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Socioeconomic disadvantages and neural sensitivity to infant cry: role of maternal distress

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Abstract

Socioeconomic disadvantage such as poverty can increase distress levels, which may further make low-income mothers more vulnerable to difficulties in the transition to parenthood. However, little is known about the neurobiological processes by which poverty and maternal distress are associated with risks for adaptations to motherhood. Thus, the current study examined the associations between income and neural responses to infant cry sounds among first-time new mothers (N = 28) during the early postpartum period. Lower income was associated with reduced responses to infant cry in the medial prefrontal gyrus (involved in evaluating emotional values of stimuli), middle prefrontal gyrus (involved in affective regulation) and superior temporal gyrus (involved in sensory information processing). When examining the role of maternal distress, we found a mediating role of perceived stress, but not depressive symptoms, in the links between income and prefrontal responses to infant cry. Reduced neural responses to infant cry in the right middle frontal gyrus and superior temporal gyrus were further associated with less positive perceptions of parenting. The results demonstrate that perceived stress associated with socioeconomic disadvantages may contribute to reduced neural responses to infant cry, which is further associated with less positive perceptions of motherhood.

Key words: neuroimaging; socioeconomic status; perceived stress; maternal brain; infant cry

Introduction

The early postpartum period is an exciting yet stressful time of life. New mothers, particularly first-time mothers, tend to report feeling overwhelmed, unprepared, drained and isolated (Barclay et al., 1997; Mistry et al., 2007). A wealth of literature provides understanding of psychological and neurobiological changes during the first few months postpartum that support new mothers in coping with parenting-associated stress (Fleming et al., 1990; Lonstein et al., 2014). On the other hand, exposure to chronic and severe stressors that are associated with socioeconomic disadvantages interfere with normative psychological and neurobiological changes that support motherhood during the early postpartum period (Kim and Bianco, 2014). Indeed, higher levels of maternal distress in new mothers living in poverty compared to their counterparts is one of the major reasons for more negative transitions to motherhood (Goyal et al., 2010), which may further be associated with suboptimal infant development (Blair et al., 2011; Brooks-Gunn et al., 1995). However, little is known about the neural processes by which socioeconomic disadvantages are related to difficulties in the transition to parenthood for new mothers.

During the early postpartum period, new mothers exhibit enhanced neural sensitivity to infant cues, including infant crying sounds. Neuroimaging studies with mothers provide evidence for increased activity in response to infant cues in neural regions including the midbrain; medial, middle and lateral prefrontal cortex (PFC); and sensorimotor and auditory cortex (Barrett and Fleming, 2011; Swain *et al.*, 2014; Feldman, 2015; Kim *et al.*, 2016; Lonstein *et al.*, 2015). Increased activations in the sensorimotor and auditory cortices in response to infant cry sounds suggest heightened neural processing of sensory information (Sander *et al.*, 2007; Swain, 2010). When mothers hear infant cry, inputs from the sensorimotor and auditory cortices activate the midbrain and striatum, neural regions that are part of the dopaminergic mesolimbic circuit, and critically involved in caregiving motivation (Ferris *et al.*, 2005; Strathearn *et al.*, Downloaded from http://scan.oxfordjournals.org/ at University of Denver on June 28, 2016

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2008). In animals, lesions in the midbrain and striatum significantly impair maternal caregiving motivation and behaviors during the early postpartum period (Numan and Insel, 2003). Furthermore, inputs from the midbrain and striatum are processed in the medial cortex and ventral ACC, regions that are involved in evaluation of affective and reward values of stimuli (Etkin et al., 2011). The middle and lateral PFC are involved in attention and emotion regulation, and decision-making (Wager et al., 2008; Ochsner et al., 2012). Activations of these regions in response to infant cry sounds suggest their role in regulation of mothers' own distress in the context of infant cry sounds, as well as making appropriate and sensitive responses to the infant (Barrett and Fleming, 2011;Rutherford et al., 2015; Kim et al., 2016). Increased responses to infant cues in these neural regions have been positively associated with maternal sensitivity observed during interactions with infants (Atzil et al., 2011; Kim et al., 2011; Musser et al., 2012). Thus, enhanced neural sensitivity to infant cry in brain regions involved in maternal motivation, affective valuations and regulation, and sensory information processing may play an important role for new mothers' normative adjustment to motherhood and development of positive relationships with their infants.

On the other hand, mothers with socioeconomic disadvantages are more likely to exhibit difficulties in adjusting to motherhood. As demonstrated by Conger and Elder's (1994) Family Stress Model, living in a low-income environment can lead to higher levels of psychological distress among mothers, which in turn increases risks for negative mother-child relationships (Newland et al., 2013). In studies with rodents and primates, conditions that induce high levels of stress such as unstable living arrangements are shown to cause more anxious behaviors and reduced maternal motivation to care for offspring among new mothers (Herzog et al., 2009). During the postpartum period, socioeconomic disadvantages have been associated with high levels of depressive symptoms, suggesting greater psychological distress among lower-income new mothers (Séguin et al., 1999; Goyal et al., 2010). Socioeconomic disadvantages have also been associated with perceived stress levels, an individual's perception of life as being unpredictable, uncontrollable and overloading (Cohen, 1986; Adler et al., 1993; Cohen et al., 1999). These aspects are found to predict negative health outcomes and poor well-being, independent of depressive symptoms (Cohen, 1986). Causal relations between socioeconomic disadvantages such as poverty and distress levels, including perceived stress and depressive symptoms, have been identified in intervention studies (Haushofer and Fehr, 2014). Higher levels of maternal perceived stress and depressive symptoms have been identified as risk factors for difficult adaptation to motherhood (Reece and Harkless, 1998; Delmore-Ko et al., 2000; Goodman, 2007; Razurel et al., 2013).

We propose that the higher levels of distress associated with socioeconomic disadvantages may influence mother's adaptation to motherhood through altered neural regulation of negative emotion and parental motivation. Exposure to povertyrelated stress has been associated with reduced connectivity between the striatum and medial PFC regions for affective and reward processing (Gianaros *et al.*, 2011) and ineffective suppression of amygdala activity by the lateral PFC during emotion regulation among adults (Kim *et al.*, 2013a). Long-term exposure to childhood poverty was also associated with reduced activation in the striatum among non-parent young adult females in response to infant cry sounds (Kim *et al.*, 2015a). Thus, it is plausible that exposure to socioeconomic disadvantages may lead to high levels of maternal distress, which may disrupt normative neurobiological adaptations for emotion regulation and maternal motivation during the early postpartum period. However, the underlying neurobiological mechanisms that explain how socioeconomic disadvantages and maternal distress may result in difficulties in transitioning to parenthood remain largely unexplored.

The current study with new first-time mothers examined whether socioeconomic disadvantages (indexed by low incometo-needs ratio) may be associated with neural responses to infant cues, specifically cry sounds. We hypothesized that lowincome mothers would exhibit reduced neural responses to their own infant cry sounds in brain regions related to maternal motivation (midbrain and striatum), affective valuations (medial PFC) and affective regulation (middle and lateral PFC). We further examined whether maternal distress at a normal range, assessed by perceived stress and depressive symptoms, would mediate the links between poverty and neural responses to infant cry. We hypothesized that low income would be linked to higher levels of perceived stress and depressive symptoms, which would in turn explain the reduced neural responses to infant cry. Finally, we tested the associations between neural responses to infant cry and subjective perceptions of parenting and own infant (Kim et al., 2013a) among the new first-time mothers. We hypothesized that reduced neural sensitivity to infant cry among low-income mothers would be associated with less positive perceptions of parenting and own infant, indicating subjective difficulties in transitioning to motherhood.

Materials and methods

Participants

Forty women with their first biological infants at age 0-6 months were recruited. Through dissemination of fliers and brochures in metro Denver areas, mothers were recruited from the community, in particular from the WIC (Women, Infant, and Children) and Colorado state Prenatal Plus programs. Eligible mothers were English-speaking and free from the following: pregnancy-related or infant medical illnesses involving more than a one-night stay in the neonatal intensive-care unit (NICU), current or historical psychiatric/neurological illness other than depression or anxiety diagnoses (to keep a controlled but ecologically valid community sampling approach), psychoactive drug use and magnetic metal in the body. Lower income women were oversampled to be nearly half of the sample (see 'Family Income of the Measures' section for more details). Of the 40 participants, 12 mothers were excluded from analyses because they did not have complete fMRI data (5 completed only home visits, 2 mothers were claustrophobic and 5 had technical problems during the scan). Thus, a total of 28 mothers were included in the analyses presented here. Their demographic characteristics are described in Table 1. There were no differences in the demographic characteristics between mothers who participated only in the home visits and those included in the current analysis.

Procedures

Mothers were initially contacted by phone to assess their eligibility for the study. If eligible, a home visit was scheduled. During the home visit, mothers reviewed and signed an IRBapproved consent form with a trained researcher, then completed questionnaires and interviews on income, mood and parenting. Trained research assistants also recorded naturally

Table 1. Characteristics of the participants

	N (%)	$\text{Mean} \pm \text{SD}$	Range
Maternal age (years)		25.07 ± 5.64	18–36
Maternal race/ethnicity			
Caucasian	12 (43)		
Hispanic	11 (39)		
African-American	3 (11)		
Others	2 (7)		
postpartum month at the time of fMRI scans		3.68 ± 1.75	0.89–6.96
Infant sex (female)	19 (68%)		
Income-to-needs ratio	, , ,	2.66 ± 1.54	0.44-6.34
Depressive mood		6.82 ± 4.82	0–17
Perceived stress		5.11 ± 2.91	0–11
Mood disorder history (Yes)	6 (21)		
Interval between home and fMRI visits (months)		0.84 ± 0.70	0.07-3.42
Breastfeeding (and/or daily pump; but not exclusive formula-feeding)	26 (93)		
Right handedness	24 (86)		

occurring infant cry sounds using a portable digital audio recorder. In a subsequent visit for the fMRI portion of the study, mothers visited the Intermountain Neuroimaging Center at the University of Colorado – Boulder. The average interval between home and fMRI visits was around 3 weeks (Table 1). All participants reviewed and signed an IRB-approved consent form with a trained researcher. Participants received monetary compensation for taking part in the study, and child care and transportation support were provided to participants when needed.

Measures

- 1. Family income. Family income was assessed based on an income-to-needs ratio, calculated by dividing total family income by the poverty threshold specified by the U.S. Census Bureau. The range of annual income was \$11 200-\$157 126 and the poverty threshold of a family with two adults and one child was \$16 317 in 2014. The range of the income-to-needs ratio was 0.44–6.34 (Table 1), and 43% of the sample lived in poverty (income-to-needs ratio ≤ 1) or near poverty (income-to-needs ratio ≤ 2).
- 2. Maternal distress
- 3. Perceived stress. Participants completed the perceived stress scale (Cohen et al., 1983; Cohen and Williamson, 1988). The self-report 4-item questionnaire measured the levels of stress experienced in the last month. The 4-item scale yields adequate reliability and validity (Cohen et al., 1983; Cohen and Williamson, 1988) and is a widely used measure of perceived stress across diverse demographic backgrounds including the perinatal population (Lobel et al., 2008; Kramer et al., 2009). The items (e.g. In the past month, how often have you felt it was difficult to control the important things in your life?) were rated using a 5-point scale (0 = never, 4 = very often). Thus, the range of the total score was 0–12. In a sample of over 2000 adults in the US, using the 4-item version, the mean was 4.49 and standard deviation was 2.96 (Cohen and Williamson, 1988). In the current study, the mean and standard deviation is presented in Table 1. The range was 0-11 while 57% of the sample reported a total score above 5, and 25% of the sample reported a total score above 8 (greater than the mean plus one standard deviation from the population study).
- Depressive mood. Participants completed the Beck Depression Inventory (BDI) (Beck et al., 1988). The BDI consists of 21

items, with each item answered on a scale of 0 (symptom is absent) to 3 (symptom is severe). The questionnaire has also been widely used across diverse demographic backgrounds including the perinatal population (O'Hara *et al.*, 1984; Gotlib *et al.*, 1989; O'hara and Swain, 1996).

5. Subjective perceptions of parenting and own infant. During the home visit, two subscales of the Yale Inventory of Parental Thoughts and Actions - Revised (YIPTA-R) interview (Leckman et al., 1999; Kim et al., 2013b), Positive Thoughts on (i) Own infant and (ii) Parenting, were conducted with mothers by trained researchers. The semi-structured interview has been used previously to assess cognitive and emotional adjustment to parenthood in new mothers (Feldman et al., 1999; Leckman et al., 1999; Kim et al., 2013b). Mothers were asked to select from a list of adjectives the words that best described their perception of their own infant or experience as a mother. For the positive thoughts on own infant, the list included 13 positive words including 'Beautiful', 'Ideal', 'Perfect' and 'Special'. For the positive thoughts on parenting, this list included 32 positive words including 'Blessed', 'Content', and 'Proud'. The sum of the positive words mothers chose was included as a variable in this study. Thus, positive thoughts on own infant and positive thoughts on parenting scores ranged between 0–13 and 0–32, respectively.

fMRI paradigm

The infant cry fMRI paradigm (Swain et al., 2008) has been previously shown to enhance activity of the neural correlates of parenting among new mothers during the postpartum period in many studies, including our own (Kim et al., 2010b, 2011, 2015b). Own infant cry samples were recorded as they naturally occurred during the home visit. The cries largely related to being hungry (50%), seeking attention (29%) and a normal range of discomfort (e.g. diaper change or being placed on a weighing scale; 11%). A control baby cry sample from a mother who did not participate in the current study was recorded using a consistent sampling method (i.e. during diaper change but not while the baby was in pain). The control infant cry sample was the same for all participants. Any non-cry noise and background sounds for both own and control infant cry sounds were removed from the recording using sound editing software (Cool Edit Pro Version 2.0, Syntrillium Software, Phoenix, AZ). The own infant cry and control infant cry sounds were matched for volume. White noises were synthesized by generating a spectral average of the cry, which was then matched to the gross temporal envelope of the own infant and control infant cry sounds.

In the MRI scanner, mothers listened to auditory stimuli through headphones. The task was organized into two functional runs, in which blocks of cry stimuli and control sounds lasted 20 s. Each stimulus block was separated by an average 10second rest period (ranging from 8 to 12 s) at which time only background scanner noise could be heard. Each run contained blocks of four sound stimuli—(A) own infant cry, (B) control infant cry, (D) own infant cry matched noise and (D) control infant cry matched noise. The order of the blocks was randomized and each block was repeated five times, thus a total of 10 times per condition. Mothers were asked to pay attention to each sound and experience feelings and thoughts as they naturally occurred.

fMRI data acquisition and processing

Scanning took place in a 3.0 T Siemens magnet scanner using a standard 32-channel head coil. Functional data were acquired (540 T2*-weighted echo-planar-imaging (EPI) volumes; TR = 2300 ms; TE = 27 ms; flip angle = 73; field of view = 192 mm; matrix size, 64×64 ; 36 axial slices; voxels = 3 mm³). High-resolution anatomical T1-weighted images using the 3D magnetization-prepared rapid gradient-echo (MPRAGE) protocol were also acquired.

Analysis of Functional Neuroimages software (AFNI) (Cox, 1996) was used for preprocessing and statistical analysis. The first two images of each run were discarded to account for magnetic equilibrium. After slice time correction, images within each run were realigned to the third image to correct for movement. Images with motion greater than 0.5 mm in any direction were censored. The range of number of volumes censored was 0–90 ($M = 15.36 \pm 22.64$; below 17% of the total volumes). Thus, at least 143 volumes for each condition were included in the analysis. After motion correction, realigned functional images were co-registered to anatomical images and functional images were spatially smoothed with a 6-mm root-mean-square deviation Gaussian blur.

At the individual participant level, general linear models were used to estimate the shape of the hemodynamic response to each stimulus (own infant cry, control infant cry, own infant cry matched noise and control infant cry matched noise). All regressors—four conditions and six motion parameters—were convolved with a gamma-variate hemodynamic response function. The beta images, which represented estimated activation in each condition for each participant, were then used in group level analyses.

Analysis

Analysis of Functional Neuroimages softwares (AFNI's) 3dLME was utilized to create a whole-brain linear mixed effects model with income-to-needs ratio as a between-subjects quantitative variable, and sound (cry vs noise) and condition (own vs control) as within-subjects factors. Although neither variables were correlated with income-to-needs ratio, postpartum month at the time of the fMRI scan and mothers' history of mood disorder status (depression and/or anxiety) were included as covariates to rule out their potential effects on neural structure for parenting (Kim et al., 2010a) and neural structure for emotion

regulation (Drevets *et al.*, 2008), respectively. To identify brain regions that were associated with income-to-needs ratio, we examined interaction effects and main effects with income. To explore the effects of sound type (cry *vs* noise), condition (own *vs* control) and postpartum month, we also examined the interactions and main effects among the variables (Supplementary material). The cluster extent threshold was set to $k \ge 23$ with a height threshold of P < 0.005, equivalent to a whole brain corrected false positive probability of P < 0.05, as calculated by 3dClustSim. To characterize significant interactions, post-hoc analyses were performed in SPSS statistical software using values extracted and averaged from the clusters.

Mediation analyses of maternal distress (perceived stress and depressive mood) were performed using PROCESS (Hayes, 2013). The indirect effect of income-to-needs ratio on neural activation through maternal distress was tested using 95% biascorrected Confidence Intervals with bootstrapping procedures (10 000 bootstrap resamples) (Preacher and Hayes, 2008). The 95% bias-corrected Confidence Intervals without the inclusion of 0 indicates a statistically significant indirect relationship, P < 0.05 (Preacher and Hayes, 2008).

Results

Characteristics of the sample

Table 1 includes descriptive statistics for the participants. No demographic variables (i.e. maternal age, race/ethnicity, hand-edness, mood disorder status, breastfeeding status, infant's age and intervals between home and fMRI visits) were associated with income-to-needs ratio. The only two variables that were correlated with income were depressive mood, r(28) = -0.46, P < 0.05, and perceived stress levels, r(28) = -0.38, P < 0.05.

fMRI analysis of the associations between income and neural activation

The three-way interaction of income-to-needs ratio X sound (cry vs noise) X condition (own infant vs control infant) did not reveal a significant cluster. The two-way interaction of income X sound revealed four significant clusters (Table 2)-the left medial frontal gyrus (also including the anterior cingulate cortex) (Figure 1a), right superior temporal gyrus and the bilateral middle frontal gyrus (also including the inferior frontal gyrus; Figure 2a), P < 0.05, corrected. Post-hoc analysis revealed that in all four clusters, family income-to-needs ratio was positively associated with neural responses to infant cry sounds across own and control infant cry sounds (Table 1, Ps < 0.05; Figures 1b and 2b). Thus, lower income-to-needs ratio was associated with dampened neural responses to infant cry sounds. In the left medial frontal gyrus, family income was negatively associated with neural responses to noise sounds across own cry-matched and control cry-matched noise. Thus, lower income-to-needs ratio was associated with elevated responses to noise sounds.

Two-way interaction of income-to-needs ratio X condition and the main effect of income were not significant. The sound X condition interaction revealed significant clusters in left medial frontal gyrus and left brainstem (P < 0.05, corrected), indicating greater responses to own infant cry sounds compared to control infant cry and own cry-matched noise sounds in both regions (Supplementary material, Table S1). The sound X postpartum month interactions indicated negative associations between postpartum month and neural responses to cry sounds in



Fig. 1. (a) The left medial frontal gyrus (BA9/32; x, y, z = -22, 47, 11, k = 93) in a red circle showing income-to-needs ratio × sound interaction, P < 0.05, corrected; (b) a scatterplot describing the positive associations between income-to-needs ratio and the neural responses to cry sounds (both own and control infant cry sounds) in the left medial frontal gyrus; (c) a path diagram showing a mediation model with the unstandardized coefficients for each association. Perceived stress mediated the relationship between income-to-needs ratio and neural responses to cry sounds in the left medial frontal gyrus; (**P < 0.05, **P < 0.01, *P < 0.05.

bilateral middle temporal gyri and right insula (Supplementary material, Table S2).

Mediation analysis of maternal distress for linking income and neural activation

We next tested whether distress levels indicated by depressive mood and perceived stress mediated the relations between family income-to-needs ratio and neural responses to cry and noise sounds identified above. Elevated perceived stress levels, but not depressive mood, mediated the associations between family income-to-needs ratio and reduced responses to cry sounds in the left medial frontal gyrus (Figure 1c). The addition of perceived stress shrank the beta weight for income-to-needs ratio 33% (Indirect effect = 0.01, 95%CIs = 0.002-0.03). Elevated perceived stress levels, but not depressive mood, also mediated the associations between family income-to-needs ratio and reduced responses to cry sounds in the left middle frontal gyrus and right middle frontal gyrus. The addition of perceived stress shrank the beta weight for income 25% (Indirect effect = 0.01, 95%CIs = 0.002–0.03) in the right middle frontal gyrus (Figure 2c) and 8% (Indirect effect = 0.02, 95%CIs = 0.006–0.06) in the left middle frontal gyrus. No mediation was detected in the right superior temporal gyrus responses to cry sounds and the left medial frontal gyrus responses to noise sounds. When perceived stress was included in the mediation model alone, the findings of its mediating role remained consistent. When depressive symptoms were included in the mediation model alone, no mediation role was identified.

Associations between neural responses and psychological adjustment to parenthood

We then examined whether the neural responses to cry sounds may be associated with subjective perception of parenting and mothers' own infant. Among the suprathreshold clusters identified to be associated with income-to-needs ratio, the right superior temporal gyrus, r(28) = 0.42, P < 0.05, and the right middle frontal gyrus, r(28) = 0.40, P < 0.05 (Figure 3) responses to cry sounds were associated with greater positive perceptions of being a parent across the new mothers. No clusters were associated with positive perceptions of mother's own infant.

Discussion

The first few months postpartum constitute a critical adjustment period to parenthood for first-time mothers. However, little is known about the role of socioeconomic disadvantages and associated stress in the neurobiological adjustment to motherhood. The current study examined whether socioeconomic disadvantages were associated with neural sensitivity to infant cry among first-time new mothers during the first 6 months



Fig. 2. (a) The right middle frontal gyrus (BA10/46; x, y, z = 32, 41, 8, k = 33) in a red circle showing income-to-needs ratio × sound interaction, P < 0.05, corrected; (b) a scatterplot describing the positive associations between income-to-needs ratio and the neural responses to cry sounds (both own and control infant cry sounds) in the right middle frontal gyrus; (c) a path diagram showing a mediation model with the unstandardized coefficients for each association. Perceived stress mediated the relationship between income-to-needs ratio and neural responses to cry sounds in the right middle frontal gyrus; *P < 0.01, *P < 0.05.

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Regions	BA	Side	х	у	z	Cluster size	F (1,24)	Association with income
Medial frontal gyrus	9/32	L	-22	47	11	93	17.51	Cry: r(28) = 0.51**; Sound: r(28) = -0.49**
Superior temporal gyrus	41	R	41	-37	5	35	19.53	Cry: r(28) = 0.48*; Sound: n.s.
Middle frontal gyrus	10/46	R	32	41	8	33	14.43	Cry: r(28) = 0.50**; Sound: n.s.
Middle frontal gyrus	46/10	L	-37	35	17	27	12.21	Cry: r(28) = 0.46*; Sound: n.s.

P < 0.05, corrected; for post-hoc analysis.

**P<0.01.

*P < 0.05.

 $n.s.\,{=}\,not\,significant.$

postpartum. We found that lower income-to-needs ratio was related to dampened neural responses to infant cry sounds in the medial frontal gyrus, middle frontal gyrus and superior temporal gyrus. Next, we conducted mediation analyses and found that perceived stress levels mediated the link between incometo-needs ratio and prefrontal region responses to infant cry. The results suggest that first-time mothers with socioeconomic disadvantages are more likely to experience higher levels of stress, which may be further associated with impaired neural adaptation to parenthood, indicated by dampened responses to infant cry. Reduced neural responses to cry sounds in the right middle frontal gyrus and the superior temporal gyrus were further associated with less positive perceptions of parenting reported by new first-time mothers. These findings provide important information for more targeted intervention efforts to reduce perceived stress levels and improve coping abilities among new first-time mothers with socioeconomic disadvantages.

While the prefrontal regions we identified, specifically the medial frontal gyrus and middle frontal gyrus, are involved in a wide range of tasks, their critical role for affective valuations of infant cues and emotion regulation has been discussed extensively (Barrett and Fleming, 2011; Moses-Kolko *et al.*, 2014; Lonstein *et al.*, 2015; Rutherford *et al.*, 2015). Heightened activation in response to infant cues including cry sounds, as well as



Fig. 3. The right middle frontal gyrus (BA10/46; x, y, z = 32, 41, 8, k = 33) in a red circle and a scatterplot describing the positive associations between the right middle frontal gyrus activation and positive perception of parenting, r(28) = 0.40, P < 0.05.

anatomical growth in these prefrontal regions have been consistently observed in both animal and human new mothers (Afonso et al., 2007; Febo et al., 2010; Kim et al., 2010a). Thus, changes in these regions are considered to be important neural adaptations to motherhood that enhance a mother's ability to evaluate emotional and social information from infant cues as well as to regulate her own emotions. Indeed, maternal sensitivity observed during mother-infant interactions has been positively associated with activations in prefrontal cortex regions in response to infant cues (Atzil et al., 2011; Kim et al., 2011; Musser et al., 2012; Hipwell et al., 2015), while difficulties in emotion regulation, such as instances of maternal depression, have been associated with reduced activation in prefrontal cortex regions (Laurent and Ablow, 2012). Moreover, the finding that lower-income mothers exhibited dampened responses to infant cry but heightened responses to white noise sounds in the medial frontal gyrus further suggest disruption in the typical neural adaptation of increased sensitivity to infant cry among mothers with socioeconomic disadvantages during the early postpartum period.

We also observed that low income was associated with dampened activation in the superior temporal gyrus, including the auditory cortex, in response to infant cry. This region is involved in processing of emotional prosody, particularly positive prosody in auditory stimuli (Johnstone et al., 2006). Auditory cortex activation has been reliably observed in previous studies using infant cry sounds (Sander et al., 2007; Kim et al., 2010b; Montoya et al., 2012), and greater response in the auditory cortex has been associated with parenting and stress factors such as maternal sensitivity (Musser et al., 2012; Hipwell et al., 2015), breastfeeding (Kim et al., 2011) and childhood parenting quality (Kim et al., 2010b). Heightened neural responses to infant cry have been interpreted as indicators of increased neural sensitivity for processing emotional information embedded in the sounds, as well as indicators of increased parental motivation. Thus, together with findings in the prefrontal cortex, our study extends the current understanding by providing evidence that a new mother's exposure to harsh circumstances, such as low income or poverty, may be associated with dampened neural sensitivity to infant cry sounds, which reflects risks for neural adaptation to motherhood.

As a potential support for such speculation, we found that reduced neural responses to infant cry in the superior temporal gyrus and the middle frontal gyrus across own and control cry sounds were associated with less positive subjective perceptions of parenting, with mothers less likely to endorse statements such as 'fulfilling' and 'rewarding'. These points to associations between neural and behavioral adaptations to parenting. On the other hand, among neural regions showing reduced activation to infant cry among lower income mothers, mother's subjective perception of her own infant (e.g. 'blessed', 'special') was not associated with neural responses to infant cry. In a previous study, positive perceptions of one's infant was associated with anatomical changes in the midbrain regions 2010a). Thus, we speculate that the null (Kim et al., findings with positive perceptions of one's own infant may be associated with the fact that income was associated with neural responses to infant cry in brain regions largely involved in emotion regulation, but not directly linked to maternal motivation.

Importantly, we identified that maternal distress mediated the links between socioeconomic disadvantages and neural responses to infant cry sounds among first-time new mothers. Lower income-to-needs ratio was associated with higher distress levels, including mothers' perceived stress and depressive symptoms. However, when both perceived stress and depressive symptoms were included in the mediation analysis, perceived stress, but not depressive symptoms, mediated the links between income-to-needs ratio and dampened neural responses to infant cry sounds in the prefrontal regions (right medial frontal cortex and bilateral middle frontal cortex). That is, lower income-to-needs ratio was associated with higher levels of perceived stress, which were further associated with reduced neural responses to infant cry sounds.

Poverty has been associated with greater levels of subjective stress, which have been identified as significant risk factors for psychological adjustment and physical health (Cohen *et al.*, 1993; Steptoe *et al.*, 1996). Our findings suggest that the high levels of perceived stress experienced by new mothers, particularly those with socioeconomic disadvantages, may contribute to difficulties in neural adaptations to parenting, indicated by reduced neural responses to infant cry sounds. It is interesting that depressive symptoms were not associated with neural adaptations to parenting in the current study, which calls for further investigation. One possible explanation is that most of the mothers exhibited no (75% of the sample) to mild (25% of the sample) depression with no mothers scoring above the cutoff for moderate depression (\geq 18) (Beck *et al.*, 1988). Thus, although the range of both measures reflects normal levels of daily stress, it is possible that perceived stress is more strongly associated with neural responses to infant cry among mothers with low to mild depressive symptoms.

It was somewhat unexpected that income-to-needs ratio was associated with neural activations across own infant and control cry sounds, rather than specifically own infant cry sounds. The results suggest the potential impact of socioeconomic disadvantages on mothers' neural sensitivity to infant cry sounds in general, particularly in prefrontal regions that are involved in emotion regulation and emotional information processing. Meta-analysis suggests that greater neural sensitivity to one's own infant cues compared to unknown infant cues is particularly pronounced in mid brain regions (including the thalamus, substantia nigra and striatum) (Rocchetti et al., 2014) that are critically involved in maternal motivation (Numan and Woodside, 2010; Numan, 2014). In rats, lesions in midbrain regions directly impair the onset of maternal behaviors (Numan and Stolzenberg, 2009), while lesions in medial prefrontal regions are not directly associated with maternal behaviors but rather with deficits in integrating complex behaviors involved in parenting (Afonso et al., 2007). Thus, we speculate that mothers with socioeconomic disadvantages may have intact neural systems of maternal motivation, but reduced neural regulation and processing of emotion, which may contribute to difficulties in regulating their own emotions in response to infant cry in general.

The findings from the current study should be considered in light of limitations. First, the study employed a cross-sectional design, therefore the temporal direction of associations among income, maternal distress, neural and psychological responses to infant and parenting cannot be determined. Future research is needed to examine the prospective role of socioeconomic disadvantages in maternal distress and neural responses to infant cry sounds. Second, both maternal distress and adjustment to parenthood were based on self-report. While these variables were assessed by widely used and appropriate measures, selfreport data are at risk for bias due to mood and stress, thus future work may include clinical interviews regarding depression. Moreover, although the perceived stress scale has been widely used to measure psychological distress, it does not distinguish between parenting-related and non-parenting related perceived stress among new parents. Future research using observational measures of parenting will also be important to confirm whether subjective perceptions of parenting may be associated with difficulties in adaptation to motherhood. Third, although our findings were not specific to own vs. control cry sounds, the intensity of the own cry and control cry sounds were not rated by third-party participants (participants not related to babies from the study), thus it is not clear whether the intensity levels of own and control cry stimuli were matched. Based on previous literature, control cry sounds and own baby cry sounds of the current study are likely to represent low intensity compared to cries reported during painful procedures (e.g. heel stick, circumcision) that are more high intensity (Stallings et al., 2001). Previous literature suggests that mothers' physiological responses to baby cries differ by intensity. Mothers exhibit higher levels of sympathy, negativity and alertness in response to high intensity pain cries compared to lower intensity hunger cries (Stallings et al., 2001). Teenage mothers show more negative responses to pain cries, but not to hunger cries, compared to adult mothers (Giardino et al., 2008), which may indicate that mothers at risk for harsh parenting exhibit differences in response to particularly high intensity pain cry. Thus, future studies should examine the role of infant cry intensity in maternal neural responses among at-risk mothers. Fourth, it will be important to study the associations with postpartum hormones and neural adaptations to parenting. Mothers undergo drastic changes in levels of several hormones including oxytocin and cortisol during the early postpartum period, and these changes are thought to support adaptations to parenthood (Kendrick, 2000; Gordon et al., 2010a,b). In children and adults, exposure to chronic stress has been associated with increased cortisol (Kim et al., in press) and reduced oxytocin levels (Fries et al., 2005). These hormones are important for stress regulation and positive emotional bonding between mothers and infants during the postpartum period (Bridges, 2015; Lonstein et al., 2015; Monk et al., 2012). Thus, it will be important to examine the role of chronic stress exposure in hormonal regulation during postpartum depression, and its relationship to maternal distress regulation and neural sensitivity to infant cues.

In sum, the current study demonstrated the associations between family income-to-needs ratio and neural adaptation to motherhood among first-time new mothers during the postpartum period. Low-income mothers exhibited dampened responses to infant cry sounds in frontal brain regions involved in affective valuation and regulation, as well as auditory information processing. Mothers from lower income households reported higher levels of perceived stress, which were in turn associated with reduced neural responses to infant cry. Dampened neural responses in the middle frontal gyrus and superior temporal gyrus were further associated with less positive perceptions of parenting. Together these findings suggest that low income-to-needs ratio and related distress can disrupt normative adaptations to motherhood, including neural sensitivity to infant cry sounds and positive perceptions of parenting during the transition to parenthood. These disruptions may have a long-term impact on a mother's ability to build a relationship with her infant, thereby affecting both maternal health and infant development.

Several government- or state-funded intervention programs exist that offer support and assistance specifically to lowincome new mothers and their infants. The neuroimaging evidence supports intervention efforts, such as nurse home visitation programs, that improve mothers' transition to parenthood by focusing on mothers' well-being and stress reduction. This in turn can help two generations - both mothers and their infants (Kim and Watamura, 2015). Our study also suggests that low-income mothers with relatively low to moderate depressive symptoms may benefit from interventions that help them cope with poverty-associated perceived stress levels. Thus, interventions focused on the well-being of mothers with socioeconomic disadvantages with or without high depressive symptoms may ultimately promote optimal development of the next generation, and reduce the intergenerational transmission of socioeconomic disadvantages and harsh environments (Kim and Bianco, 2014).

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Supplementary data

Supplementary data are available at SCAN online.

Conflict of interest. None declared.

References

- Adler, N.E., Boyce, W.T., Chesney, M., Folkman, S., Syme, S.L. (1993). Socioeconomic inequalities in health: No easy solutions. Journal of the American Medical Association, 269, 3140–5.
- Afonso, V.M., Sison, M., Lovic, V., Fleming, A.S. (2007). Medial prefrontal cortex lesions in the female rat affect sexual and maternal behavior and their sequential organization. Behavioral Neuroscience, **121**(3), 515–26. doi: 10.1037/0735-7044.121.3.515
- Atzil, S., Hendler, T., Feldman, R. (2011). Specifying the neurobiological basis of human attachment: brain, hormones, and behavior in synchronous and intrusive mothers. *Neuropsychopharmacology*, **36**(13), 2603–15. doi: 10.1038/ npp.2011.172
- Barclay, L., Everitt, L., Rogan, F., Schmied, V., Wyllie, A. (1997). Becoming a mother—an analysis of women's experience of early motherhood. *Journal of Advanced Nursing*, 25(4), 719–28.
- Barrett, J., Fleming, A.S. (2011). Annual Research Review: all mothers are not created equal: neural and psychobiological perspectives on mothering and the importance of individual differences. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, **52**(4), 368–97. doi: 10.1111/j.1469-7610.2010.02306.x
- Beck, A.T., Steer, R.A., Garbin, M.G. (1988). Psychometric properties of the Beck Depression Inventory: twenty-five years of evaluation. *Clinical Psychology Review*, 8, 77–100.
- Blair, C., Granger, D.A., Willoughby, M., et al. (2011). Salivary cortisol mediates effects of poverty and parenting on executive functions in early childhood. Child Development, 82(6), 1970–84.
- Bridges, R.S. (2015). Neuroendocrine regulation of maternal behavior. Frontiers in Neuroendocrinology, 36, 178–96. doi: http://dx. doi.org/10.1016/j.yfrne.2014.11.007
- Brooks-Gunn, J., Klebanov, P.K., Liaw, F.R. (1995). The learning, physical, and emotional environment of the home in the context of poverty: the Infant Health and Development Program. *Children and Youth Services Review*, 17(1), 251–76.
- Cohen, S. (1986). Contrasting the Hassles Scale and the Perceived Stress Scale: who's really measuring appraised stress? *American* Psychologist, **41**, 716–8.

- Cohen, S., Kamarck, T., Marmelstein, R. (1983). A global measure of perceived stress. *Journal of Health and Social Behavior*, **24**, 385–96.
- Cohen, S., Kaplan, G.A., Salonen, J.T. (1999). The role of psychological characteristics in the relation between socioeconomic status and perceived health. *Journal of Applied Social Psychology*, **29**(3), 445–68.
- Cohen, S., Tyrrell, D.A., Smith, A.P. (1993). Negative life events, perceived stress, negative affect, and susceptibility to the common cold. *Journal of Personality and Social Psychology*, **64**(1), 131–40.
- Cohen, S., Williamson, G.M. (1988). Perceived stress in a probability sample of the United States. In: Oskamp, S.Spacapan, S., editors. The Social Psychology of Health: Claremont Symposium on Applied Social Psychology. Los Angeles: SAGE Publications, 31–67.
- Conger, R. D., & Elder, G. H. (1994). Families in troubled times: adapting to change in rural america. New York: Aldine de Gruyter.
- Cox, R.W. (1996). AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. Computers and Biomedical Research, 29(3), 162–73.
- Delmore-Ko, P., Pancer, S.M., Hunsberger, B., Pratt, M. (2000). Becoming a parent: The relation between prenatal expectations and postnatal experience. *Journal of Family Psychology*, 14(4), 625.
- Drevets, W.C., Price, J.L., Furey, M.L. (2008). Brain structural and functional abnormalities in mood disorders: implications for neurocircuitry models of depression. Brain Structure and Function, **213**(1–2), 93–118.
- Etkin, A., Egner, T., Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in Cognitive Sciences*, **15**(2), 85–93. doi: 10.1016/j.tics.2010.11.004
- Febo, M., Felix-Ortiz, A.C., Johnson, T.R. (2010). Inactivation or inhibition of neuronal activity in the medial prefrontal cortex largely reduces pup retrieval and grouping in maternal rats. *Brain Research*, **1325**, 77–88.
- Feldman, R. (2015). The adaptive human parental brain: implications for children's social development. Trends in Neurosciences, 38(6), 387–99. doi: 10.1016/j.tins.2015.04.004
- Feldman, R., Gordon, I., Schneiderman, I., Weisman, O., Zagoory-Sharon, O. (2010). Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent-infant contact. Psychoneuroendocrinology, 35(8), 1133–41.
- Feldman, R., Weller, A., Leckman, J.F., Kuint, J., Eidelman, A.I. (1999). The nature of the mother's tie to her infant: maternal bonding under conditions of proximity, separation, and potential loss. *Journal of Child Psychology and Psychiatry*, **40**(06), 929–39.
- Ferris, C.F., Kulkarni, P., Sullivan, J.M., Jr., Harder, J.A., Messenger, T.L., Febo, M. (2005). Pup suckling is more rewarding than cocaine: evidence from functional magnetic resonance imaging and three-dimensional computational analysis. *Journal of Neuroscience*, 25(1), 149–56. doi: 10.1523/jneurosci.3156-04.2005
- Fleming, A.S., Ruble, D.N., Flett, G.L., Van Wagner, V. (1990). Adjustment in first-time mothers: changes in mood and mood content during the early postpartum months. *Developmental Psychology*, 26(1), 137.
- Fries, A.B., Ziegler, T.E.K., Jacoris, J.R., Pollak, S. S.D., (2005). Early experience in humans is associated with changes in neuropeptides critical for regulating social behavior. Proceedings of the National Academy of Sciences of the United States of America, 102, 17237–40.

- Gianaros, P.J., Manuck, S.B., Sheu, L.K., et al. (2011). Parental education predicts corticostriatal functionality in adulthood. *Cerebral Cortex*, **21**(4), 896–910. doi: 10.1093/cercor/bhq160
- Giardino, J., Gonzalez, A., Steiner, M., Fleming, A.S. (2008). Effects of motherhood on physiological and subjective responses to infant cries in teenage mothers: a comparison with nonmothers and adult mothers. Hormones and Behavior, 53(1), 149–58. doi: http://dx.doi.org/10.1016/j.yhbeh.2007.09.010
- Goodman, S.H. (2007). Depression in mothers. Annual Review of Clinical Psychology, **3**, 107–35.
- Gordon, I., Zagoory-Sharon, O., Leckman, J.F., Feldman, R. (2010a). Oxytocin and the development of parenting in humans. Biological Psychiatry, 68(4), 377–82.
- Gordon, I., Zagoory-Sharon, O., Leckman, J.F., Feldman, R. (2010b). Oxytocin, cortisol, and triadic family interactions. Physiology and Behavior, **101**(5), 679–84.
- Gotlib, I.H., Whiffen, V.E., Mount, J.H., Milne, K., Cordy, N.I. (1989). Prevalence rates and demographic characteristics associated with depression in pregnancy and the postpartum. *Journal of Consulting and Clinical Psychology*, 57(2), 269.
- Goyal, D., Gay, C., Lee, K.A. (2010). How much does low socioeconomic status increase the risk of prenatal and postpartum depressive symptoms in first-time mothers? Womens Health Issues, 20(2), 96–104.
- Haushofer, J., Fehr, E. (2014). On the psychology of poverty. Science, **344**(6186), 862–7.
- Hayes, A.F. (2013). Introduction to Mediation, Moderation, and Conditional Process Analysis: A regression-Based Approach. New York: The Guilford Press.
- Herzog, C., Czéh, B., Corbach, S., et al. (2009). Chronic social instability stress in female rats: a potential animal model for female depression. Neuroscience, 159(3), 982–92.
- Hipwell, A.E., Guo, C., Phillips, M.L., Swain, J.E., Moses-Kolko, E.L. (2015). Right frontoinsular cortex and subcortical activity to infant cry is associated with maternal mental state talk. *Journal* of Neuroscience, **35**(37), 12725–32. doi: 10.1523/jneurosci.1286-15.2015
- Johnstone, T., van Reekum, C.M., Oakes, T.R., Davidson, R.J. (2006). The voice of emotion: an FMRI study of neural responses to angry and happy vocal expressions. Social Cognitive and Affective Neuroscience, 1(3), 242–9. doi: 10.1093/scan/nsl027
- Kendrick, K.M. (2000). Oxytocin, motherhood and bonding. Experimental Physiology, 85 Spec No, 111S–24S.
- Kim, P., Bianco, H. (2014). How motherhood and poverty change the brain. Zero to Three, 34(4), 29–36.
- Kim, P., Evans, G.W., Angstadt, M., et al. (2013a). Effects of childhood poverty and chronic stress on emotion regulatory brain function in adulthood. The Proceedings of the National Academy of Sciences of the United States of America, 110(46), 18442–7.
- Kim, P., Evans, G.W., Chen, E., Miller, G.E., Seeman, T.E. (in press). How socioeconomic disadvantages get under the skin and into the brain across the lifespan. In: Halfon, N., Forrest, C., Lerner, R., Faustman, E., editors. The Handbook of Life Course Health Development. New York, NY: Springer.
- Kim, P., Feldman, R., Mayes, L.C., et al. (2011). Breastfeeding, brain activation to own infant cry, and maternal sensitivity. *Journal* of Child Psychology and Psychiatry and Allied Disciplines, 52(8), 907–15. doi: 10.1111/j.1469-7610.2011.02406.x
- Kim, P., Ho, S.S., Evans, G.W., Liberzon, I., Swain, J.E. (2015a). Childhood social inequalities influences neural processes in young adult caregiving. *Developmental Psychobiology*, 57(8), 948–60.
- Kim, P., Leckman, J.F., Mayes, L.C., Feldman, R., Wang, X., Swain, J.E. (2010a). The plasticity of human maternal

brain: longitudinal changes in brain anatomy during the early postpartum period. *Behavioral Neuroscience*, **124**(5), 695–700. doi: 10.1037/a0020884

- Kim, P., Leckman, J.F., Mayes, L.C., Newman, M.A., Feldman, R., Swain, J.E. (2010b). Perceived quality of maternal care in childhood and structure and function of mothers' brain. *Developmental Science*, **13**(4), 662–73. doi: 10.1111/j.1467-7687.2009.00923.x
- Kim, P., Mayes, L., Feldman, R., Leckman, J.F., Swain, J.E. (2013b). Early postpartum parental preoccupation and positive parenting thoughts: relationship with parent infant interaction. *Infant Mental Health Journal*, **34**(2), 104–16. doi: Doi 10.1002/ Imhj.21359.
- Kim, P., Rigo, P., Leckman, J.F., et al. (2015b). A prospective longitudinal study of perceived infant outcomes at 18–24 months: neural and psychological correlates of parental thoughts and actions assessed during the first month postpartum. Frontiers in Psychology 6, 1772.
- Kim, P., Strathearn, L., Swain, J.E. (2016). The maternal brain and its plasticity in humans. Hormones and Behavior, **77**, 113–23.
- Kim, P., Watamura, S.E. (2015). Two Open Windows: Infant and Parent Neurobiologic Change [Ascend]. Washington, DC: The Aspen Institute.
- Kramer, M.S., Lydon, J., Séguin, L., et al. (2009). Stress pathways to spontaneous preterm birth: the role of stressors, psychological distress, and stress hormones. American Journal of Epidemiology, 169(11), 1319–26.
- Laurent, H.K., Ablow, J.C. (2012). A cry in the dark: depressed mothers show reduced neural activation to their own infant's cry. Social Cognitive and Affective Neuroscience, 7(2), 125–34. doi: nsq091 [pii] 10.1093/scan/nsq091
- Leckman, J.F., Mayes, L.C., Feldman, R., Evans, D.W., King, R.A., Cohen, D.J. (1999). Early parental preoccupations and behaviors and their possible relationship to the symptoms of obsessive-compulsive disorder. Acta Psychiatrica Scandinavica. Supplementum, 396, 1–26.
- Lobel, M., Cannella, D.L., Graham, J.E., DeVincent, C., Schneider, J., Meyer, B.A. (2008). Pregnancy-specific stress, prenatal health behaviors, and birth outcomes. *Health Psychology*, 27(5), 604–15.
- Lonstein, J.S., Lévy, F., Fleming, A.S. (2015). Common and divergent psychobiological mechanisms underlying maternal behaviors in non-human and human mammals. Hormones and Behavior, 73, 156–85. doi: http://dx.doi.org/10.1016/j.yhbeh. 2015.06.011
- Lonstein, J.S., Maguire, J., Meinlschmidt, G., Neumann, I.D. (2014). Emotion and mood adaptations in the peripartum female: complementary contributions of GABA and oxytocin. *Journal of Neuroendocrinology*, 26(10), 649–64.
- Mistry, R., Stevens, G.D., Sareen, H., De Vogli, R., Halfon, N. (2007). Parenting-related stressors and self-reported mental health of mothers with young children. *American Journal of Public Health*, **97**(7), 1261–88.
- Monk, C., Spicer, J., Champagne, F.A. (2012). Linking prenatal maternal adversity to developmental outcomes in infants: the role of epigenetic pathways. *Development and Psychopathology*, 24(4), 1361–76.
- Montoya, J.L., Landi, N., Kober, H., et al. (2012). Regional brain responses in nulliparous women to emotional infant stimuli. PLoS One, 7(5), e0036270. doi: 10.1371/journal.pone.0036270
- Moses-Kolko, E.L., Horner, M.S., Phillips, M.L., Hipwell, A.E., Swain, J.E. (2014). In search of neural endophenotypes of postpartum psychopathology and disrupted maternal caregiving. *Journal of Neuroendocrinology*, **26**(10), 665–84. doi: 10.1111/ jne.12183

- Musser, E.D., Kaiser-Laurent, H., Ablow, J.C. (2012). The neural correlates of maternal sensitivity: an fMRI study. *Developmental Cognitive Neuroscience*, **2**(4), 428–36. doi: 10.1016/j.dcn.2012.04.003
- Newland, R.P., Crnic, K.A., Cox, M.J., Mills-Koonce, W.R. (2013). The family model stress and maternal psychological symptoms: mediated pathways from economic hardship to parenting. Journal of Family Psychology, **27**(1), 96–105.
- Numan, M. (2014). Neurobiology of Social Behavior: Toward an Understanding of the Prosocial and Antisocial Brain. London: Academic Press.
- Numan, M., Stolzenberg, D.S. (2009). Medial preoptic area interactions with dopamine neural systems in the control of the onset and maintenance of maternal behavior in rats. Frontiers in Neuroendocrinology, **30**, 46–64.
- Numan, M., Insel, T.R. (2003). The Neurobiology of Parental Behavior. New York: Springer.
- Numan, M., Woodside, B. (2010). Maternity: neural mechanisms, motivational processes, and physiological adaptations. Behavioral Neuroscience, **124**(6), 715–41. doi: 10.1037/a0021548
- O'Hara, M.W., Neunaber, D.J., Zekoski, E.M. (1984). Prospective study of postpartum depression: prevalence, course, and predictive factors. *Journal of Abnormal Psychology*, **93**(2), 158–71. doi: 10.1037/0021-843X.93.2.158
- O'hara, M.W., Swain, A.M. (1996). Rates and risk of postpartum depression-a meta-analysis. International Review of Psychiatry, **8**(1), 37–54.
- Ochsner, K.N., Silvers, J.A., Buhle, J.T. (2012). Functional imaging studies of emotion regulation: a synthetic review and evolving model of the cognitive control of emotion. *Annals of the New* York Academy of Sciences, **1251**(1), E1–E24. doi: 10.1111/j.1749-6632.2012.06751.x
- Preacher, K.J., Hayes, A.F. (2008). Asymptotic and resampling strategies for assessing and comparing indirect effects in multiple mediator models. *Behavior Research Methods*, **40**(3), 879–91.
- Razurel, C., Kaiser, B., Sellenet, C., Epiney, M. (2013). Relation between perceived stress, social support, and coping strategies and maternal well-being: a review of the literature. Women and Health, 53(1), 74–99.
- Reece, S.M., Harkless, G. (1998). Self-efficacy, stress, and parental adaptation: applications to the care of childbearing families. *Journal of Family Nursing*, **4**(2), 198–215.

- Rocchetti, M., Radua, J., Paloyelis, Y., et al. (2014). Neurofunctional maps of the "maternal brain" and the effects of oxytocin: a multimodal voxel-based meta-analysis. Psychiatry and Clinical Neurosciences, 68(10), 733–51. doi: 10.1111/ pcn.12185
- Rutherford, H.J.V., Wallace, N.S., Laurent, H.K., Mayes, L.C. (2015). Emotion regulation in parenthood. *Developmental Review*, **36**, 1–14. doi: http://dx.doi.org/10.1016/j.dr.2014.12.008
- Sander, K., Frome, Y., Scheich, H. (2007). FMRI activations of amygdala, cingulate cortex, and auditory cortex by infant laughing and crying. *Human Brain Mapping*, **28**(10), 1007–22.
- Séguin, L., Potvin, L., St-Denis, M., Loiselle, J. (1999). Depressive symptoms in the late postpartum among low socioeconomic status women. Birth, 26(3), 157–63. doi: 10.1046/j.1523-536x.1999.00157.x
- Stallings, J., Fleming, A.S., Corter, C., Worthman, C., Steiner, M. (2001). The effects of infant cries and odors on sympathy, cortisol, and autonomic responses in new mothers and nonpostpartum women. *Parenting*, 1(1–2), 71–100.
- Steptoe, A., Wardle, J., Pollard, T.M., Canaan, L., Davies, G.J. (1996). Stress, social support and health-related behavior: a study of smoking, alcohol consumption and physical exercise. *Journal of Psychosomatic Research*, **41**(2), 171–80.
- Strathearn, L., Li, J., Fonagy, P., Montague, P.R. (2008). What's in a smile? Maternal brain responses to infant facial cues. *Pediatrics*, **122**, 40–51.
- Swain, J.E. (2010). The human parental brain: in vivo neuroimaging. Progress in Neuro-Psychopharmacology and Biological Psychiatry, 35(5), 1242–54. doi: S0278-5846(10)00390-8 [pii] 10.1016/j.pnpbp.2010.10.017
- Swain, J.E., Kim, P., Spicer, J., et al. (2014). Approaching the biology of human parental attachment: brain imaging, oxytocin and coordinated assessments of mothers and fathers. Brain Research, **1580**, 78–101. doi: 10.1016/j.brainres.2014.03.007
- Swain, J.E., Tasgin, E., Mayes, L.C., Feldman, R., Constable, R.T., Leckman, J.F. (2008). Maternal brain response to own baby-cry is affected by cesarean section delivery. *Journal of Child Psychology and Psychiatry*, **49**(10), 1042–52. doi: 10.1111/j.1469-7610.2008.01963.x
- Wager, T.D., Davidson, M.L., Hughes, B.L., Lindquist, M.A., Ochsner, K.N. (2008). Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*, 59(6), 1037–50. doi: 10.1016/j.neuron.2008.09.006