

Studies report similar properties of pet-directed and infant-directed speech (Burnham et al., 2002; Hirsh-Pasek & Treiman, 1982; Mitchell, 2001). For example, pet-directed speech (doggerel) shares similar properties (well-formedness, short utterances, frequency, and high pitch) with infant-directed speech (motherese). A naturalistic observation of communication with pets and infants (Mitchell, 2001) found that the limited attention and reciprocity of pets and infants warrants the speaker to modulate their attention with exaggerated gestures and intonation to generally express friendliness and affection. Despite the many similarities between attachment to children and to pets, there are differences as well. For instance, adult affective speech (measured by intonation and rhythm) was shown to be greater when directed at infants in comparison to when it was directed at pets (Burnham et al., 2002). Also, unlike children, pets have a more "flexible" role in the family hierarchy across the developmental stages of the family life cycle; in the absence of a young child the family pet serves the role of a child, but not in the presence of a young child (Owens & Grauerholz, 2019; Turner, 2005).

Given the established effects of sex on attitudes about children and childcare, in this study, we investigated the following: (1a) whether the established main effect of sex on negative reactions to children and childcare (NRC) was moderated by current pet ownership; (1b) whether the established main effect of sex on positive feelings about children (PFC) was moderated by current pet ownership; (2a) whether the established main effect of sex on negative reactions to children and childcare (NRC) was moderated by lifetime experience caring for pets; and (2b) whether the established main effect of sex on positive feelings about children (PFC) was moderated by lifetime experience caring for pets. Based on previous studies showing that non-parent males are the least child-centric group and given the more positive responsiveness to children by females compared to males, we hypothesize that the moderating effects of pet ownership and/or lifetime experience caring for pets on attitudes about children and childcare would be greatest among males in a sample of non-parents.

Methods

Participants

Data from 173 participants (74 non–pet owners, 99 pet owners) were analyzed in this study. English-speaking respondents from the United States completed an online survey advertised via a link posted on SurveyMonkey.com. A total of 432 respondents completed the survey. Respondents were included as participants in this study if they were non-parents, between the ages of 18 and 45, and completed questions regarding age, sex, parental status, and whether or not they are currently pet owners. Pet owners were excluded from data analysis if they had pets other than dog(s) and/or cat(s) that they consider a companion (*n* = 19). Also, respondents were excluded if they did not consider their pet a companion animal; that is, if participants answered "no" to currently owning a pet that they consider a companion, but "yes" to currently owning a dog and/or cat (*n* = 21). The study was approved by the Research Ethics Board of the University of Toronto, Toronto, ON, Canada.

Procedures and Questionnaires

Participants completed a survey on SurveyMonkey.com (duration: ~20 min). In addition to standard questions regarding demographic information, the survey includes questions about participants' history, attitudes, and feelings towards pets and children. Relevant questionnaires are described in Table 1.

Predictors

Sex. Self-reported sex with the following options: male or female.

Current pet ownership. Participants were labeled as a pet owner only if they currently have a pet (specifically dog[s] and/or cat[s]) that they consider to be a companion. Participants were labeled as non–pet owners if they do not currently have a pet (dog[s] and/or ca([s]). In this sample, non–pet owners could have owned a pet that they considered a companion in the past—as a child (*n* = 12), an adult (*n* = 6), or both (*n* = 20) (Table 3).

Lifetime experience caring for pets. Responses to items were used to compute a mean score. A higher score indicates greater lifetime experience caring for pets (Table 1).

Outcomes

Negative reactions to children and childcare (NRC). This factor corresponds to instrumental aspects of caregiving. Responses to items were used to compute mean NRC scores. A higher score indicates greater negative reactions to children and the instrumental aspects of childcare (Table 1).

Positive feelings about children (PFC). This factor corresponds to affectionate/warm aspects of caregiving. Responses to items were used to compute mean PFC scores. A higher score indicates more positive and affectionate feelings about children (Table 1).

Potential Confounds

To control for their potential confounding effects, we included empathy (Christov-Moore et al., 2014), experience caring for children (Fleming et al., 1993, 1997, 2002), and age as covariates in our models.

Empathy. This factor was created by computing the mean of items indicated in Table 1. A higher score indicates greater levels of empathy.

Lifetime experience caring for children. This factor was created by computing the mean of items indicated in Table 1. A higher score indicates greater experience caring for children.

Table 1. Description of the Questionnaires

Factor & Questionnaires	Questions	Score	α
Positive feelings about children (PFC) corresponding to affectionate aspects of caregiving (Chico et al., 2014; Giardino et al., 2008; Krpan et al., 2005; Teberg et al., 1983). From: Childbearing Attitudes Questionnaire (CAQ) (Fleming, Ruble, Flett, & Shaul, 1988; Ruble et al., 1990).	1. Just the sight of a small child makes me smile. 2. Whenever I see a baby, I feel like picking it up. 3. Just thinking of a baby makes me feel good.	Seven-point Likert scale: 1 = "strongly disagree" to 7 = "strongly agree" A higher score indicates more positive and affectionate feelings about children.	.89
Negative reactions to children and childcare (NRC) corresponding to instrumental aspects of caregiving (Chico et al., 2014; Giardino et al., 2008; Krpan et al., 2005; Teberg et al., 1983). From: Childbearing Attitudes Questionnaire (CAQ) (Fleming, Ruble, Flett, & Shaul, 1988; Ruble et al., 1990).	1. I try to avoid places where I think there will be a lot of infants and small children. 2. Child care is repetitive and boring. 3. The messes that babies make bother me a lot.	Seven-point Likert scale: 1 = "strongly disagree" to 7 = "strongly agree" A higher score indicates greater negative reactions to children and instrumental aspects of childcare.	.80
Lifetime experience caring for pets From: Companion Animal Bonding Scale (CABS) (Poresky et al., 1987) and the Pet Attachment Scale (PAS) (Geller, 2005).	1. How often are you responsible for the pet's care? 2. How much experience with pets have you had? 3. How much time have you spent looking after, playing with, cleaning [up] after, or walking pets?	Five-point Likert scale: 1 = "none" to 5 = "a lot" A higher value represents more experience caring for pets.	.82
Empathy From: Interpersonal Reactivity Index (Davis, 1980, 1983).	1. When I see another person who is hurt or upset, I feel sorry for them. 2. When I see someone being bullied, I feel sorry for them. 3. I feel bad for other people who are sad or have problems. 4. Before criticizing somebody, I try to imagine how I would feel if I were in their place. 5. If I'm sure I'm right about something, I don't waste much time listening to other people's arguments. (reversed) 6. I sometimes try to understand my friends better by imagining how things look from their perspective. 7. I believe that there are two sides to every question and try to look at them both. 8. I sometimes find it difficult to see things from the other person's point of view. (reversed) 9. I try to look at everybody's side of a disagreement before I make a decision. 10. When I'm upset at someone, I usually try to "put myself in his/her shoes" for a while.	Five-point Likert scale: 1 = "does not describe me well" to 5 = "describes me very well" A higher score represents greater levels of empathy.	.82

(*continued*)

Table 1. (*Continued*)

Factor & Questionnaires	Questions	Score	α
Lifetime experience caring for children From: Child Experience Inventory (Fleming et al., 1993, 1997, 2002).	1. How much experience with infants under one [year] have you had? 2. How much volunteer work with infants younger than one year have you had? 3. How much time have you spent looking after or playing with brothers, sisters, nieces, nephews, friends' babies under the age of one year?	Five-point Likert scale: 1 = None, 5 = A lot A higher value represents more experience caring for children.	.86

Note: α = Cronbach alpha. All participants were evaluated for lifetime experience caring for pets.

Age. Given that we found a significant sex difference in age in our sample (see section on participant characteristics in results section and Table 2), we controlled for the potential confounding effects of age.

Data Analysis Strategy

Missing data. Missing data were addressed using multiple imputations (n = 50) with the Markov chain Monte Carlo (MCMC) method (Kenward & Carpenter, 2007; Schafer, 1997). We used the bar procedure in the Statistical Package for the Social Sciences (SPSS, version 24.0) software to pool the multi-imputed data frames into a single data frame. The percentage of missing values for the data analyzed in this study (n = 173) ranged from 0.5% (n = 1) to 11.3% (n = 22) for PAS and CABS questionnaires, respectively, and 11.3% (n = 22) for CAQ. According to Little's Missing Completely at Random (MCAR) test, data was missing at random (χ^2 = 23.90, df = 20.51, p = .24). Independent variables and demographic data were not imputed including socioeconomic status (SES) (missing values 1.2%; n = 2), cohabitating status (missing values 2.9%; n = 5) and quantity of pets (missing values 2.9%; n = 5). We ran the same models with unimputed data (including missing data); results using unimputed data were largely similar but less strong due to reduced power.

Statistical analysis. We used chi-square tests of homogeneity (χ^2) to compare the distribution of counts between females and males on all categorical demographic variables (e.g., age, socioeconomic status [SES], and cohabitating status). We used t-tests to compare females and males on continuous variables (e.g., empathy, lifetime experiences caring for pets, and lifetime experience caring for children; see Table 2). To control for their potential confounding effects, we included empathy, lifetime experience caring for children, and age as covariates in all the models. All statistical analyses were performed using SPSS version 24.0 (IBM Corp., Armonk, NY).

Current pet ownership. To determine (a) whether the established main effect of sex on negative reactions to children and childcare (NRC) was moderated by current pet ownership, and (b) whether the established main effect of sex on positive feelings about children (PFC) was moderated by current pet ownership, we computed 2 (male, female) x 2 (pet, no pet) between-participants ANCOVAs independently for NRC and PFC as the outcome variable. Standard post-hoc Tukey HSD tests were computed where relevant.

Lifetime experience caring for pets. To determine (a) whether the established main effect of sex on negative reactions to children and childcare (NRC) was moderated by lifetime experience caring for pets, and (b) whether the established main effect of sex on positive feelings about children (PFC) was moderated by lifetime experience caring for pets, we ran hierarchical multiple linear regression (HMLR) analyses with three blocks independently for NRC and PFC as the dependent variable. Block 1 included the covariates (age, empathy, and lifetime experiences caring for children) to control for their potential confounding effects. Block 2 included sex as the main predictor and lifetime experience caring for pets as the moderator. Conceptually, the reason for choosing sex as a main predictor of NRC/PFC is two-fold: sex chronologically precedes lifetime experience of care for pets, and there is an established sex effect on interest and attitudes about children (for a review see Berman, 1980; Kringelbach et al., 2016; also see Maestripieri & Pelka, 2002; Parsons et al., 2017). Block 3 included the interaction term (sex x lifetime experience caring for pets). In that sense, results from this last block allows testing the hypothesis that lifetime experience caring for pets moderates or changes the direction and/or strength of the relation between sex and attitudes about children and childcare (NRC/PFC).

Prior to conducting a HMLR, the relevant assumptions were tested. A sample size of 173 participants was deemed adequate given five independent variables to be included in the analysis (Tabachnick & Fidell, 2001). The assumption of singularity was also met as the independent variables (lifetime experience caring for children, empathy, age, sex, and lifetime experience caring for pets) were not a combination of other independent variables. An examination of correlations (see Table 4) revealed that no independent variables were highly correlated ($r > 0.70$) (Hinkle et al., 2003; Mukaka, 2012). Finally, the predictor "lifetime experience caring for pets" was mean centered by computing standardized z-scores.

Note on interpreting effect size. For ANCOVAs, the effect size estimates for individual variables are partial eta squared (η^2) and for the whole model it is adjusted R^2 values. For regression models, the effect size estimates are standardized β coefficients for individual variables and adjusted R^2 values for the whole model. In HMLR, the ΔR^2 indicates the change in R^2 from the previous model to the current model indicating whether the current model significantly explains more variance in the outcome than the previous model, that is, if ΔR^2 is significant, then the current model explains more variance in the outcome than the previous model.

Results

Participant Characteristics by Sex

We found a significant sex difference in current non–pet owners, with more males than females indicating that they did not own a pet (χ^2 [1, N = 173] = 4.00, p = .045). We also found sex differences in age (χ^2 [1, N = 173] = 16.00, p = .001) with more females in the 18–25 years old age group compared to males, and more males in the 36–45 years old age group compared to females. Also compared to males, females had higher levels of empathy (p = .001), and more lifetime experience caring for children (p = .001) (Table 2). Therefore, we controlled for the potentially confounding effects of empathy, lifetime experience caring for children, and age in all models.

Pet-Related Characteristics

We found that compared to current non–pet owners (M = 2.96, SD = 1.06), current pet owners (M = 4.54, SD = .53) showed greater levels of lifetime experience caring for pets (t[171] = 11.74, p = .001). Further, Table 3 describes the characteristics of current pet ownership in our sample; the majority of current pet owners are dog owners, have more than one pet, and have always had pets (in childhood, adulthood, and now).

Significant Sex by Current Pet Ownership Interaction on Attitudes about Children and Childcare

Negative reactions to children and childcare (NRC). We found a main effect of sex on NRC (F[1, 166] = 4.708, p = .031, partial η^2 = .028); compared to females, males reported higher NRC scores (more negative reactions to children and childcare). There was a significant sex by current pet ownership interaction on NRC (F[1, 166] = 4.634, p = .033, partial η^2 = .027) such that current pet ownership eliminated the sex difference in NRC (Figure 1a). The adjusted R^2 for the model was equal to 0.127.

Post-hoc tests revealed that in comparison to female current non–pet owners, male current non–pet

Table 2. Participant Characteristics by Sex

Variables (*n* = 173)	Females (*n* = 83)	Males (*n* = 90)
Current pet ownership, *n* (%)*		
Pet owners	54 (54.5)	45 (45.5)
Non-pet owners	29 (39.2)	45 (60.8)
Age (years), *n* (%)*		
18–25	41 (67.2)	20 (32.8)
26–35	27 (43.5)	35 (56.5)
36–45	15 (30)	35 (70)
SES, *n* (%)		
<50 K	40 (44.0)	51 (56.0)
50–74 K	18 (62.1)	11 (37.9)
75–99 K	12 (63.2)	7 (36.8)
>100 K	8 (38.1)	13 (61.9)
Prefer not to answer	4 (36.4)	7 (63.6)
Cohabitating, *n* (%)		
No	47 (46.5)	54 (53.5)
Yes	35 (52.2)	32 (47.8)
Empathy, *Mean* (*SD*)*	4.07 (.58)	3.59 (.76)
Lifetime experience caring for children, *Mean* (*SD*)*	2.94 (1.25)	2.16 (1.01)
Lifetime experience caring for pets, *Mean (SD)**	4.04 (1.09)	3.70 (1.13)

Note: SES = socioeconomic status; * significant differences between females and males, $p < .05$. Independent (sex, current pet ownership) and demographic variables (SES, cohabitating status) were not imputed (see Data Analysis Strategy under Methods). SES (missing 1 female; 1 male), cohabitating status (missing 1 female; 4 males).

owners reported higher NRC (hence more negative reactions); however, current pet owners reported similar levels of NRC regardless of their sex (Figure 1a).

Positive feelings about children (PFC). We did not find main effects nor interactions between sex and current pet ownership on PFC (Figure 1b). The adjusted R^2 for the model was equal to 0.349.

These analyses show that the interaction between sex and current pet ownership on attitudes about children and childcare is specific to NRC but not PFC (Figure 1).

Lifetime Experience Caring for Pets Moderated the Relationship between Sex and Attitudes about Children and Childcare

Negative reactions to children and childcare (NRC). The hierarchical multiple linear regression (HMLR) revealed that at block one, “Lifetime experience caring for children” and “Empathy” contributed significantly to the regression model (p = .001) and accounted for 11.6% of the variance in NRC. When introducing “Sex” and “Lifetime

Table 3. Description of Pet-Related Variables by Current Pet Ownership

Pet status variables (*n* = 173)	Current Pet Owner (*n* = 99)	Current Non–Pet Owner (*n* = 74)
Pet Type, *n* (%)		
No Pets	–	74 (42.8)
Just Dog(s)	53 (30.6)	–
Just Cat(s)	20 (11.6)	–
Cat(s) and Dog(s)	26 (15.0)	–
Quantity of Pets, *n* (%)		
None	–	71 (42.3)
One	41 (24.4)	–
Two or more	56 (33.3)	–
History of having a pet, *n* (%)		
Never had	–	31 (18.7)
Childhood only	–	12 (7.2)
Adulthood, not now	–	6 (3.6)
Childhood and adulthood	–	20 (1.2)
Adulthood and currently	10 (6)	–
Always (childhood, adulthood, and now)	87 (52.4)	–

experience caring for pets" at block two, ΔR^2 was not significant (p = .136). However, adding the interaction term "Sex by Lifetime experience caring for pets" at block three explained 16.4% of the variance in NRC and this ΔR^2 was significant (p = .02). Block three of the regression model showed that the strongest predictors of NRC were "Lifetime experience caring for children" and the interaction term "Sex by Lifetime experience caring for pets" (see Table 5).

To determine which sex was driving the statistically significant interaction between "Sex" and "Lifetime experience caring for pets" on NRC, we ran simple linear regression analyses independently for males and females. These analyses revealed that experience caring for pets predicted NRC for males (β = -.271; SE = .149; constant = 3.888; p = .01, adjusted R^2 = 0.063), but not for females (β = .123; SE = .159; constant = 3.125, p = .27, adjusted R^2 = 0.003). For a visual representation of this sex difference on NRC moderated by lifetime experiences caring for pets see Figure 2a; the dashed line representing males has a negative slope, thus, males with more experience caring for pets show less NRC compared to males with lower experience caring for pets. The slope of the line for females does not show significant changes, such that for females, lifetime experience caring for pets was not associated with NRC.

Positive feelings about children (PFC). The HMLR revealed that only block one with "Lifetime experience caring for children" and "Empathy" contributed significantly to the regression model (p = .001) and accounted for 36.2% of the variance in PFC. The model was not significant when

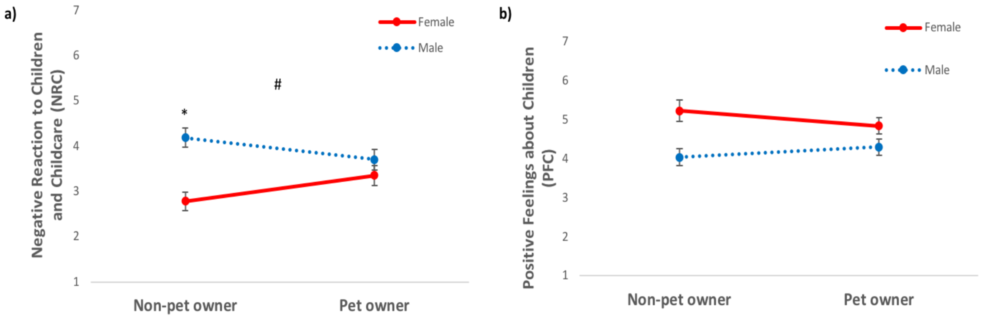

Figure 1. Interaction between sex and current pet ownership on attitudes about children and childcare.
Means ± SEMs of attitudes about children and childcare depicting the interaction between sex and current pet ownership on (a) negative reactions to children and childcare (NRC), and (b) positive feelings about children (PFC). Significant sex by current pet ownership interactions are represented by #, main effects of sex are represented by *. There are no sex differences within current pet owners; however, within current non-pet owners, males reported more negative attitudes about children and childcare (higher NRC) compared to females. # ,* *p* < .05.

Table 4. Correlation Table

	1	2	3	4	5	6	7
1. PFC	1						
2. NRC	**-.442****	1					
3. Sex[1]	**-.268****	**.268****	1				
4. Current pet ownership[2]	0.029	-0.041	**-.152***	1			
5. Lifetime experience caring for pets	0.054	-0.125	**-.150***	**.700****	1		
6. Lifetime experience caring for children	**.476****	**-.290****	**-.326****	0.057	0.042	1	
7. Empathy	**.475****	**-.232****	**-.337****	**.196****	**.269****	**.254****	1

Note: Pearson correlation was used to evaluate the association between continuous variables and also for the association between continuous variables and dummy variables (Sex and Current pet ownership) ([1]coding for sex: female = 0, male = 1; [2]coding for current pet ownership: non-pet owner = 0, pet owner = 1). Spearman correlation was used to evaluate the association between the dichotomous categorical variables (Sex with Current Pet Ownership). *p < .01 (bilateral); ** p < .001 (bilateral).

introducing variables for blocks two and three (*p* = .471 and *p* = .541 respectively) (Figure 2b). This showed that the strongest predictors of PFC were "Lifetime experience caring for children" and "Empathy." Also, none of the following variables significantly predicted PFC: "Age," "Sex," "Lifetime experience caring for pets," nor the interaction term "Sex by Lifetime experience caring for pets" (see Table 6).

Discussion

This is the first study to explore the effects of current pet ownership and lifetime experiences caring for pet(s) on sex differences in attitudes about children and childcare. We found a sex effect in attitudes about children and childcare such that compared to males, females had less negative attitudes about children and childcare. This is consistent with previous

Table 5. Hierarchical Multiple Linear Regression for Variables Predicting Outcome Variable NRC

		Unstandardized coefficients		*Standardized coefficients*						
Block	*Independent variables*	*B*	*SE*	*β (SE)*	*p-value*	R^2	*Adjusted* R^2	ΔR^2	*F*	*p*
1						.116	.101	.116	7.421	**.001**
	Lifetime experience caring for children	-.301	.093	-.241 (.075)	**.002**					
	Empathy	-.320	.157	-.155 (.076)	**.04**					
	Age	.142	.137	.077 (.074)	.30					
2						.137	.111	.021	2.022	.136
	Lifetime experience caring for children	-.261	.096	-.209 (.077)	**.007**					
	Empathy	-.214	.165	-.104 (.080)	.19					
	Age	.091	.141	.049 (.076)	.52					
	Sex[1]	.414	.242	.140 (.082)	.09					
	Lifetime experience caring for pets	-.100	.111	-.068 (.075)	.37					
3						.164	.134	.026	5.257	**.02**
	Lifetime experience caring for children	-.222	.096	-.178 (.077)	**.02**					
	Empathy	-.228	.163	-.111 (.079)	.17					
	Age	.108	.139	.058 (.075)	.44					
	Sex	.438	.239	.148 (.081)	.07					
	Lifetime experience caring for pets	.169	.161	.114 (.109)	.30					
	Sex by Lifetime experience caring for pets	-.498	.217	-.244 (.106)	**.02**					

Note: *B weight* = B coefficient (slope of the line, indicates the direction of the relationship between two variables); *SE* = standard error; *β* = beta weight (standardized B weights); ΔR^2 = change in R^2. The predictor "Lifetime experience caring for pets" was centered (*z*-scores were used). [1]Sex was coded as follows: 0 female; 1 male; indicating that males are the reference group, thus the table represents changes pertaining to males when compared to females. Bold values indicate statistical significance at the $p < 0.05$ level.

studies showing an established sex effect on attitudes about children (Berman, 1980; Kringelbach et al., 2016; Maestripieri & Pelka, 2002; Parsons et al., 2017). However, we found that this was only true for participants who currently did not own a pet as well as for participants who had low levels of lifetime experiences caring for pets. For current pet owners and those with high levels of lifetime experiences caring for pets, both females and males had similar attitudes about children and childcare. Specifically, males with higher levels of experience caring for pets showed less negative reactions to children and childcare (NRC) compared to males with lower levels of lifetime experiences caring for pets. These results are consistent with our hypothesis stating that the moderating effects of pet ownership or lifetime experience caring for pets on the established relationship between sex and attitudes about children and childcare would be greatest among males in our study sample of non-parents: the group that is the least child-centric.

Greater positive attitudes about children and childcare have been linked to higher quality of caregiving (Bader et al., 2019; Daggett et al., 2000). As described above, we found that males who had the most lifetime experiences caring for pets showed greater positive attitudes about children and childcare compared to males with less lifetime experiences caring for pets. Although not directly investigated, our results suggest that lifetime experiences caring for pets may function to prepare males, more than females, for parenthood; or, that experience caring for

Table 6. Hierarchical Multiple Linear Regression for Variables Predicting Outcome Variable PFC

		Unstandardized coefficients		*Standardized coefficients*						
Block	*Independent variables*	*B*	*SE*	*β (SE)*	*p-value*	R^2	*Adjusted* R^2	ΔR^2	*F*	*p*
1						.362	.350	.362	31.93	**.001**
	Lifetime experience caring for children	.486	.081	.382 (.064)	**.001**					
	Empathy	.808	.136	.385 (.065)	**.001**					
	Age	.058	.119	.031 (.064)	.63					
2						.367	.349	.006	.756	.471
	Lifetime experience caring for children	.472	.084	.371 (.066)	**.001**					
	Empathy	.835	.145	.397 (.069)	**.001**					
	Age	.082	.123	.044 (.066)	.51					
	Sex[1]	-.114	.212	-.038 (.071)	.59					
	Lifetime experience caring for pets	-.112	.097	-.074 (.064)	.25					
3						.369	.346	.001	.376	.541
	Lifetime experience caring for children	.481	.085	.378 (.067)	**.001**					
	Empathy	.831	.145	.396 (.069)	**.001**					
	Age	.086	.123	.046 (.066)	.49					
	Sex	-.109	.212	-.036 (.070)	.61					
	Lifetime experience caring for pets	-.048	.143	-.032 (.095)	.74					
	Sex by Lifetime experience caring for pets	-.118	.192	-.057 (.093)	.54					

Note: *B weight* = B coefficient (slope of the line, indicates the direction of the relationship between two variables); *SE* = standard error; *β* = beta weight (standardized B weights); ΔR^2 = change in R^2. The predictor "Lifetime experience caring for pets" was centered (*z*-scores were used). [1]Sex was coded as follows: 0 female; 1 male; indicating that males are the reference group, thus the table represents changes pertaining to males when compared to females. Bold values indicate statistical significance at the $p < 0.05$ level.

pets may prepare the couple as their attitudes about children converge. Whereas our results reflect the interaction between sex and current pet ownership on attitudes about children and childcare, a longitudinal study design would be best suited to address the question of causality. It is important to note that the small effect sizes reported in this study reflect the subtle nature of the effects of currently owning a pet and lifetime experiences caring for pets on attitudes about children and childcare.

Lifetime Experiences Caring for Pets

Owning a pet does not necessarily mean taking care of it. Pet care activities include instrumental and affectionate aspects. Examples of instrumental care include providing daily fresh food and water, a clean shelter, exercise, enrichment, training, and grooming (August, 2011). Affectionate care includes petting, playing, and cuddling (August, 2011). In contrast to affectionate care, instrumental care may be overwhelming, especially to children who generally delegate those instrumental responsibilities to their parents (Muldoon et al., 2015). In this study, the factor "Lifetime experience caring for pets" measures the extent of caring for, playing with, cleaning or walking the pets. It is possible that caregiving interactions between humans and their pets also contribute to sensitive behavior and more positive attitudes toward children. For example, caretaking

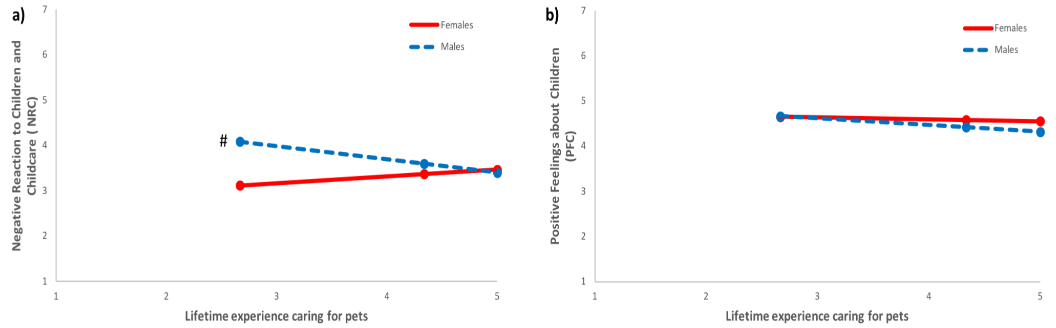

Figure 2. Visual representation of the interaction between sex and lifetime experience caring for pets on attitudes about children and childcare.
(a) Visual representation of block 3 of the hierarchical regression analysis showing the moderating effect of lifetime experience caring for pets on the relationship between sex (main predictor) and NRC. # indicates that lifetime experience caring for pets significantly predicted NRC for males using the post-hoc linear regression for males (β = -.271; SE = .149; constant = 3.888; p = .01, adjusted R^2 = 0.063). (b) Visual representation of block 3 of the hierarchical regression analysis showing no relationship between sex and PFC and no moderating effect of lifetime experience caring for pets on the relationship between sex and PFC. Values for moderator (not centered: Lifetime experience caring for pets) are at the 16th, 50th, and 84th percentiles. Although centered values of the moderator were used in the analyses, the graph shows noncentered values for better interpretability of the graphs. We chose to orient Figure 2 as we did (Lifetime experience caring for pets on the x-axis and Sex presented as two separate lines) given that "Sex" is a dichotomous variable so easily represented by two different lines, and to graph a continuous variable like "Lifetime experience caring for a pet" required artificial dichotomization. This presentation, while contravening traditional statistical style conventions, aids in interpretability of the figure.

interactions contribute to the dyadic bond between mothers and their babies (Barrett & Fleming, 2011; Cassidy, 2008) and more experienced mothers exhibit more sensitive mothering behavior toward their infants (Fleming et al., 1993, 1997, 2002).

Our study provides evidence showing that greater levels of lifetime experiences caring for pets is associated with decreased NRC (hence increased positive attitudes generally) about children and childcare in males—suggesting that the bond between the human-pet dyad could generalize beyond that dyad to include children. Similarly, the human–pet relationship is associated with attitudes about other humans, animals, and environmental issues (Amiot & Bastian, 2015; Muldoon et al., 2015). Among adults, pet ownership was found to be associated with less negative attitudes toward romantic partners (Bonas et al., 2000; Cloutier & Peetz, 2016; Guthrie et al., 2018; McConnell et al., 2019). Among children, pet ownership was associated with positive attitudes toward other animals (Bowd, 1984) and increased environmentally conscious attitudes and behaviours (Torkar et al., 2020). Our results add to this literature by demonstrating that among male non-parents, current pet ownership and lifetime experiences caring for pets are associated with less negative attitudes about children and childcare.

Lifetime Experiences Caring for Pets Increase Males' "Caregiving Portfolio"

Our results provide first insights into the moderating effects of lifetime experiences caring for pets on the relationship between sex and attitudes about children and childcare. Consistent with the literature showing that women spend more time with babies and children compared to men (Craig, 2006; Rossi, 1984), in a sample of non-parents, we found that females had higher levels of experience caring for children compared to males. In addition to being the main caregiver to an infant, observational studies show that mothers tend to be the main caregiver of the family pet (Fifield & Forsyth, 1999; Muldoon et al., 2015). These studies suggest that females tend to have a greater "caregiving portfolio" compared to males. This begs the question: would males show equivalent attitudes about children and childcare if they had an equivalent "caregiving portfolio"? A study by van Polanen and colleagues (2017) on caregiving professionals with similar levels of experience with children found no gender differences in caregiving behaviors on dimensions of attention, sensitivity, and stimulation. This shows that experience caring for children is an important factor associated with increased positive attitudes about children. Similarly, our findings suggest that lifetime experiences caring for pets may increase males' "caregiving portfolio" to a level that is similar to females, thus showing more positive attitudes about children. It is plausible that the extent of experience as a caregiver increases attitudes not only for the individual who is being cared for, but possibly increases positive attitudes toward other living beings.

Differences between NRC and PFC

We investigated whether sex in interaction with current pet ownership and/or lifetime experience caring for pets was associated with two components of attitudes about children and childcare: negative reactions to children and childcare (NRC) and positive feelings about children (PFC). We found that the interaction between sex and current pet ownership as well as an interaction between sex and lifetime experience caring for pets on attitudes about children was specific to NRC. PFC is a measure of warm affectionate emotional attitudes about children, while NRC is a measure of negative attitudes about the physical or instrumental aspects of childcare. In line with our results, and using similar factors for measures of NRC and PFC, Ruble and colleagues (1990) also found significant effects of NRC but not PFC while measuring change in these attitudes across the peripartum period; NRC decreased across the transition to motherhood (from prepregnant to postpartum), but PFC did not. A possible explanation for this may be due to the fact that the two components examine different aspects of caregiving. Caregiving behavior consists of multiple aspects (Cancian & Oliker, 2000), which include instrumental (Barrett & Fleming, 2011; Lomanowska et al., 2017; Lonstein et al., 2015) and affective aspects of caregiving (Atkinson et al., 2000; Fleming et al., 2002; Lomanowska et al., 2017). Therefore, it makes sense that NRC (which addresses reactions about child *care*) would be more sensitive to the moderating effects of lifetime experiences of *care* for pets compared to PFC (which addresses *feelings* about children). While the two factors measure attitudes about the emotional and physical aspects of childcare, it is important to note that they are not measures of behavior per se.

Limitations and Future Directions

Our findings can be considered with the following limitations in mind. The results are limited by a relatively small sample size and the correlational nature of the study. Although current pet ownership eliminated the sex differences in negative attitudes about children and childcare—an effect driven by differences between males with and without pets—it is possible that males who are more inclined to own a pet are also more inclined to care and therefore report more positive attitudes about dependents (children or pets). Further, despite evidence pointing to the importance of the social environment on responsiveness to infant stimuli (Berman, 1980), it was not possible to control the social environment as participants completed the survey online. It is important to note that the small effect sizes reported in this study reflect the subtle nature of the effects of owning and caring for a pet on attitudes about children and childcare. Attitudes about children form a complex psychological phenotype, and this study's objectives were limited by design to explore the interplay between sex and pet ownership/care on attitudes toward children. Future work should include a larger sample size with both parents and non-parents. Also, our group is investigating the effects of pet ownership on well-being including mental health during the COVID-19 pandemic. Further, to determine whether the association between sex and pet ownership on attitudes about children is causal, it would be paramount to investigate these effects through a longitudinal and experimental design including behavioral and attitudinal end points.

Conclusion

In this sample of non-parents, males reported greater negative reactions to children and childcare (NRC) compared to females. However, this sex difference was eliminated within the current pet owners' group as well as among participants with the greatest lifetime experiences caring for pets. Males and females who were either currently pet owners or had more lifetime experience caring for pets had similar NRC levels. This was driven by changes in males' attitudes, such that males with the greatest lifetime experience caring for pets had less NRC compared to males with the least lifetime experience caring for pets. Taken together, these results suggest that owning and specifically caring for pets was associated with increased positive attitudes about children and childcare and may be preparatory for parenthood in male non-parents.

Summary for Practitioners

It is well established that compared to females, males report less positive (i.e., more negative) attitudes about children and childcare (ACC). Given the similarities between parent–infant and owner–pet attachment, we investigated whether these established sex differences in ACC were moderated by owning a pet and/or by lifetime experiences caring for pets—particularly dogs and/or cats—in non-parents. We found that compared to females, males reported more NRC if they were non–pet owners; however, among pet owners, there were no sex differences in NRC. Similarly, we found no sex differences among participants who had more lifetime experience caring for pets; however, at lower levels of lifetime experience caring for pets, males reported more NRC (more negative attitudes) compared to females. This effect was driven by the males, such that compared to males with low lifetime experiences of care for pets, males with higher levels of lifetime experiences of care for pets reported less NRC (more positive attitudes). It is therefore plausible that benefits of the human–pet bond generalize beyond that dyad to include children. Based on this pattern of results, it is not surprising that young couples often acquire a shared pet before they have children. Adding more caregiving experience to their "caregiving portfolio" may afford young couples "practice" or preparation for impending parenthood.

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Chapter 6

General Discussion

6.1 Contributions to the current understanding of brain (amygdala) and affective responses to infant pictures in women

Novelty statement. Studies 1 and 2 (presented in chapter 2 and 3) add to the literature on the neural correlates of postpartum depression (PPD). In study 1 (chapter 2), we investigated the brain (amygdala) and subjective affective response to pictures of *positive* infant faces—which is less often done—as a function of depression status in mothers (PPD vs Non-PPD). In study 2 (chapter 3), we investigated both depression status and maternal status using a 2x2 design (depressed and non-depressed mothers and non-mothers). Results from these studies advance the current (at the time of writing) understanding of: the normative neurobiology underlying the maternal brain, the neurobiology underlying PPD (advance the search for a neural signature for PPD), provide evidence supporting the notion that PPD is distinct from depression occurring outside the postpartum period, the neuroplasticity of the human maternal brain as a result of maternal experience (maternal status and parity).

For the first time, we found that the PPD group had an elevated amygdala response to positive pictures of unfamiliar infants compared to the Non-PPD group as well as to the MDD group. Also for the first time, we found a differential functional connectivity pattern as a function of depression status in mothers during the own vs unfamiliar infant contrast. Further, despite the exploratory nature of these analyses, this was the first report of the effects of maternal experience (parity) on brain response to infant pictures in mothers with and without PPD. Previous fMRI studies comparing mothers with and without PPD were conducted at 1-3 months postpartum (Chase et al., 2014; Deligiannidis et al., 2013; Moses-Kolko et al., 2011, 2010, Silverman et al., 2011, 2007) or 15-18 months postpartum (Laurent & Ablow, 2012, 2013). This study adds to this literature by investigating mothers at 2-5 months postpartum. To the best of my knowledge at the time of writing, study 2 is the only head-to-head investigation to compare depression within and outside the postpartum period (PPD vs MDD).

Response to own infant. We found that all mothers, regardless of depression status, showed greater amygdala and subjective affective responses to their own infant's positive pictures compared to an unfamiliar infant's positive pictures. In non-depressed mothers (Non-PPD), we found that bilateral amygdalae showed a greater response to own infant compared to unfamiliar infant. This finding is a replication of a previous study from our group investigating brain response to infant pictures in a community sample of mothers (Barrett et al., 2012). This result is also in line with studies showing greater amygdala responsiveness to own infant cues compared to an unfamiliar infant's cues across different sensory modalities in healthy mothers (non-depressed community samples) (Barrett et al., 2012; Hipwell et al., 2015; Kim et al., 2011; Leibenluft et al., 2004; Olsavsky, Stoddard, Erhart, Tribble, & Kim, 2021a; Ranote et al., 2004; Seifritz et al., 2003; Strathearn & Kim, 2013; Swain, 2008). For the first time, we found that this effect was not limited to non-depressed mothers, but that the right amygdala of mothers with PPD displayed the same preference to positive pictures of their own infant compared to an unfamiliar infant. Similarly, in a more recent study, researchers asked mothers to observe and empathize with infant pictures and found that mothers at risk for PPD had elevated right amygdala response to their own infant's pictures (both joy and in distress) compared to healthy controls (Lenzi et al., 2016). Given that a mother's own infant is socially, emotionally, and motivationally relevant, these results are also consistent with the evidence showing that the amygdala is specifically responsive to stimuli that is emotionally and motivationally salient to the individual (Cunningham & Brosch, 2012).

Although we did not find group differences (PPD vs Non-PPD) in amygdala response to the own-unfamiliar infant contrast, we found a differential association between the activity of the bilateral amygdalae and the right insular cortex (i.e., functional connectivity) comparing mothers with and without PPD. Specifically, while viewing positive pictures of own infant contrasted to pictures of an unfamiliar infant (own-unfamiliar contrast), PPD mothers showed *decreased* functional connectivity while Non-PPD mothers showed an *increased* functional connectivity between the amygdalae and the right insular cortex. Similarly, depression (measured using EPDS) and anxiety (measured using STAI-T) symptom severity in this sample of mothers was negatively associated with the functional connectivity between the bilateral amygdalae and the right-insular cortex during the own-unfamiliar infant contrast. In other words, mothers scoring higher on depression and anxiety metrics had *decreased* functional connectivity between the bilateral amygdalae and the right insular cortex—the insula is a brain region that has been implicated in processing many cognitive functions including empathy (Singer, Critchley, & Preuschoff, 2009; Uddin, Nomi, Hébert-Seropian, Ghaziri, & Boucher, 2017). This was consistent with our hypothesis of a differential top-down cortico-limbic functional connectivity pattern as a function of depression status in mothers (PPD vs Non-PPD). The hypothesis stems from mounting evidence supporting the notion of dysregulated cortico-limbic connectivity in MDD (Disner et al., 2011; Mayberg et al., 1999; Seminowicz et al., 2004), and in PPD (investigated in the absence of a task, i.e., resting state functional connectivity) (Chase et al., 2014; Deligiannidis et al., 2013).

Response to unfamiliar infant. Compared to Non-PPD mothers, PPD mothers showed an elevated right amygdala response to the positive picture of the unfamiliar infant. This finding was maintained when data from more PPD (+4 PPD, n=32) and Non-PPD (+9 Non-PPD, n=26) mothers were analyzed (see Chapter 3). These findings are in contrast to the majority of fMRI studies on PPD showing a hypoactive amygdala in response to negative words (Silverman et al., 2011, 2007) and angry or fearful pictures of adult faces (Moses-Kolko et al., 2010). It is therefore possible that the direction of amygdala activation in PPD is dependent on the emotional valence of the stimuli as well as the social salience of the stimulus (infant vs non-infant). Nonetheless, given that all mothers (depressed and not) had similar elevated amygdala response to their own infant but only the PPD group showed an elevated amygdala response to the unfamiliar infant pictures shows that the unique amygdala response to positive pictures of one's own infant was blunted in PPD compared to Non-PPD. This fits with hypoactive amygdala response found in PPD compared to Non-PPD groups found in previous studies (Moses-Kolko et al., 2010; Silverman et al., 2011, 2007).

Maternal experience.

Maternal status (mothers vs non-mothers). Although we expected a greater amygdala response to unfamiliar infant pictures in healthy mothers compared to healthy non-mothers, we did not find differences in amygdala responsiveness to positive infant pictures as a function of maternal status. One potential explanation is that the value or meaning of an infant cue is different for parents compared to non-parents. This is clearly demonstrated in work done on non-human mammals. For instance, in response to pup cues virgin female rats—typically neophobic—will either avoid the pups or behave aggressively towards them. In contrast, rat dams (i.e., mothers) attend to their pups or foster pups by approaching them and displaying a range of maternal behaviours towards them. Maternal behaviour within the rat include grooming behaviour, licking, retrieval back to the nest, and crouching over the pups to expose nipples for nursing. In humans, however, the difference between parents and non-parents is more subtle (Lonstein et al., 2015). Another possible explanation is that in-design, mothers viewed a picture of their own infant in addition to the unfamiliar infant, while the non-mothers only viewed pictures of unfamiliar infants. Therefore, it is possible that the cognitive appraisal of the unfamiliar infant by the mother was affected by viewing pictures of their own infant in the same paradigm. Future studies are encouraged to add a comparable familiar condition for the non-moms in the paradigm, or to present infant pictures that are unfamiliar to both mothers and non-mothers.

Parity. Exploratory results from study 1 (chapter 2) showed (marginal) interaction effects between parity and depression status in amygdala response and connectivity while viewing infant cues. Among multiparous mothers, PPD mothers showed an elevated amygdala response to own infant compared to Non-PPD mothers. In contrast, amygdala response to own infant was elevated among primiparous mothers regardless of their depression status. Therefore, among Non-PPD mothers, amygdala response to own infant *decreased* with more maternal experience; whereas, among PPD mothers, amygdala response to own infant *increased* with more maternal experience. Further, amygdala-insula functional connectivity *increased* in Non-PPD mothers but is low in PPD mothers regardless of maternal experience. Evidence from experimental studies in animal models robustly demonstrate the structural and functional neuroplasticity of the maternal brain as a result of pregnancy, parturition, and sensory interactions with the young (i.e., experience-dependent neuroplasticity) (reviewed by Barba-Müller, Craddock, Carmona, & Hoekzema, 2019). Despite the dearth of investigations into the human structural maternal neuroplasticity, recent work in humans (using MRI) shows similar structural changes in brain regions associated with caregiving in the postpartum period (Barba-Müller et al., 2019; Hoekzema et al., 2017; Kim et al., 2010). For example, a study found reductions in overall brain size during pregnancy that return to pre-pregnancy levels throughout the postpartum period (Oatridge et al., 2002). Similarly in a prospective study, Hoekzema and colleagues (2017) found *decreased* gray matter volume in brain regions associated with the mentalizing (i.e., theory of mind) neural network comparing pre-and post-pregnancy (~2 months postpartum) that lasted up to 2 years postpartum in primiparous (i.e., first-time) mothers. In contrast, another prospective study by Kim and colleagues (2010) showed *increased* gray matter volume in several brain regions including the amygdala and insula at 3-4 months postpartum compared to 2-4 week postpartum. Regarding functional brain plasticity, study 1 (chapter 2) for the first time demonstrated functional brain plasticity as a function of parity. The interaction between parity and depression status on amygdala response to own infant pictures adds to the aforementioned literature on brain plasticity. Further, while we found a decreased amygdala response to own infant pictures with more maternal experience in healthy mothers, a recent study by Parsons et al. (2017) found the opposite pattern of amygdala response to unfamiliar infant (vs adult vocalizations) as a function of maternal experience (measured by infant age). Despite these seemingly conflicting results, it is important to note the differences between the two studies. While study 1 (chapter 2) investigated brain response to own infant pictures, Parsons et al. (2017) investigated brain response to unfamiliar infant (vs adult) vocalizations. Critically, the group of mothers assessed by Parsons et al. (2017), were all primiparous and maternal experience was defined by infant age; whereas, the group of mothers assessed in study 1 (chapter 2) included both primiparous and multiparous women and maternal experience was defined by parity. Due to the paucity of studies investigating the structural and functional brain plasticity across the postpartum period, it is difficult to interpret these conflicting findings. However, taken together, these results show that structural and functional brain plasticity is occurring in the postpartum period.

Contributions to the notion that PPD is distinct from MDD. Whether or not PPD is distinct from depression occurring outside the postpartum period is an area of ongoing debate (Batt et al., 2020). Nonetheless, mounting evidence is pointing to a unique pathophysiology underlying a subset of women in PPD relative to MDD (Payne & Maguire, 2019). Study 2 (chapter 3) provides evidence in support of the notion that PPD is distinct from MDD. We found that compared to depressed non-moms (MDD), the PPD group had a greater amygdala response to unfamiliar infants. This elevated amygdala response in the PPD group is in contrast to the decreased amygdala response to affectively negative stimuli observed in PPD (Moses-Kolko et al., 2010; Silverman et al., 2011, 2007). This differential amygdala responsiveness as a function of stimuli valence has been shown in the relatively more extensive fMRI literature on major depressive disorder (MDD) outside the postpartum period. While it is clear that the amygdala in MDD (vs Non-MDD) is hyperresponsive to negative stimuli, evidence on the MDD-amygdala response to positive stimuli is mixed; both hyperactive and hypoactive amygdala response to positive stimuli have been reported in MDD populations (vs healthy controls) (Jaworska et al., 2015).

Clinical symptom severity in this sample. There was considerable variability in symptom severity within the PPD group, and some showed asymptomatic or subclinical depression levels at the time of the fMRI scan. Nonetheless, all mothers in the PPD group had at least one major depressive episode (MDE) during their most recent peripartum period as diagnosed by the resident psychiatrist at an outpatient clinic. Despite this, we still do see group differences between the PPD and Non-PPD group. Further, it is important to note that the PPD group reported feeling more anxious than depressed. This is because while the EPDS scores in the PPD group ranged from 3.85 to 12.73 which is below the typical cut-off for EPDS of 12, trait anxiety scores (measured by the STAI-T) ranged between 36.71-53.01 which is above the clinical cut-off of 34. This adds another layer of understanding to the elevated amygdala response in the PPD group compared to all other groups (see Figure 4 in study 2). Recent evidence points to a specific 'biotype' of depression that presents with more anxious symptomology which is characterized by *decreased* functional connectivity between the amygdala and the cortical regions (Drysdale et al., 2017). Results from study 1 (chapter 2) show the same pattern of decreased functional connectivity (amygdalae-insula) in mothers with PPD (vs Non-PPD). Although depression and anxiety conditions are typically comorbid, this study was designed to study postpartum depression specifically. As such, we call upon future studies to tease out brain response differences comparing postpartum depression and postpartum anxiety.

Limitations and future directions. The limitations inherent to the study design ought to be considered when interpreting results from studies 1 and 2 (for a detailed discussion see the limitations sections in chapters 2 and 3). In addition to the future directions discussed in chapters 2 & 3, here, I briefly present two possibilities for future directions of this work.

Sleep deprivation. Not only is the amygdala's function at the intersection of the maternal and affective neural networks, recent evidence suggests that the amygdala activity (measured by fMRI-BOLD) is particularly sensitive to changes in sleep quantity and quality. Specifically, lack of sleep was shown to elevate amygdala reactivity (Killgore, 2013; Krause et al., 2017; Yoo, Gujar, Hu, Jolesz, & Walker, 2007). For instance, lack of sleep was shown to elevate amygdala reactivity; one night of sleep deprivation led to elevated amygdala response to emotionally negative pictures (reviewed by Goldstein & Walker, 2014). Further, the relationship between sleep and mood disorders is well established (Benca et al., 1997; Plante & Winkelman, 2008). Given that new mothers are chronically sleep deprived (Cárdenas, Kujawa, & Humphreys, 2020; Hall et al., 2009), and the elevated PPD-amygdala response to positive infant pictures demonstrated in study 1 & 2, it would be interesting/important to investigate the relationship between sleep deprivation and the neural response to infant pictures as a function of maternal status and depression. Interestingly, sleep deprivation acts as an antidepressant for a subset of depressed patients (Gillin, Buchsbaum, Wu, Clark, & Bunney, 2001; Ioannou et al., 2021). For those patients, several studies have demonstrated elevated glucose metabolism in the several brain areas including the amygdala and limbic regions (Drevets et al., 2002; Wu et al., 1992). Therefore, future studies investigating sleep deprivation ought to account for this subgroup.

Toward an understanding of large-scale brain network dynamics. Focusing on apriori anatomically defined regions of interest is a targeted and hypothesis driven approach to understanding the neural correlates underlying mood disorders. However, there has been a paradigm shift toward understanding the role of large-scale brain networks as opposed to a localized approach in understanding neurocognitive function (Friston, 2011). Menon (2011) proposed a unifying triple network model for conceptualizing and understanding psychopathology. The triple network model involves aberrant interactions between the 3 intrinsic neural networks: the default mode network (DMN), the salience network (SN), and the central executive network (CE). The insula is part of the salience network (SN) which is thought to mediate switching between the default mode network (DMN) and the central executive network (CE) in healthy participants. The DMN is a collection of brain regions that are active at rest or during mind wandering (i.e., when not attending to a task). In contrast, the CE is a collection of brain regions that are active when performing a cognitive task requiring executive functioning such as solving a mathematical problem (Menon, 2011). Given the negative functional coupling (i.e., decreased functional connectivity) between the amygdala and right insular cortex in PPD (study1), it would be interesting to investigate the interplay between the 3 large scale networks while depressed and non-women (mothers and non-mothers) viewed pictures of infants.

6.2 Contributions to the current understanding of infant cuteness

Novelty statement. To the best of my knowledge, this is the first study to empirically investigate ethological postulations regarding the relationship between cuteness and emotion. This is also the first study to develop a data-driven infant (DDI) cuteness metric.

In the third study (chapter 4), we deepened our understanding of the stimuli (positive infant pictures) used to elicit a brain response in chapters 2 & 3. In this study, we developed a novel data-driven approach to quantify infant cuteness into a single metric. The metric is based on morphological facial characteristics of infant pictures. Previous attempts to quantify infant cuteness were limited by the use of line measurements that captured differences across a few selected facial features (Alley, 1981; Hildebrandt & Fitzgerald, 1979; Sternglanz et al., 1977). This study contributes to the literature on quantifying infant cuteness. In contrast to approaches used in previous studies, this was the first study to use a data-driven approach to quantify infant cuteness into a single metric using face-morphing software (Psychomorph). Compared to earlier approaches, this approach allows for delineation of the facial features at a higher resolution (using 206 facial markers forming 43 lines). The approach also mathematically accounts for the relationship between facial features as well as the curvature of facial features. Using this data-driven approach, we found that the following morphological components were associated with subjective ratings of infant cuteness: large and wide forehead relative to a small and narrow chin, roundness of the face, a big smile, and long asymmetrical features. Also, a square face silhouette with a square jawline—typical characteristics of a masculine adult face—was a component that was negatively associated with subjective ratings of infant cuteness. These morphological descriptions are consistent with ethological descriptions and line measurements of infant cuteness (Kringelbach et al., 2016).

Using the data-driven infant (DDI) cuteness metric, we found that infant cuteness was positively correlated with positive emotions and negatively correlated with negative emotions in nulliparous females. Specifically, higher infant cuteness elicited greater: positive affect, feelings of sympathy, delight, calm, interest, and more of a need to respond. In contrast, higher infant cuteness elicited less: disturbed, distressed, and irritated emotional responses. These findings are consistent with ethological notions regarding cuteness as an evolutionarily conserved protective mechanism to ensure the survival of the young by modulating emotional responses to the infants (eliciting positive and decreasing negative emotion) (Kringelbach et al., 2016; Lorenz, 1943). Subsequent to this study, findings from a recent study corroborate these results showing that baby schema/cuteness elicits positive affect, caring, and smiling response from adults regardless of parental status and gender (Löwenbrück & Hess, 2021).

Limitations and future directions. While the perception of infant cuteness is a multisensory experience that likely includes infant vocalizations and movements, the DDI cuteness metric is limited to facial features. Further, the metric is limited to assessing the variance across 72 photographs of infants' faces. Some of the variance quantified across those pictures is related to camera angles; pictures were not perfectly standardized based on lighting and angle. Therefore, some of the components explaining the variance between pictures are related to camera angles relative to the infant's face. Nonetheless, this provides ecological validity to the metric and understanding of infant cuteness as interactions between adults and infants occur in three-dimensional space and thus involves a variety of angles and vantage points. Another limitation is related to the fixed (as opposed to randomized) order of questions. Subjective ratings of cuteness and emotional responses to infant pictures were collected from a sample of nulliparous females. While the order of infant pictures was randomized across trials, the order of questions was fixed; rating on the cuteness dimension preceded other emotional dimensions. This fixed order could have resulted in a halo effect.

Beyond understanding the morphological and emotional correlates of infant cuteness, we quantified infant cuteness into a single metric using a novel data-driven approach. Next steps are to use this cuteness metric to empirically investigate the relationships between cuteness, brain response to infants, and the quality of maternal/parental behaviour that a child receives. According to Belsky's model on the determinants of parenting, the characteristics of the child are one of three domains that determine the quality of parenting that a child receives. A study by Langlois and colleagues (1995) showed that mothers of infants that were rated as highly cute—by independent raters—were more affectionate and playful compared to mothers of infants that were rated as low on cuteness. Further, cuter infants were shown to elicit a rapid neural response in brain regions implicated in the reward neural network such as the nucleus accumbens (NAc) (Glocker, Langleben, Ruparel, Loughead, Valdez, et al., 2009; Kringelbach et al., 2016). Using the DDI cuteness metric, future studies ought to expand on those findings in mothers with and without postpartum depression. Therefore, future studies ought to investigate the interplay between cuteness, postpartum depression, neural response to infant cues and the quality of maternal behaviour. Drawing on logic from Belsky's model (1984) on the determinants of parenting, one could hypothesize that effect of infant cuteness on maternal response and behavior would be more pronounced in mothers who are non-depressed (vs mothers with PPD). This is because child characteristics (i.e., cuteness) are conceptualized to be the least influential element on parenting compared to the psychological and personal resources of the parent (including maternal mood and thus depression) and contextual resources of stress and support (Barrett & Fleming, 2011; Belsky, 1984).

6.3 Contributions to the current understanding of the relationships between sex and pet ownership on attitudes about children

Novelty statement. To the best of my knowledge, this is the first and only study to investigate the moderating effects of pet ownership and experiences caring for pets on the relationship between sex and attitudes about children and childcare. Results from this study contribute to the current understanding of: human-pet relationships, sex differences in experiences of care and their relation to attitudes about children.

In the fourth and final study (chapter 5), we investigated whether pet ownership and/or lifetime experiences caring for a pet would moderate the established relationship between sex and attitudes about children and childcare in a community sample of non-parents. Consistent with previous studies (Berman, 1980; Kringelbach et al., 2016; Maestripieri & Pelka, 2002), we found that males reported more negative reactions to children and childcare compared to females. Critically, we found that pet ownership as well as lifetime experiences caring for pets moderated the relationship between sex and attitudes about children. Sex differences in attitudes about children and childcare were eliminated as a function of pet ownership and lifetime experiences caring for pets. Specifically among non-pet owners, males reported more negative reactions about children and childcare (NRC) compared to women; whereas among pet owners, males and females did not differ in NRC. Similarly, the extent of lifetime experiences of care for a pet moderated the relationship between sex and NRC. This effect was driven by males and not females; the extent of lifetime experiences caring for pets predicted attitudes about children and childcare in males but not in females. Specifically compared to males with very few lifetime experiences caring for pets, males with a lot of lifetime experience caring for pets reported more favorable attitudes about children and childcare (less negative NRC, thus more positive attitudes). This is consistent with our hypothesis stating that the moderating effects of pet ownership/care would be the greatest among the least child-centric group (i.e., non-parent males).

The results from this study contribute to our understanding of human-pet relationships (Amiot & Bastian, 2015; Muldoon et al., 2015). In particular, these results support the notion that people's attitudes about human-pet relationships are similar to their attitudes about human-human relationships (Bastian et al., 2012; Costello & Hodson, 2010; Guthrie et al., 2018; McConnell et al., 2011, 2019) as well as attitudes about other animals and the environment (Amiot & Bastian, 2015; Muldoon et al., 2015). For example, pet ownership was found to be positively associated with enhanced attitudes about romantic partners (Bonas et al., 2000; Cloutier & Peetz, 2016; Guthrie et al., 2018; McConnell et al., 2019), other animals (Bowd & Santrock, 1984), and environmentally conscious attitudes (Torkar et al., 2020). Results from this study extend these findings to include the positive association between pet ownership/care (human-pet relationship) and favorable attitudes about children and childcare (human-human relationship). However, we found that this association was unique to non-parent males; we did not find an association between pet ownership/care and attitudes about children and childcare in non-parent females. This is in line with the gender specific differences in the association between pet ownership and favorable health and wellbeing outcomes has been reported by previous studies (Guthrie et al., 2018; Parslow et al., 2005; Tower & Nokota, 2006). For instance, Guthrie and colleagues (2018) found that, among non-parents, men and women had the inverse pattern of association between attitudes about pets and the level of social support they received. Specifically, men who had more positive attitudes about pets also had more social support and more relationship satisfaction with their current romantic partner. Therefore, men’s attitudes about their pets were related to their attitudes about their own human-human relationships. However, this was not the case for females. For women, attitudes about pets were not related with how satisfied they felt about their current romantic partner. Therefore for women, a positive human-pet relationship was not predictive of having positive human-human relationships. Also for women, positive attitudes towards pets were associated with decreased levels of social support—a direct contrast to what was found in men (Guthrie et al., 2018). Two epidemiological studies suggest that the gender differences in the association between pet ownership and health outcomes is dependent on relationship status (Parslow et al., 2005; Tower & Nokota, 2006). For instance, Tower & Nokota (2006) found that among unmarried women, pet owners (vs non-pet owners) had lower depressive symptoms while among married women, pet owners (vs non-pet owners) had higher depressive symptoms. Within the family structure, mothers have been shown to be the primary caregiver of the pet (Fifield & Forsyth, 1999; Muldoon et al., 2015). Therefore, one interpretation is that while pet ownership may act as a buffer against lack of social connection for unmarried women, for married women—who are caring for their children and husband—caring for a pet may increase the caregiving burden and thus is associated with lower health outcomes. Men had the inverse pattern. Among unmarried men, pet owners had higher depressive symptoms while among married men there were no association between pet ownership and depression scores. One interpretation is that for unmarried men, pets may be a way by which they seek social relationships; however, the protective effects of social connectedness may be already fulfilled among married men.

Caregiving experiences with pets: adding to a general 'caregiving portfolio'. The notion that more experienced caregivers provide higher quality caregiving compared to inexperienced caregivers has been robustly demonstrated in studies on non-human mammals (Lonstein et al., 2015; Numan et al., 2006). Similarly, studies in humans point to the importance of the effects of caregiving experiences on attitudinal and behavioural responsiveness to infants and children (Bleichfeld & Moely, 1984;

Fleming et al., 1997; Krpan et al., 2005; Numan et al., 2006; Stallings et al., 2001). For instance among mothers, greater experience caring for children prior to having their own children predicted more favorable attitudes and responses to infant cues (Bleichfeld & Moely, 1984; Fleming et al., 1997; Stallings et al., 2001). Results from this study add to these findings, extending the effect of caring for the young conspecifics on attitudes about children to the effect of caring for a member of another species (companion animal, i.e., pet) on attitudes about children. As aforementioned, we found that among non-parent males, greater levels of lifetime experience caring for a pet was associated with more positive/favorable attitudes about children and childcare. This effect was unique to males. A possible explanation for this sex-specific association is due to the differences between male and female 'caregiving portfolios'. We found that compared to males, females had more experience caring for children and had more positive attitudes about children and childcare. These findings are consistent with findings from previous studies showing that compared to men, women tend to spend more time with infants and children (Craig, 2006; Rossi, 1984), and that women have more favorable attitudes about children (Berman, 1980; Kringelbach et al., 2016; Maestripieri & Pelka, 2002). Therefore, women have a higher baseline 'caregiving portfolio'. Given that it was males, and not females, driving the mediating effect of pet care on attitudes about children and childcare, we wonder whether caring for pets elevated males' caregiving portfolio to a level that is similar to females such that their attitudes about children converged. Similarly among caregiving professionals, van Polanen et al. (2017) found that sex differences in caregiving behaviour towards children were eliminated when both males and females had similar levels of experience in caring for children. We suggest the idea of a caregiving portfolio as an important factor for attitudes about children and that the experience of caregiving need not be restricted to the young of one's own species but also to pets as a form of cross-species caregiving. Taken together, results of this study suggest that cross-species caregiving has similar effects to same-species caregiving. This begs the question of whether owning a pet is preparatory for parenthood for young couples, especially in non-parent males.

Limitations and future directions. Interpretation of the aforementioned results are limited by the cross-sectional and correlational design of the study. As such, we are unable to make inferences about the causal effects of owning/caring for pets on attitudes about children and childcare. However, this study acts as the initial step for future studies to investigate whether pet ownership/care prepares non-parents for parenthood. Drawing from Belsky's model on the determinants of parenting, pet ownership/care could fall under the parent's personal and psychological resources, or under contextual sources of stress or support. There is a large variability in the amount of prior caregiving experience that parents have before entering parenthood. More prior experiences caring for an infant are associated with more favorable maternal behaviour/outcomes (Bleichfeld & Moely, 1984; Fleming et al., 1997; Krpan et al., 2005; Numan et al., 2006; Stallings et al., 2001). Does having more experiences caring for a pet aid the parent's personal and psychological resources? Would having to care for a pet in addition to a child be a source of stress for the family? Would that differ based on sex? A longitudinal and interventional/experimental design would be best suited to answer such questions to determine whether pet ownership/care is preparatory for parenthood in prospective parents and whether it would have enhancing/detrimental influences on parental behaviour among current parents.

Further, although previous studies demonstrate that attitudes about children are related to the quality of caregiving behaviour (Bader, Fouts, & Jaekel, 2019; Daggett, O'Brien, Zanolli, & Peyton, 2000), the current study investigated attitudes about children and childcare but not caregiving behaviour per se. As such, future studies are encouraged to include caregiving behavioural endpoints.

6.4 General Conclusions

In conclusion, we found that infant-related amygdala response and connectivity were altered in PPD, infant cuteness was associated with more positive and less negative emotional responses, and previous experiences of caregiving even to a member of a different species were associated with more favorable attitudes about children and childcare in non-parent males. These investigations of brain, affective, and attitudinal responses to infants and children as a function of maternal mood (PPD), infant characteristics (cuteness), and previous experiences of caregiving (to pets and other children) contribute to the current understanding of human caregiving.

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