Development and Psychopathology (2020), **32**, 1534–1543
doi:10.1017/S0954579419001469

CAMBRIDGE
UNIVERSITY PRESS

Regular Article

Neglectful maternal caregiving involves altered brain volume in empathy-related areas

María José Rodrigo[1,2], Inmaculada León[1,2], Lorna García-Pentón[3], Juan Andrés Hernández-Cabrera[1,2] and Ileana Quiñones[4]

[1]Instituto Universitario de Neurociencia, La Laguna, Canary Islands, Spain; [2]Facultad de Psicología. Universidad de La Laguna, La Laguna, Canary Islands, Spain; [3]Department of Psychology at Scarborough; University of Toronto,Toronto, Canada and [4]Basque Center on Cognition, Brain, and Language, Donostia-San Sebastián, Basque Country, Spain.

Abstract

The maternal brain undergoes adaptations to sensitive caregiving that are critical for infant well-being. We investigated structural alterations associated with neglectful caregiving and their effects on mother–child interactive behavior. High-resolution 3D volumetric images were obtained on 25 neglectful (NM) and 23 non-neglectful control (CM) mothers. Using voxel-based morphometry, we compared differences in gray and white matter (GM and WM, respectively) volume. Mothers completed an empathy scale and participated with their children in a play task (Emotional Availability Scale, EA). Neglectful mothers showed smaller GM volume in the right insula, anterior/middle cingulate (ACC/MCC), and right inferior frontal gyrus and less WM volume in bilateral frontal regions than did CM. A greater GM volume was observed in the right fusiform and cerebellum in NM than in CM. Regression analyses showed a negative effect of greater fusiform GM volume and a positive effect of greater right frontal WM volume on EA. Mediation analyses showed the role of emotional empathy in the positive effect of the insula and right inferior frontal gyrus and in the negative effect of the cerebellum on EA. Neglectful mothering involves alterations in emotional empathy-related areas and in frontal areas associated with poor mother–child interactive bonding, indicating how critical these areas are for sensitive caregiving.

Keywords: empathy, maternal neglect, mother–child interaction, volume alterations, voxel-based morphometry

(Received 23 April 2019; revised 7 September 2019; accepted 11 September 2019)

The experience of being a mother involves functional and structural brain changes that support the establishment of sensitive caregiver responses to infants (Kim, Strathearn, & Swain, 2016). Mothers, compared with non-mothers, have been shown to exhibit a specific right prefrontal response when discriminating infant facial expressions (Nishitani, Doi, Koyama, & Shinohara, 2011). Mothers also respond to their own versus unfamiliar infants' cry sounds and faces with a more intense activation in regions involved in viso-emotional processing, empathy, or emotion regulation (Kim et al., 2016; Rocchetti et al., 2014). A higher activation is also found when mothers are responding to an emotional face-matching task during the late than in the early postpartum period, which may reflect long-lasting adjustments in emotional empathy-related areas such as the insula and the middle and inferior frontal gyrus (IFG; Gingnell et al., 2015). Brain changes before and after pregnancy are associated with pronounced and long-lasting gray matter (GM) volume reductions in empathy areas such as the superior temporal sulcus, anterior cingulate cortex, and middle and inferior frontal gyrus, among others (Hoekzema et al., 2017). Moreover, some of these areas also undergo structural increases in GM during the postpartum period, suggesting maternal brain adaptations to the child's evolving needs (Barba-Müller, Craddock, Carmona, & Hoekzema, 2019). From a complementary perspective, the current study examined possible volume differences in those mothers exhibiting a drastic disregard of their own child's needs compared with those showing sensitive caregiving as well as whether these volumetric differences are functionally related to observed mother–child interactive behavior. Finding this association may further illustrate how critical the empathy-related areas are for appropriate mother–child bonding interactions.

An example of extremely insensitive caregiving is maternal neglect that consists of the mothers' failure to provide for the child food, clothing, shelter, medical care, supervision, or emotional support. It is the most common and severe form of child maltreatment that puts the child's safety at risk (Petersen, Joseph, & Feit, 2014; Stoltenborgh, Bakermans-Kranenburg, & van IJzendoorn, 2013). Negligence also disrupts the establishment of a child's secure attachment and healthy psychosocial development (Weinfield, Sroufe, Egeland, & Carlson, 2008), and it entails negative and cumulative behavioral and neurobiological alterations for the offspring (see a review by Teicher, Samson,

Author for Correspondence: María José Rodrigo, Facultad de Psicología, Campus de Guajara, Universidad de La Laguna, La Laguna, Canary Islands, Spain; E-mail: mjrodri@ull.es

Cite this article: Rodrigo MJ, León I, García-Pentón L, Hernández-Cabrera JA, Quiñones I (2020). Neglectful maternal caregiving involves altered brain volume in empathy-related areas. *Development and Psychopathology* **32**, 1534–1543. https://doi.org/10.1017/S0954579419001469

Anderson, & Ohashi, 2016). Studying the neurobiological basis of maternal neglect could help in the tuning of intervention efforts directed at reducing risk and promoting infant health.

Our first objective was to examine GM and WM volume differences between neglectful (NM) and non-neglectful control (CM) mothers who are sociodemographically similar. In searching for brain differences between NM and CM, we expected that at least part of the volumetric differences would overlap with empathy-related areas. Those areas undergo functional and structural adaptations to sensitive caregiving in normal mothering (Kim et al., 2016). Parental empathy, defined as the appropriate perception, understanding, and experience of an infant's emotional states, is one of the crucial abilities for providing caring responses to one's own infant's needs that is lower in NM (León et al., 2014; Rodrigo et al., 2011). The lower empathic skills that have been observed in NM seem to be tightly coupled with their lower brain reactivity to infant cues. Compared with CM, NM showed a generic attenuated response to infant and adult crying faces in viso-limbic areas such as the bilateral lingual, bilateral cerebellum, bilateral fusiform gyrus, right hippocampus, parahippocampal gyrus, and right amygdala (León et al., 2019). Lesser activations in NM than in CM were also specifically shown to infant crying faces in the left, middle, frontal, and anterior cingulate areas, underscoring their difficulties with responding to the infant's emotional cues (León et al., 2019). In this study, brain differences were assessed using voxel-based morphometry (Ashburner & Friston, 2000), an approach used to quantify structural brain properties for the investigation of volume differences in brain anatomy.

With respect to the GM volume, studies have shown that adults with higher scores on the emotional Empathic Concern (EC) scale of the Interpersonal Reactivity Index (Davis, 1980), defined as the embodied simulation of and sympathy with others' emotions, showed greater GM volume in the anterior insula (Eres, Decety, Louis, & Molenberghs, 2015; Mutschler, Reinbold, Wankerl, Seifritz, & Ball, 2013) and the IFG (Banissy, Kanai, Walsh, & Rees, 2012) than those with lower scores. In turn, adults with higher scores on the cognitive the Perspective Taking (PT) scale of the Interpersonal Reactivity Index, defined as the mental-state understanding and perspective taking from others, showed greater GM volume in the middle cingulate cortex and the adjacent dorsomedial prefrontal cortex than those with lower scores (Eres et al., 2015). Importantly, GM volume increases in sensitive mothers with perceived higher parental care in childhood were also found in the superior/middle frontal areas, orbitofrontal gyrus, superior temporal gyrus, and fusiform gyrus (Kim et al., 2010). Given these findings, we expected to find some volumetric differences between NM and CM in empathy-related areas, given the severe disregard of the child's needs and the lower scores in empathic concern that have been observed in NM (León et al., 2014; Rodrigo et al., 2011).

Structural differences in WM volume are also expected between NM and CM. White matter disruption has been reported in postpartum depression in the fronto-thalamic circuit and in interhemispheric connectivity (Silver et al., 2018). In turn, a higher EC score in adults has been shown to be positively associated with greater WM structural integrity in the tracts linking areas involved in affective processing of infant faces such as the inferior longitudinal fasciculus and the inferior fronto-occipital fasciculus (IFOF; Parkinson & Wheatley, 2012). Given that NM compared with CM showed a volume reduction in the inferior longitudinal fasciculus and IFOF in a diffusion tensor imaging study (Rodrigo et al., 2016), we also expected a smaller WM volume in NM than in CM in those areas traversed by these tracts.

As a second objective, we examined the functional effects of GM and WM volume differences between NM and CM on Emotional Availability (EA), as a proxy for the quality of mother–child bonding interactions. A play task that measures the ability to read and respond appropriately to each other's emotional signals in mother–child dyads has been used to assess EA (Biringen, 2000; Biringen, Derscheid, Vliegen, Closson, & Easterbrooks, 2014). Emotional availability is also predictive of the mothers' reported child attachment (Altenhofen, Clyman, Little, Baker, & Biringen, 2013). A previous study had shown lower scores in NM than in CM in EA associated with a lesser volume in the inferior longitudinal fasciculus and IFOF (Rodrigo et al., 2016). Therefore, we expected to find a positive association between smaller GM and WM volumes and lower EA scores in NM compared with CM.

Once the possible effect of volumetric differences on maternal sensitivity between NM and CM had been tested, we wanted to go a step further in determining the possible role of trait emotional and cognitive empathy in that relationship. A higher score on EC has been associated with the intention to provide needed care to the child (Lin & McFatter, 2012) and the expression of maternal warmth and positive affect (Stern, Borelli, & Smiley, 2015). In turn, a higher score on PT has been related to increases in one's own infant's pupil dilation in response to others' emotional displays, an early precursor of empathy (Upshaw, Kaiser, & Sommerville, 2015). Therefore, if volumetric differences are found in areas corresponding either to the emotional or cognitive empathy circuits, we expected that introducing EC or PT, respectively, as mediators would increase the possibilities of finding an association between volumetric differences and EA.

Altogether, this study can provide evidence of the volumetric alterations underlying neglectful mothering and the role played by the emotional and cognitive empathy-related brain areas in maternal caregiving.

Methods

Participants

Forty-eight mothers (25 NM and 23 CM) voluntarily participated in the experiment. They were all recruited through the same primary health center in Tenerife, Spain. Written consent was obtained from all of the participants and the Ethics Committee of the University of La Laguna approved the study's protocol. General inclusion criteria were being the biological mother of a child who was under three years old who had not been placed in foster care at any point in their history and had not been born prematurely or suffered perinatal or postnatal medical complications according to the pediatricians' reports. Specific inclusion criteria for the neglectful mother group were a substantiated case of neglect registered in the last 12 months by Child Protective Services and complying with the indicators of the Maltreatment Classification System for severe neglect (Barnett, Manly, & Cicchetti, 1993) according to the pediatrician of the primary health center in charge of the case. Thus, these mothers scored positively on physical neglect (inadequate food, hygiene, clothing, and medical care), lack of supervision (child is left alone or in the care of an unreliable caregiver), and educational neglect (lack of cognitive and socioemotional stimulation and lack of attention to the child's education). Inclusion criteria

https://doi.org/10.1017/S0954579419001469 Published online by Cambridge University Press

for the control group were negative scores in all of the Maltreatment Classification System neglect indicators, also according to the pediatrician, and the absence of Child Protective Services or Preventive Services records for the family. As for the sociodemographic profile of mothers, which was reported by the social worker, they were all in their early 30s; they had a similar number of children and mean age of the target child; the NM were more likely than CM to live in one-parent families and to receive financial assistance, indicating an overload in their caregiver task and financial difficulties; and the groups shared similar, low socioeconomic backgrounds (Table 1). According to the neglect risk profile rated by the social workers on the presence or absence of risk indicators for neglect, most mothers in the neglectful group had a history of childhood maltreatment or neglect (of the mother when she was a child). They also scored positively in poor household management, disregard of the child's needs, and rigid/inconsistent discipline norms [see Appendix 1 for details on the risk profile measures].

Table 1. Sociodemographic and neglect risk profile in Neglectful and Control groups

	Neglectful group ($n = 25$) M (SD) or %	Control group ($n = 23$) M (SD) or %	t (46) or $\chi 2$
Sociodemographic profile			
Mean age of mother	29.2 (7.0)	33.43 (3.4)	−2.63*
Number of children	2.08 (0.8)	1.65 (0.6)	1.93
Mean age of the target child	2.8 (1.5)	2.1 (1.8)	1.5
Rural areas (%)	45.8	37.5	0.61
Level of education (%):			2.93
Primary	72	47.0	
Secondary school	16	30.0	
>Secondary school	12	21.7	
One-parent family	48	13	5.28*
Employment (%)	44	34	5.32
Financial assistance	84	13	21.37***
Neglect risk profile			
History maltreatment/ neglect (%)	68	17.4	10.49***
Intimate partner conflict (%)	5	0	3.68
Chronic physical illness (%)	4	0	2.51
Poor household management (%)	84.2	0	24.29***
Disregard health/ education needs (%)	57	0	12.79***
Disregard emotion/ cognitive needs (%)	89	0	27.24***
Rigid/inconsistent norms (%)	68	0	16.83***

Note: Group comparisons with mean scores were performed with t tests, while those with percentage values were performed with the chi-Square (χ^2) statistic. $^*p < .05$ $^{***}p < .001$.

Behavioral and personality measures

The Mini International Neuropsychiatric Interview

(M.I.N.I. 6.0, Spanish version; Ferrando, Bobes, Gibert, Soto, & Soto, 2000). All of the participants completed the M.I.N.I., which includes 15 major psychiatric disorders (Table 2). The two groups mainly differed on five psychopathological variables (marked in italics) that survived the Bonferroni correction, which were evaluated by using a principal component analysis. The results yielded a one factor solution: "Psychiatric Disorders," with moderate intercorrelations among the five variables, KMO = 0.68, eigenvalue = 2.74, with explained variance of 55%, and the coefficient scores in Psychiatric Disorders being higher in neglectful ($M = 0.63$, $SD = 1.02$) than in control mothers ($M = -0.69$, $SD = 0.21$); t (46) = 6.3, $p = .000$; $\delta = 1.82$. None of the mothers in either group were being medicated for psychiatric disorders at the time of testing. The coefficient score for Psychiatric Disorders (PD) was used as a regressor in the statistical parametric mapping (SPM) model. Given that the dichotomized variables (Group for mothers and PD) were certainly related ($r = 0.67$), we previously ruled out their potential multicollinearity before including each in the model as a covariate. Research shows that the magnitude of such a correlation is not a reliable indicator when there are problems with collinearity between two variables (Belsley, 1991). Therefore, we tested whether our use of "psychiatric disorders" as a covariate in the SPM model with Group had the potential for problematic multicollinearity. We calculated the variance inflation factor, the tolerance, and the condition number, associating each predictor variable with the group as well as the shared variance of the psychiatric variables with the group [See Appendix 2, Table A1]. Once evidence of noncollinearity was obtained, PD was included as a covariate in the SPM model to control as much as possible for its effect on brain volumetric differences. All of the analyses were performed with R (R Core Team, 2019).

Emotional Availability (EA)

This variable was measured in the context of mother–child free play using the EA Scale: Infancy to Early Childhood Version (Easterbrooks & Biringen, 2005). This scale operationalizes parental and child behavior on six subscales that were factorized into one factor, EA, by using principal component analysis, given the high intercorrelations among the scales. Two external observers who were blind to the mothers' grouping made the ratings from the videos, and the inter-rater reliability of the ratings in each scale was adequate [see Appendix 3 and Table A2 for the scales and testing]. The EA factor score was lower in the neglectful dyads ($M = -0.61$, $SD = 0.92$) than in control dyads ($M = 0.66$, $SD = 0.55$); t (46) = −5.75, p = 1.66, and it was used as a dependent variable.

Interpersonal Reactivity Index

(IRI; Spanish version; Pérez-Albéniz, De Paúl, Etxeberría, Montes, & Torres, 2003). Only the Empathic Concern (EC) and the Perspective Taking (PT) scales were used. The EC scale assesses the respondents' feelings of warmth, compassion, and concern for others (emotional empathy), whereas the PT scale describes the tendency to spontaneously adopt others' points of view in everyday life (cognitive empathy). The scores on EC and PT were lower in NM ($M = 26$, $SD = 3.59$; $M = 23.56$, $SD = 4.35$, respectively) than in CM ($M = 28.08$, $SD = 3.56$; $M = 26.21$, $SD = 3.74$, respectively), and t (46) = −2.01, $p = .05$; $\delta = 0.58$; $t(46) = -2.25$; $p = .05$; $\delta = 0.65$, respectively.

Table 2. Psychopathological conditions stratified by group

	Neglectful group ($n = 25$) M (SD)	Control group ($n = 23$) M (SD)	t (46)	Effect size δ
Major Depressive Episode	2.0 (2.6)	0.2 (0.5)	3.36**	0.97
Dysthymia	1.6 (2.2)	0.3 (0.5)	2.75**	0.79
Suicidality	0.5 (0.8)	0	2.79*	0.81
Hypo/Manic Episode	1.8 (2.1)	0.1 (0.3)	3.94**	1.14
General Panic Disorder	6.8 (5.7)	0.7 (2.1)	4.93***	1.42
Agoraphobia	0.7 (1)	0.2 (0.4)	2.33*	0.70
Social Phobia	0.6 (1)	0	2.50*	0.75
Obsessive-Compulsive	1.2 (1.6)	0.2 (0.6)	2.46*	0.74
Post-traumatic Stress Disorder	1.6 (2.6)	0.9 (1.8)	0.96	0.29
Alcohol Dependence/Abuse	0.1 (0.2)	0.2 (0.5)	0.78	0.23
Drug Dependence/Abuse	0.2 (0.4)	0	1.89	0.57
Psychotic Disorders	0.7 (1.4)	0.2 (0.5)	1.68	0.49
Bulimia Nervosa	0.1 (0.2)	0	1	0.29
Generalized Anxiety Disorder	3.4 (3.4)	0.6 (0.9)	3.76***	1.08
Antisocial Personality	1.2 (1.2)	0.1 (0.3)	4.08***	1.18

Note: Variables that are shown in italics were submitted to principal component analysis. *$p \leq 05$ **$p \leq .01$ ***$p \leq .001$

Procedure

After the selection of the sample, social workers reported on the sociodemographic and neglect risk profile and asked mothers for permission to be contacted by phone. Those mothers who gave permission were contacted by our collaborator and were informed about the general goal of the study (to participate in a study about mother–child relationships avoiding the use of the term neglect in any case) and the procedure to be followed upon their acceptance. Then, the collaborator picked them up at their homes at their convenience to bring them to the scanning session at the hospital where they gave their informed written consent and passed the MRI sequence under a resting state condition without stimuli being presented. In a second session carried out at their homes, the same collaborator collected the mothers' response to the questionnaire, gave a gift to the child, and video recorded the mother–child play interaction. At the end of the session, the mothers were given a monetary compensation (100 euros).

MRI Processing and Analysis

Structural Image Acquisition

High-resolution T1-weighted MPRAGE anatomical volumes were acquired on a General Electric 3T scanner located at the university hospital's magnetic resonance service for biomedical research at the University of La Laguna. A total of 196 contiguous 1mm sagittal slices were acquired with the following parameters: repetition time = 8.716 ms, echo time = 1.736 ms, field of view = 256×256 mm^2, in-plane resolution = 1 mm × 1 mm, flip angle = 12.

Voxel-Based Morphometry Processing

T1 images were preprocessed using the Voxel-Based Morphometry toolbox (http://dbm.neuro.uni-jena.de/vbm.html) and the SPM8 software package. The images were corrected for bias-field inhomogeneity, and the tissue was then classified into gray and white matter and cerebrospinal fluid and registered to standard space using high-dimensional DARTEL normalization (Ashburner, 2007). The segmentation approach that was used is based on an adaptive maximum a posteriori technique, which does not need a priori information about tissue probabilities (Rajapakse, Giedd, & Rapoport, 1997). This procedure was further refined by accounting for partial volume effects and by applying a hidden Markov random field model, which incorporates spatial prior information of the adjacent voxels into the segmentation estimation (Tohka, Zijdenbos, & Evans, 2004). To measure regional differences in absolute GM and WM volumes in the obtained volumetric segmentations, the warped images were modulated. All of the normalized modulated images were smoothed with a filter of a 10-mm Gaussian kernel. An additional quality check based on the sample homogeneity was conducted.

Statistical Analyses of GM and WM volumes

General linear model analyses (i.e., in SPM, full factorial design (Gläscher & Gitelman, 2008) were performed using the individual gray/white matter volumetric segmentations as dependent variables and including Group (Control vs. Neglectful mothers) as a between-subject factor. The models included one regressor described above as Psychiatric Disorders. The age of the mothers (mean centered) was also included as a nuisance covariate.

The resulting statistical parametric maps were thresholded at a peak level of $p < 0.001$ (uncorrected), adjusting the cluster spatial extent to capture only those clusters corrected for multiple comparisons using the whole-brain or the small-volume FWE corrections (p < 0.05). The second-level inferences were tested using a threshold of $p < 0.001$ (uncorrected), with a voxel extent adjusted such that only those peaks or clusters with a p-value corrected for multiple comparisons using family-wise error (Nichols & Hayasaka, 2003) were considered to be significant. All local maxima were reported as Montreal Neurological Institute coordinates.

https://doi.org/10.1017/S0954579419001469 Published online by Cambridge University Press

Gray matter regions were labeled with reference to the Automated Anatomical Labeling atlas (AAL; Tzourio-Mazoyer et al., 2002).

Statistical Analyses of Brain-Behavior Associations

As a first step, regression analysis was performed with the whole sample to test the hypothesis of whether the presumable group volumetric differences in GM and WM were associated with the mother–child emotional availability in the play task (EA). Based on the results of the second level whole-brain analysis previously described, the volume per region of interest per subject was extracted. Five GM and two WM variables were used. To examine possible Group interaction effects on EA, we first performed a regression analysis in which Group was included with the volumetric variables. Maltreatment status was also included due to its potential association with EA. Because Group did not show any interaction effects with volumetric measures and Maltreatment effects on EA disappeared due to the high redundancy with Group (17 out 25 in NM were maltreated), Group was removed from the regression. Therefore, the regression analysis that is reported includes Maltreatment status and the volumetric variables in the whole sample to determine their effects on EA.

As a second step, we performed mediation analyses with those volumetric variables not exhibiting a direct association with EA in the reported regression model to further test whether they were related to EA through the mediation of EC and PT. For each mediation model with EC/PT, each of the aforementioned brain areas acted as the independent variable, EC/PT as a mediator, and EA as the dependent variable.

Results

Volumetric differences in GM and WM in neglectful as compared with control mothers

The voxel-based morphometry analysis showed three distributed clusters with a pattern of smaller GM volume in NM than in CM. Each of these clusters spanned several contiguous anatomical regions in both hemispheres (Table 3 and Figure 1). Cluster 1 included a large midline region comprising the anterior/middle cingulate (ACC/MCC) cortex with extension to both hemispheres, superiorly to the left precentral gyrus, the left superior frontal gyrus, and the most inferior part of the right supplementary motor area. Cluster 2 involved a broad region from the pars triangularis within the IFG to the adjacent part of the middle frontal gyrus. Cluster 3 was circumscribed to the posterior part of the right insula. In addition, the voxel-based morphometry analysis showed one posterior cluster exhibiting the opposite pattern, that is, greater GM volume in NM than in CM. As this cluster comprised a broad region, it was anatomically divided into two distinct areas, fusiform and cerebellum, to test their effects separately.

The WM analyses showed two frontal bilateral clusters of smaller WM volume in NM than in CM, traversed by the association fiber tracts sensitive to individual differences in empathic concern (See Table 3 and Figure 2). For visualization purposes, the significant WM clusters were used to build the 3D regions of interest that are represented in Figure 2 (below). The surrounding pathways were reconstructed using the Q-Space diffeomorphic reconstruction (Yeh & Tseng, 2011) in Montreal Neurological Institute space implemented in DTI Studio (Jiang, Van Zijl, Kim, Pearlson, & Mori, 2006). Thus, bilaterally, clusters comprised the IFOF, the corpus callosum, and the anterior corona radiata. The left WM cluster also included the anterior thalamic radiation (Oishi, Faria, Van Zijl, & Mori, 2010). The smaller WM volume in the frontal clusters was located adjacent to the smaller GM volume in the two frontal clusters (Figure 3).

Effects of differences in GM and WM volumes on Emotional Availability

For the regression analyses, the maltreatment classification (21 maltreated and 27 non-maltreated mothers), the five GM areas (ACC/MCC, right inferior frontal gyrus, Insula, Fusiform_R, and Cerebellum) and the two WM areas (WM_L and WM_R frontal areas) showing volumetric differences in the previous section were used as predictors of EA. The results showed as significant regressors the volumetric measures in the GM of Fusiform_R, in the WM of Frontal_R, and Maltreatment status, F (3,44) = 7.98, p < 0.001, explaining a moderate proportion of the variance in EA, $R^2 = 0.352$; $AdjR^2 = 0.308$. Greater volume in frontal WM_R was associated with higher scores in EA, Estimate = 3.73; t (44) = 2.08, p = .04, whereas greater GM volume in Fusiform_R, Estimate = −3.35; t (44) = −1.94, p = .05, and belonging to the maltreatment group, Estimate = −0.69; t (44) = −2.74, p = .01, were associated with lower scores in EA (Figure 4a & b).

Empathic Concern and Perspective Taking as mediators of the effects of GM and WM volumes on Emotional Availability

We performed mediation analyses (Tingley, Yamamoto, Hirose, Keele, & Imai, 2014) to further test whether those five areas not directly linked to EA in the regression model (ACC/MCC, IFG_R, Insula_R, Cerebellum, and WM_L) would be related through the mediation of EC and PT. Three of the five mediating models showed significant relations. Using a bootstrap resampling procedure, their parameters fell outside the confidence intervals, indicating that the results are not likely to be random. The analysis indicated that EC mediated in the positive relationship that was observed for both the IFG (Average Causal Mediation Effects, $ACME = 4.03$, $p = 0.001$) and the Insula ($ACME = 3.39$, $p = 0.03$) on EA (Figure 4c) and in the negative relationship that was observed for the Cerebellum ($ACME = -2.56$, $p = 0.04$) on EA (Figure 4d). Neither mediated nor direct significant effects were found for EC in relation to ACC/MCC and WM_L and EA, and no effect was found for PT for any of the models.

Discussion

This study revealed brain differences between NM and CM consisting of a smaller GM volume for critical empathy-related areas of the maternal brain including the right and left ACC and MCC, right insula, and right IFG, corresponding to those areas showing greater GM volume in high empathic adults. The insula-cingulate structures function as an alarm system to infant signals of pain and distress, whereas the right IFG is a core region of the mirror neuron system, which enables parents to intuitively resonate with the child's actions and facial expressions while observing them (Fan, Duncan, de Greck, & Northoff, 2011; Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). The NM group also showed a pattern of greater GM volume in areas crucially involved in emotional face processing including the cerebellum (Adamaszek et al., 2017) and right fusiform (Weiner & Zilles, 2016) than the CM group.

Table 3. Gray and white matter volumetric differences showing cingulate, frontal, and insula smaller GM volume clusters (NM < CM); one posterior (cerebellum and fusiform) greater GM volume cluster (NM > CM); and one frontal smaller WM volume cluster (NM < CM).

	Coordinates (mm)			Cluster level		Peak level
	x	y	z	*p*-values (FWE-corr)	Cluster size (voxels)	*T* scores
Neglectful < Control Mothers (GM volume)						
Cingulum_Mid_R	6	38	32	0.000	7776	5.804
Cingulum_Mid_L	−6	15	36			5.227
Cingulum_Mid_R	5	20	32			5.029
Supp_Motor_Area_R	8	2	51			4.899
Precentral_L	−29	−12	65			4.783
Frontal_Sup_L	−24	3	68			4.677
Cingulum_Ant_L	−3	36	29			4.639
Frontal_Sup_Medial_R	5	27	42			4.405
Frontal_Inf_Tri_R	43	38	27	0.011	1104	5.402
Frontal_Mid_R	27	47	29			3.993
Insula_R	59	−13	7	0.132*	525	4.520
Neglectful > Control Mothers (GM volume)						
Cerebellum_9_R	21	−41	−48	0.001	4035	4.483
Cerebellum_8_R	17	−60	−50			3.830
Cerebellum_Crus2_R	50	−69	−39			3.583
Fusiform_R	33	−62	−18			3.041
Neglectful < Control Mothers (WM volume)						
Cluster Frontal_L	−32	11	29	0.000	4707	5.673
	−15	12	48			4.843
	−8	27	51			4.555
Cluster Frontal_R	41	21	24	0.042	1805	4.503
	33	29	23			4.173
	15	29	32			3.345

Note: Whole-brain voxel corrections were applied. All of the reported local maxima belong to a significant cluster (*p*-value FWE corrected < 0.05) with the exception of the probability value signaled with an asterisk, indicating that this cluster was significant after a small volume correction (cluster-level *p*-value (FWE-corr) = 0.001; peak-level *p*-value (FWE-corr) = 0.019). NM: Neglectful mothers; CM: Control mothers; Sup: Superior; Ant: Anterior; Inf: Inferior; Mid: Middle; Supp: Supplementary; Tri: Triangular; R: Right; L: Left.

The different pattern of GM volumetric differences between NM and CM in the empathy-related areas (smaller frontal areas) and in the viso-emotional processing system (greater occipital areas) is quite compatible with the asymmetric pattern found in EEG rhythms in response to emotional stimuli also found in NM (León et al., 2014)—the higher the increases in theta and lower alpha oscillations in response to emotional pictures at occipital sites, the lower the increases of the same bands at frontal sites. A reversed EEG oscillatory pattern was found in CM. Therefore, both GM volume and oscillatory patterns in NM would reflect the lower engagement of frontal regulatory processes over the occipital areas in emotional processing. Brain regulatory responding to emotional information is critical for sensitive parenting and for the development of emotion regulation in early child development (Rutherford, Wallace, Laurent, & Mayes, 2015). The current results highlight the relevance of the frontal-occipital distribution of gray matter volume in the context of emotion regulation, presumably associated with sensitive parenting.

A smaller WM volume was found in frontal clusters in NM than in CM. The bilateral WM frontal clusters were traversed by fibers of the IFOF, the corpus callosum, and the anterior corona radiate, whereas the left WM frontal cluster was traversed by fibers of the anterior thalamic radiation. These results greatly converge with those found in diffusion tensor imaging studies showing less integrity in the same tracts in adults with lower scores in EC (Parkinson & Wheatley, 2012). Altogether, the GM and WM findings pointed to an important restriction in volume on a highly interconnected frontal region at the crossroads of viso-emotional pathways, the thalamus with the cortex, and the communication between hemispheres that may undermine the way mothers "read" the emotional cues to engage appropriately in sensitive interactions with the child.

As expected, the quality of mother–child bonding (EA) was lower in neglectful than in control dyads. Importantly, we obtained evidence of the functional influence of GM and WM volumetric differences on EA, either directly or when introducing differences in EC as a mediator. Overall, a greater GM volume in

https://doi.org/10.1017/S0954579419001469 Published online by Cambridge University Press

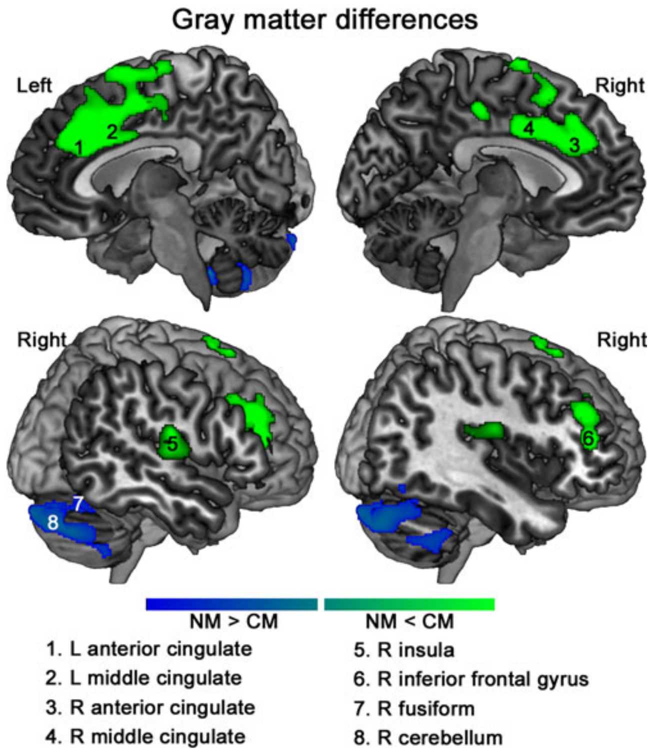

Figure 1. GM volume alterations in neglectful mothers in empathy-related regions. Smaller GM volumes in NM as compared to CM were found in the bilateral anterior/middle cingulate cortex, right posterior insula, and right inferior frontal gyrus. A reversed pattern of greater GM volume in NM as compared to CM was found in the right fusiform and the right cerebellum.

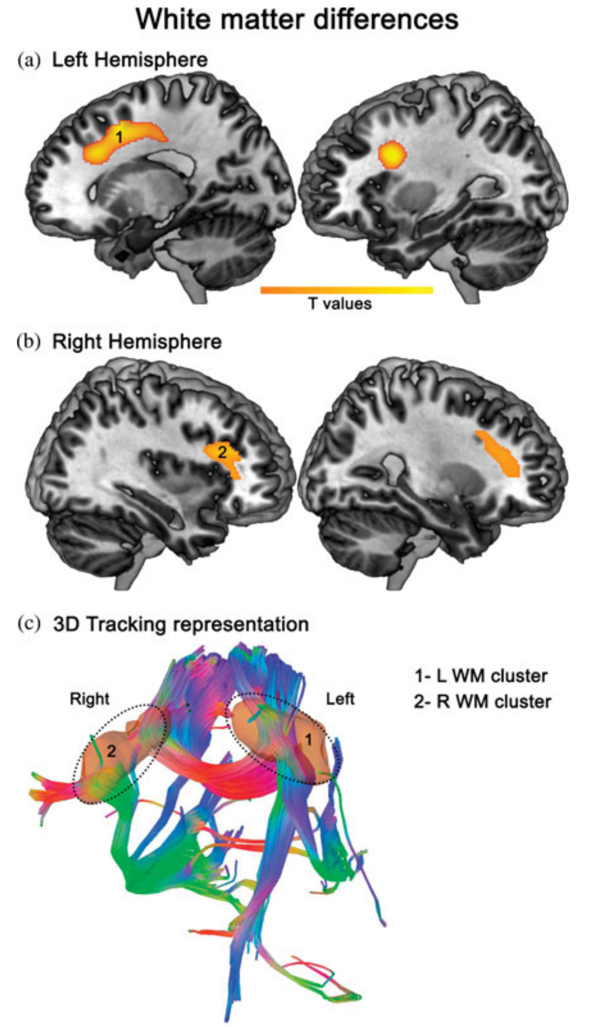

Figure 2. WM volume alterations in neglectful mothers in frontal regions. (a and b) Smaller WM volumes in NM as compared to CM were found in two frontal bilateral clusters, and (c) 3D individual tracking representation (see dotted ovals) shows that the right frontal cluster is traversed by the inferior fronto-occipital fasciculus (IFOF), the corpus callosum, and the anterior corona radiata (ACR), whereas the left frontal cluster is traversed by the anterior thalamic radiation (ATR).

right fusiform and a smaller WM volume in right frontal areas were directly associated with the lower mother–child emotional availability, once we examined the negative impact of the mothers' childhood maltreatment on the dyadic emotional availability (also found by Mielke et al., 2016). The frontal anomalies found in WM seem to correspond to the lower structural connectivity in the IFOF obtained in a diffusion tensor imaging study in NM, and they also related to poor mother–child bonding (Rodrigo et al., 2016). Although NM scored lower on both EC and PT than CM (León et al., 2014; Rodrigo et al., 2011), greater volume in emotional empathy-related areas, such as the insula and IFG, were associated with higher mother–child emotional availability only mediated by EC. In turn, greater cerebellum volume mediated by EC was associated with lower emotional availability, suggesting its implication in emotional processes (Adamaszek et al., 2017). These brain-behavior associations could be used in the future as biological indicators of dysfunctional mother–child interactive behavior.

The GM areas affected in NM associated with EA as well as the unique mediating role of EC in this relationship suggest that emotional empathy-related areas, which are responsible for the automatic perception of distress signals and involved in embodied simulation and sympathy with others' emotions, played a distinctive, prominent role in the caregiving network. The alterations in NMs' emotional empathy-related areas may disturb the so-called "intuitive parenting" (Papoušek & Papoušek, 1987) that provides a fast response to the child that is crucial to a child's secure attachment (Altenhofen et al., 2013). A convergent finding is that mothers' caregiving behavior is particularly driven by the emotion-processing network, while fathers, when acting as primary caregivers, exhibit activity in both the emotional and the cognitive empathy areas (Abraham et al., 2014). In turn, the volumetric reduction in NM compared with CM in the ACC/MCC cortex presumably related to cognitive empathy (Eres et al., 2015) was not associated with EA, confirming a less prominent role of the cognitive empathy-related areas in maternal neglectful caregiving.

Our present results converged with those found with EEG and diffusion tensor imaging studies in defining some of the alterations underlying maternal neglect (León et al., 2014; Rodrigo et al., 2011, 2016). A paradoxical result is the greater GM volume in the cerebellum and fusiform areas in NM than in CM, where an activation reduction was found in these areas in response to crying faces in an fMRI study with the same mothers (León et al., 2019). However, a greater convergence (reductions both in GM volume and activation to infant crying faces) was found in the frontal and cingulate areas in NM than in CM. More research is needed to envision how the neural organization is altered in these mothers at structural, functional, and connectivity levels and to elucidate the potential connections between levels.

https://doi.org/10.1017/S0954579419001469 Published online by Cambridge University Press

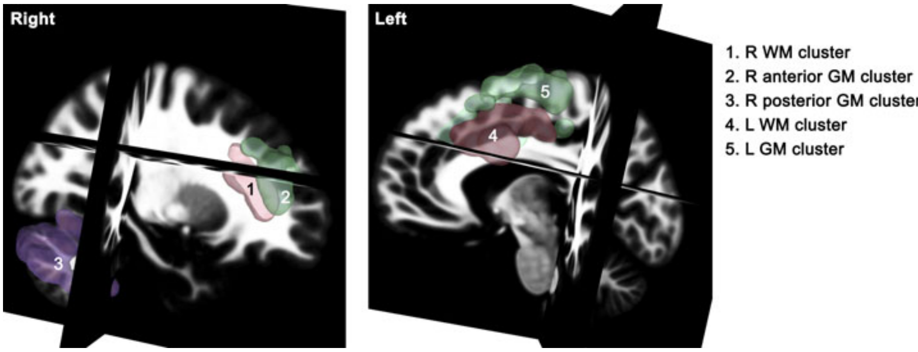

Figure 3. Overlapping of WM and GM volume frontal alterations in neglectful mothers. The smaller WM volumes in the bilateral frontal clusters were located adjacent to the two reduced GM volumes in the bilateral frontal clusters. Notice that only letter (c) in Figure 2 is in italic and should be ordinary found like (a) and (b) and like the ones in Figure 4.

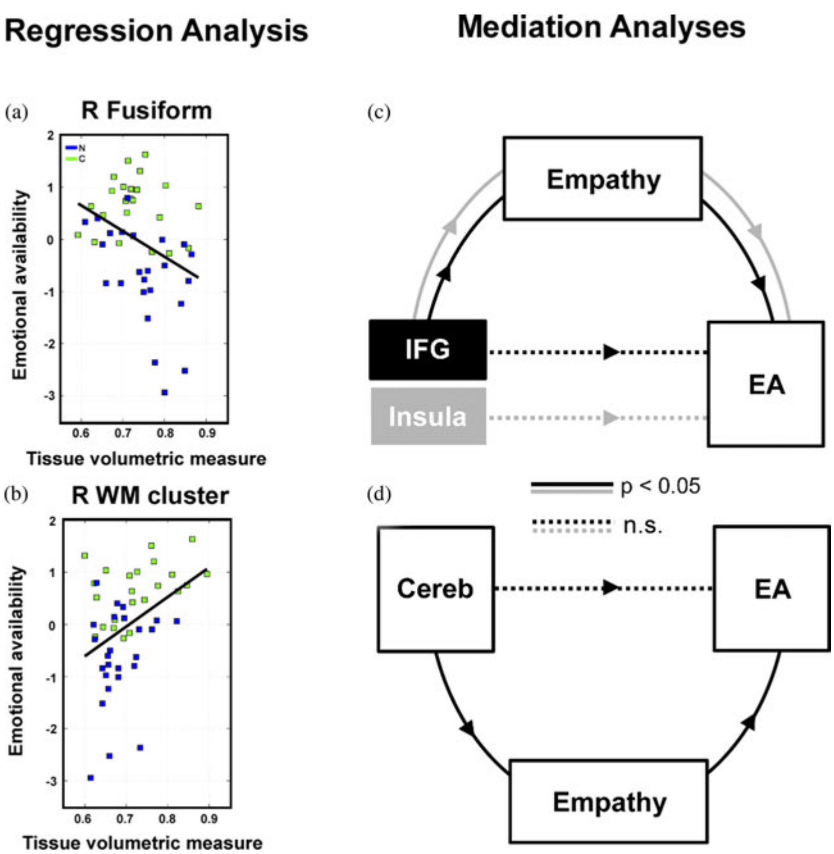

Figure 4. Regression and mediation models of brain differential areas in neglectful mothers on emotional availability (EA). The regression model shows (a) a negative relationship between greater GM volume in Fusiform_R, and (b) a positive relationship between greater WM_R volume in frontal cluster and EA. Mediation models with trait empathy show (c) that emotional concern significantly mediated the positive relationship between IFG and Insula volumetric measures and EA, with no direct effects; and (d) that emotional concern significantly mediated the negative relationship between cerebellum volumetric measures and EA, with no direct effects.

Limitations

Despite the robust results showing the first evidence of the volume differences associated with NM and the relative control of the effect of psychiatric conditions on the relation of volumetric differences with EA, the composition of the sample did not permit separating out the contribution of the psychiatric conditions to negligent motherhood. Building on the neural differences found in this study, future research with larger samples would allow for an orthogonal design crossing NM and CM with that condition and also with other risk factors (i.e., own childhood maltreatment or epigenetic factors) to determine their respective contributions to the neural alterations associated with maternal neglect. In particular, own childhood maltreatment is a dichotomic variable, and as such, it would not be appropriate to use it as a covariate in the current SPM model, especially when maltreatment status greatly overlaps with the groups. Another limitation is that a cross-sectional design does not allow disentangling whether the differences between NM and CM are related to alterations in brain plasticity when becoming a mother or whether they were already present before getting pregnant as well as whether these alterations have causal relationships with EA.

Conclusion

This study significantly contributes to the neurological characterization of neglectful mothers, also revealing as a negative photographic image the brain areas that are critical for sensitive caregiving. The greater GM volume in emotional empathy areas that are not found in the "neglectful" brain may be crucial for the intuitive parenting capacities that enable more automatic, fast, and emotional responding to the needed child. The mothers' failure of emotional attunement to the others' signal of distress may be imitated by the neglected child, leading to the poor interactive bonding exhibited by our neglectful dyads. In turn, the establishment of positive mother–child interactions also requires the greater WM volume in a highly interconnected frontal region, not found in NM, which seems to exert regulatory control over the processing of viso-emotional information. This is a new proposal that deserves closer examination by means of connectivity analyses. Altogether, neglectful mothering is characterized by GM and WM volumetric alterations, affecting both the automatic and elaborative processes that may be engaged when establishing mutual emotional bonds with the child. Prevention and intervention strategies training mothers to manage their own emotions when faced with their distressed infant and to enhance their emotional empathic responding are necessary to ensure the neural equipment that maximizes infant survival and well-being.

Supplementary Material. The supplementary material for this article can be found at https://doi.org/10.1017/S0954579419001469.

Acknowledgments. This work was supported by the Spanish Ministry of Economy and Competitiveness and the European Regional Development Fund under Grant PSI2015-69971-R to M. J. R. & I. L. We thank Dr. Alejandro Pérez for his comments on the manuscript. We also thank the Health and Social Services staff and all of the mothers and their infants who participated in this study.

References

Abraham, E., Hendler, T., Shapira-Lichter, I., Kanat-Maymon, Y., Zagoory-Sharon, O., & Feldman, R. (2014). Father's brain is sensitive to childcare experiences. *Proceedings of the National Academy of Sciences*, *111*, 9792–9797.

Adamaszek, M., D'Agata, F., Ferrucci, R., Habas, C., Keulen, S., Kirkby, K., … Verhoeven, J. (2017). Consensus paper: Cerebellum and emotion. *The Cerebellum*, *16*, 552–576.

Altenhofen, S., Clyman, R., Little, C., Baker, M., & Biringen, Z. (2013). Attachment security in three-year-olds who entered substitute care in infancy. *Infant Mental Health Journal*, *34*, 435–445. doi:10.1002/imhj.21401

Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *Neuroimage*, *38*, 95–113. doi:10.1016/j.neuroimage.2007.07.007

Ashburner, J., & Friston, K. J. (2000). Voxel-based morphometry—the methods. *Neuroimage*, *11*, 805–821. doi:10.1006/nimg.2000.0582

Banissy, M. J., Kanai, R., Walsh, V., & Rees, G. (2012). Inter-individual differences in empathy are reflected in human brain structure. *Neuroimage*, *62*, 2034–2039. doi:10.1016/j.neuroimage.2012.05.081

Barba-Müller, E., Craddock, S., Carmona, S., & Hoekzema, E. (2019). Brain plasticity in pregnancy and the postpartum period: Links to maternal caregiving and mental health. *Archives of Women's Mental Health*, *22*, 289–299. doi:10.1007/s00737-018-0889-z

Barnett, D., Manly, J. T., & Cicchetti, D. (1993). Defining child maltreatment: The interface between policy and research. *Child Abuse, Child Development, and Social Policy*, *8*, 7–73.

Belsley, D. A. (1991). A guide to using the collinearity diagnostics. *Computer Science in Economics and Management*, *4*, 33–50. doi:10.1007/BF00426854

Biringen, Z. (2000). Emotional availability: Conceptualization and research findings. *American Journal of Orthopsychiatry*, *70*(1), 104–114. doi:10.1037/h0087711

Biringen, Z., Derscheid, D., Vliegen, N., Closson, L., & Easterbrooks, M. A. (2014). Emotional availability (EA): Theoretical background, empirical research using the EA Scales, and clinical applications. *Developmental Review*, *34*, 114–167. doi:10.1016/j.dr.2014.01.002

Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS Catalog of Selected Documents in Psychology*, *10*, 85.

Easterbrooks, M. A., & Biringen, Z. (2005). The Emotional Availability Scales: Methodological refinements of the construct and clinical implications related to gender and at-risk interactions. *Infant Mental Health Journal: Official Publication of The World Association for Infant Mental Health*, *26*, 291–294.

Eres, R., Decety, J., Louis, W. R., & Molenberghs, P. (2015). Individual differences in local gray matter density are associated with differences in affective and cognitive empathy. *NeuroImage*, *117*, 305–310. doi:10.1016/j.neuroimage.2015.05.038

Fan, Y., Duncan, N. W., de Greck, M., & Northoff, G. (2011). Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. *Neuroscience & Biobehavioral Reviews*, *35*(3), 903–911. doi:10.1016/j.neubiorev.2010.10.009

Ferrando, L., Bobes, J., Gibert, J., Soto, M., & Soto, O. (2000). *MINI Entrevista Neuropsiquiátrica Internacional (MINI International Neuropsychiatric Interview, MINI). Instrumentos de Detección y Orientación Diagnóstica. Spanish Version 5.0. DSM-IV*. Madrid: Instituto IAP.

Gingnell, M., Bannbers, E., Moes, H., Engman, J., Sylvén, S., Skalkidou, A., … Sundström-Poromaa, I. (2015). Emotion reactivity is increased 4–6 weeks postpartum in healthy women: A longitudinal fMRI study. *PloS One*, *10*, e0128964. doi:10.1371/journal.pone.0128964

Gläscher, J., & Gitelman, D. (2008). Contrast weights in flexible factorial design with multiple groups of subjects. SPM@JISCMAIL.AC.UK *Sml, Editor*.

Hoekzema, E., Barba-Müller, E., Pozzobon, C., Picado, M., Lucco, F., García-García, D., … Vilarroya, O. (2017). Pregnancy leads to long-lasting changes in human brain structure. *Nature Neuroscience*, *20*, 287–296.

Jiang, H., Van Zijl, P. C., Kim, J., Pearlson, G. D., & Mori, S. (2006). DtiStudio: Resource program for diffusion tensor computation and fiber bundle tracking. *Computer Methods and Programs in Biomedicine*, *81*, 106–116. doi:10.1016/j.cmpb.2005.08.004

Kim, P., Leckman, J. F., Mayes, L. C., Newman, M.-A., Feldman, R., & Swain, J. E. (2010). Perceived quality of maternal care in childhood and structure and function of mothers' brain. *Developmental Science*, *13*, 662–673. doi:10.1111/j.1467-7687.2009.00923.x

Kim, P., Strathearn, L., & Swain, J. E. (2016). The maternal brain and its plasticity in humans. *Hormones and Behavior*, *77*, 113–123. doi:10.1016/j.yhbeh.2015.08.001

León, I., Rodrigo, M. J., El-Deredy, W., Modroño, C., Hernández-Cabrera, J. A., & Quiñones, I. (2019). Limbic-visual attenuation to crying faces underlies neglectful mothering. *Scientific Reports*, *9*, Article 6373.Retrieved from doi:10.1038/s41598-019-42908-1

León, I., Rodrigo, M. J., Quiñones, I., Hernández, J. A., Lage, A., Padrón, I., & Bobes, M. A. (2014). Electrophysiological responses to affective stimuli in neglectful mothers. *PloS One*, *9*, e87808. Retrieved from doi:10.1371/journal.pone.0087808

Lin, H.C., & McFatter, R. (2012). Empathy and distress: Two distinct but related emotions in response to infant crying. *Infant Behavior and Development*, *35*, 887–897. doi:10.1016/j.infbeh.2012.08.001

Mielke, E. L., Neukel, C., Bertsch, K., Reck, C., Möhler, E., & Herpertz, S. C. (2016). Maternal sensitivity and the empathic brain: Influences of early life maltreatment. *Journal of Psychiatric Research*, *77*, 59–66. doi:10.1016/j.jpsychires.2016.02.013

Mutschler, I., Reinbold, C., Wankerl, J., Seifritz, E., & Ball, T. (2013). Structural basis of empathy and the domain general region in the anterior insular cortex. *Frontiers in Human Neuroscience*, *7*, 177. doi:10.3389/fnhum.2013.00177

Nichols, T., & Hayasaka, S. (2003). Controlling the familywise error rate in functional neuroimaging: A comparative review. *Statistical Methods in Medical Research*, *12*, 419–446. doi:10.1191/0962280203sm341ra

Nishitani, S., Doi, H., Koyama, A., & Shinohara, K. (2011). Differential prefrontal response to infant facial emotions in mothers compared with non-mothers. *Neuroscience Research*, *70*, 183–188. doi:10.1016/j.neures.2011.02.007

Oishi, K., Faria, A. V., Van Zijl, P. C., & Mori, S. (2010). *MRI atlas of human white matter*. Academic Press.

Papoušek, H., & Papoušek, M. (1987). Intuitive parenting: A dialectic counterpart to the infant's integrative competence. In J. D. Osofsky (Ed.), *Wiley series on personality processes. Handbook of infant development* (pp. 669–720). Oxford, England: John Wiley & Sons.

Parkinson, C., & Wheatley, T. (2012). Relating anatomical and social connectivity: White matter microstructure predicts emotional empathy. *Cerebral Cortex*, *24*, 614–625. doi:10.1093/cercor/bhs347

Pérez-Albéniz, A., De Paúl, J., Etxeberría, J., Montes, M. P., & Torres, E. (2003). Adaptación de interpersonal reactivity index (IRI) al español. *Psicothema*, *15*, 267–272.

Petersen, A., Joseph, J., & Feit, M. (2014). New directions in child abuse and neglect research. *Report of the Committee on Child Maltreatment Research, Policy, and Practice for the Next Decade: Phase II*. Washington, DC: National Academies Press.

Rajapakse, J. C., Giedd, J. N., & Rapoport, J. L. (1997). Statistical approach to segmentation of single-channel cerebral MR images. *IEEE Transactions on Medical Imaging*, *16*, 176–186. doi:10.1109/42.563663

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. Retrieved from https://www.R-project.org/

Rocchetti, M., Radua, J., Paloyelis, Y., Xenaki, L.-A., Frascarelli, M., Caverzasi, E., … Fusar-Poli, P. (2014). Neurofunctional maps of the 'maternal brain'and the effects of oxytocin: A multimodal voxel-based meta-analysis. *Psychiatry and Clinical Neurosciences*, *68*, 733–751. doi:10.1111/pcn.12185

Rodrigo, M. J., León, I., Góngora, D., Hernández, J. A., Byrne, S., & Bobes, A. (2016). Inferior fronto-temporo-occipital connectivity: A missing link between maltreated girls and neglectful mothers. *Social Cognitive and Affective Neuroscience*, *11*, 1658–1665. doi:10.1093/scan/nsw080

Rodrigo, M. J., León, I., Quiñones, I., Lage, A., Byrne, S., & Bobes, M. A. (2011). Brain and personality bases of insensitivity to infant cues in neglectful mothers: An event-related potential study. *Development and Psychopathology*, *23*, 163–176. doi:10.1017/S0954579410000714

Rutherford, H. J., Wallace, N. S., Laurent, H. K., & Mayes, L. C. (2015). Emotion regulation in parenthood. *Developmental Review*, *36*, 1–14. doi:10.1016/j.dr.2014.12.008

Shamay-Tsoory, S. G., Aharon-Peretz, J., & Perry, D. (2009). Two systems for empathy: A double dissociation between emotional and cognitive empathy in inferior frontal gyrus versus ventromedial prefrontal lesions. *Brain*, *132*, 617–627. doi:10.1093/brain/awn279

Silver, M., Moore, C. M., Villamarin, V., Jaitly, N., Hall, J. E., Rothschild, A. J., & Deligiannidis, K. M. (2018). White matter integrity in medication-free women with peripartum depression: A tract-based spatial statistics study. *Neuropsychopharmacology*, *43*, 1573–1580. doi:10.1038/s41386-018-0023-y

Stern, J. A., Borelli, J. L., & Smiley, P. A. (2015). Assessing parental empathy: A role for empathy in child attachment. *Attachment & Human Development*, *17*, 1–22. doi:10.1080/14616734.2014.969749

Stoltenborgh, M., Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2013). The neglect of child neglect: A meta-analytic review of the prevalence of neglect. *Social Psychiatry and Psychiatric Epidemiology*, *48*(3), 345–355. doi:10.1007/s00127-012-0549-y

Teicher, M. H., Samson, J. A., Anderson, C. M., & Ohashi, K. (2016). The effects of childhood maltreatment on brain structure, function and connectivity. *Nature Reviews Neuroscience*, *17*, 652–666. doi:10.1038/nrn.2016.111

Tingley, D., Yamamoto, T., Hirose, K., Keele, L., & Imai, K. (2014). Mediation: R package for causal mediation analysis. *Journal of Statistical Software*, *59*. doi:10.18637/jss.v059.i05

Tohka, J., Zijdenbos, A., & Evans, A. (2004). Fast and robust parameter estimation for statistical partial volume models in brain MRI. *Neuroimage*, *23*, 84–97. doi:10.1016/j.neuroimage.2004.05.007

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., … Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage*, *15*, 273–289. doi:10.1006/nimg.2001.0978

Upshaw, M. B., Kaiser, C. R., & Sommerville, J. A. (2015). Parents' empathic perspective taking and altruistic behavior predicts infants' arousal to others' emotions. *Frontiers in Psychology*, *6*, Article 360. doi:10.3389/fpsyg.2015.00360

Weiner, K. S., & Zilles, K. (2016). The anatomical and functional specialization of the fusiform gyrus. *Neuropsychologia*, *83*, 48–62. doi:10.1016/j.neuropsychologia.2015.06.033

Weinfield, N. S., Sroufe, L. A., Egeland, B., & Carlson, E. (2008). Individual differences in infant-caregiver attachment: Conceptual and empirical aspects of security. In J. Cassidy, & P. R. Shaver (Eds.), *Handbook of attachment: Theory, research, and clinical applications* (2nd ed., pp. 78–101). New York: Guilford Press.

Yeh, F.-C., & Tseng, W.-Y. I. (2011). NTU-90: A high angular resolution brain atlas constructed by q-space diffeomorphic reconstruction. *Neuroimage*, *58*, 91–99. doi:10.1016/j.neuroimage.2011.06.021