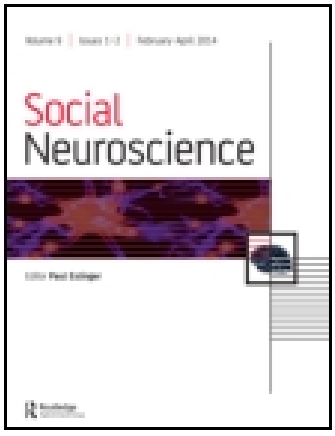




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# Neural plasticity in fathers of human infants

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# Neural plasticity in fathers of human infants

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Fathering plays an important role in infants' socioemotional and cognitive development. Previous studies have identified brain regions that are important for parenting behavior in human mothers. However, the neural basis of parenting in human fathers is largely unexplored. In the current longitudinal study, we investigated structural changes in fathers' brains during the first 4 months postpartum using voxel-based morphometry analysis. Biological fathers ($n$ = 16) with full-term, healthy infants were scanned at 2–4 weeks postpartum (time 1) and at 12–16 weeks postpartum (time 2). Fathers exhibited increase in gray matter (GM) volume in several neural regions involved in parental motivation, including the hypothalamus, amygdala, striatum, and lateral prefrontal cortex. On the other hand, fathers exhibited decreases in GM volume in the orbitofrontal cortex, posterior cingulate cortex, and insula. The findings provide evidence for neural plasticity in fathers' brains. We also discuss the distinct patterns of associations among neural changes, postpartum mood symptoms, and parenting behaviors among fathers.

***Keywords:*** Paternal brain; Father; Parenting; Postpartum; Neuroimaging.

Over the past 20–30 years, fathers' involvement in caregiving has become increasingly significant (Parke, 2002). Infancy, in particular, is a period when fathers are often most active in parental care (Yeung, Sandberg, Davis-Kean, & Hofferth, 2001). The quality of paternal care and paternal postpartum depression play important roles for infants' socioemotional and cognitive development (Bornstein, 2002; Lamb & Lewis, 2013; Leidy, Schofield, & Parke, 2013; Ramchandani et al., 2011). Furthermore, longitudinal studies demonstrate the unique contribution of sensitive father–infant interactions to the development of children's social competencies in childhood and adolescence

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across cultural contexts (Brown, Mangelsdorf, & Neff, 2012; Feldman, Bamberger, & Kanat-Maymon, 2013; Feldman, Gordon, Influs, Gutbir, & Ebstein, 2013; Feldman & Masalha, 2010). In human mothers, a growing literature of neuroimaging studies has begun to identify the neural basis of parenting behaviors (Atzil, Hendler, & Feldman, 2011; Barrett & Fleming, 2011; Kim et al., 2010; Landi et al., 2011; Michalska et al., 2014; Montoya et al., 2012; Rutherford, Potenza, & Mayes, 2013; Rutherford, Williams, Moy, Mayes, & Johns, 2011; Swain, 2010; Swain, Lorberbaum, Kose, & Strathearn, 2007; Swain et al., in press). However, to date, biobehavioral studies on the developing parent–infant relationships have mostly targeted mothers with little attention to fathers. Thus, the current longitudinal neuroimaging study examined changes in the neural anatomy of human fathers, over the course of the first 4 months postpartum.

In animal studies, several brain areas are revealed to be important for the development of paternal behaviors. Studies of the paternal brain have been focused on biparental species including California mice (*Peromyscus californicus*) and prairie voles (Kentner, Abizaid, & Bielajew, 2010). Males of these biparental species are similar to females (Fleming et al., 2002; Numan & Insel, 2003) in that the medial preoptic area (MPOA), located in the rostral hypothalamus, and its connections with the amygdala and reward regions including striatum play a critical role in the onset of paternal motivation (De Jong, Chauke, Harris, & Saltzman, 2009; Kenkel, Suboc, & Carter, 2014; Lee & Brown, 2007). Male prairie voles show increased *c-Fos* expression in the MPOA (Kirkpatrick, Carter, Newman, & Insel, 1994), which is critical for paternal behaviors (Rosenblatt & Ceus, 1998). Male prairie voles have arginine vasopressin (AVP) receptors in these regions (Wang, Young, De Vries, & Insel, 1999), and infusion of a vasopressin receptor antagonist into the lateral septum disrupts paternal activities, including grooming, crouching over young, contacting, and retrieving pups (Landgraf & Neumann, 2004). On the other hand, California male mice exhibited reduced *c-Fos* immunoreactivity in the insular cortex compared to non-paternal male species (Lambert, 2012). In primates, fatherhood was associated with higher density of the prefrontal cortex (PFC) of marmoset males (Kozorovitskiy, Hughes, Lee, & Gould, 2006). The PFC is involved in processing social information, such as infant cues, and regulating parental behaviors in animal models (Afonso, Sison, Lovic, & Fleming, 2007).

There are only a few existing neuroimaging studies that focus on human fathers. These studies suggest the importance of several brain regions including PFC, striatum, and insula for paternal responses to infants (Swain et al., in press). The first study found increased activity in brain areas similar to those found in mothers, including prefrontal regions, the orbitofrontal cortex (OFC), and striatal regions, while viewing own infant images at 2-4 months postpartum (Kuo, Carp, Light, & Grewen, 2012). The second study found responses in fathers overlapping with mothers in the inferior frontal gyrus, medial and lateral PFC, and insula, while viewing own infant at 4-6 months postpartum (Atzil, Hendler, Zagoory-Sharon, Winetraub, & Feldman, 2012). A recent study found increased activity in the medial frontal gyrus, striatum, cingulate, and thalamus in response to own child images (vs. adult images) among fathers with children at ages 1-5 years (Mascaro, Hackett, & Rilling, 2013). While animal studies suggest changes in neural structure over time, human studies with fathers have focused on functional activity. Therefore, it is unclear whether brains of human fathers also exhibit similar structural plasticity during the early postpartum period.

The current study will also examine whether postpartum outcomes among new fathers are associated with neural changes. Fathers' active engagement in parenting has been shown to play a significant role in optimal child development (Pruett, 1998; Sarkadi, Kristiansson, Oberklaid, & Bremberg, 2008). Fathers, although to a lesser degree than mothers, experience mood changes including increased levels of anxiety and distress during the early postpartum period (Kim, Mayes, Feldman, Leckman, & Swain, 2013; Leckman et al., 1999). Highly negative mood such as paternal depression during the postpartum period can have long-term negative cognitive and emotional outcomes in their children (Kim & Swain, 2007; Ramchandani & Psychogiou, 2009; Ramchandani, Stein, Evans, & O'Connor, 2005). In studies with mothers, the degree of increase in neural activity in the PFC, amygdala, and striatal regions were positively associated with the higher quality of motherinfant dyadic interactions (Atzil et al., 2011; Kim et al., 2011). On the other hand, in human mothers, low levels of neural activation in prefrontal and insula/striatal regions in response to infant stimuli have also been associated with depressive symptoms, which can disrupt the normal development of parent–infant bonding (Kingston, Tough, & Whitfield, 2012; Laurent & Ablow, 2012; Moses-Kolko et al., 2010; Noll, Mayes, & Rutherford, 2012; Swain et al., 2008). However, in human fathers, the associations between

structural plasticity in the brain, mood symptoms, and parental behaviors have never been examined.

In order to better understand neuroplasticity related to fathering during the early postpartum period, this longitudinal magnetic resonance imaging (MRI) study examined structural brain changes in human fathers from 2-4 weeks to 12-16 weeks postpartum. We employed the longitudinal voxel-based morphometry (VBM) analyses to identify changes in gray matter (GM) volume. Using the VBM analyses, we previously reported GM volume increases in a number of brain regions in human mothers, including the striatum, thalamocingulate, and PFC during the same early postpartum period (Kim et al., 2010). Multiple VBM analysis studies have also shown that intense training for 3 months leads to increased GM in hippocampal, temporal, and PFC regions in adults (Draganski & May, 2008; Gaser & Schlaug, 2003; Maguire et al., 2000; May, 2011). Thus, we hypothesized that over the 3-month period during early postpartum, fathers would exhibit GM volume increase in the brain regions that modulate motivation and decision-making—the striatum and the PFC. Based on findings from animal studies, we also hypothesized that fathers would exhibit GM volume decrease in the insula, a region involved in negative emotional information processing. Additionally, as an exploratory analysis, we planned to examine whether morphological changes were associated with individual differences in fathers' depressive symptoms and objective assessments of father–infant interactions. We hypothesized that increase in the GM volumes in the striatum and PFC and the decrease in GM volume in the insula would be associated with fewer depressive symptoms and increased sensitive and/or decreased intrusive parenting behaviors during the early postpartum period.



# METHODS

## Participants

Sixteen biological fathers of full-term and healthy infants were recruited in postpartum hospital wards at the Yale–New Haven hospital. All fathers (age M = 36.31 years, SD = 4.92) were right-handed, Caucasian, either married or cohabiting, and had a college or higher education (M = 17.25 years, SD = 3.34). Among the fathers, 7 out of 16 (44%) were first-time fathers. Exclusion criteria included any current psychiatric diagnosis and recent history of prescription medications within 2 weeks of the experiment. Informed consent was obtained from each participant in accordance with a protocol approved by the Human Research Protection Program of Yale University and the Helsinki Declaration.

## Procedure

Fathers visited the Yale Magnetic Resonance Research Center twice to acquire brain imaging data: once between 2 and 4 weeks postpartum [time 1 (T1)] and again 12-16 weeks postpartum [Time (T2)]. The average interval between two scans was 80.75 (SD = 10.67) days. A measure of depressed mood was obtained at both T1 and T2. At T2, a videotaped father–infant interaction was obtained during a home visit and then analyzed for measures of parental sensitivity and intrusiveness. For videotaped interactions, fathers were asked to interact with their infants for 5 minutes as they normally would.

## Measures

### *Beck Depression Inventory*

The measure was used to assess the level of depressive symptoms. All fathers had a score ranging 0–8, which indicates minimal levels of depression except one father who scored 14, indicating a mild depression at T1. The mean was 3.00 (SD = 3.87) at T1 and 1.93 (SD = 1.94) at T2.

### *Paternal sensitivity and intrusiveness*

Father–infant interactions were coded using the Coding Interactive Behavior (CIB) manual (Feldman, 1998). Research has shown that measures of sensitivity and intrusiveness assessed during 5-minute parent–infant interaction sessions yield important data and capture meaningful aspects of the parental repertoire. Measures of sensitivity and intrusiveness assessed with the CIB correlate with lengthy home observations, are individually stable in repeated interactions from infancy to adolescence, show differences between mother–child and father–child interaction and between interactive contexts (e.g., feeding and play), and predict developmental outcomes across childhood and adolescence, including emotion regulation, social competence, peer relationships, and empathy (Feldman, 2012; Feldman, Bamberger, et al., 2013; Feldman & Klein, 2003; Feldman & Masalha, 2010). The CIB consists of 42 parent, infant, and dyadic codes, each rated on a scale

of 1 (a little) to 5 (a lot). Interactions were videotaped at home and coded offline by trained coders. The CIB demonstrated the high test-retest reliability and construct validity for assessing the full range of the subscales and detecting differences between normal and at-risk samples (Feldman, 2012; Feldman, Greenbaum, Mayes, & Erlich, 1997; Feldman, Keren, Gross-Rozval, & Tyano, 2004). These scales were then aggregated into several composites. The sensitivity construct used in this study includes the following 11 codes ($\alpha$ = 0.91): acknowledgement of child communications, vocal clarity, positive affect, gaze, appropriate range of affect, affectionate touch, resourcefulness, imitation, consistency of style, adaptation to child signals, and supportive presence. The intrusiveness ($\alpha$ = 0.84) construct refers to a parental style that overrides the infant's signals and imposes the parental agenda and includes the following averaged five codes: forcing (e.g., parent's physical manipulation of infant's body, for instance, moving the infant's hands or feet, pulling the infant to a sitting position, or throwing the infant in space), overriding (e.g., interruption of infant's activities and parent leading the interaction), anger toward a child, hostility toward a child, and anxious behaviors. Two of the fathers were unable to provide the videotaped interactions because of scheduling conflicts. Thus, data of 14 fathers were used in the parental behavior analysis. Overall, inter-rater reliability exceeded 90% on all codes ($\kappa$ > 0.82). The mean for sensitivity was 3.88 (SD = 0.92; range = 2–5) and intrusiveness was 1.98 (SD = 0.87; range = 1–4).

## Image acquisition

High-resolution T1-weighted structural MRIs were obtained (Three Dimensional Magnetization Prepared Rapid Acquisition Gradient-echo; TR = 2530 ms; TE = 3.66 ms; matrix size 256 × 256; 176 slices; flip angle = 40°; voxel size was 1.0 × 1.0 × 1.0 mm) with a Siemens Trio 3T scanner (Erlangen, Germany).

## Voxel-based morphometry longitudinal analysis

VBM analyses (Ashburner & Friston, 2000, 2001) were performed with VBM8 toolbox (http://dbm.neuro.uni-jena.de/vbm/) for Statistical Parametric Mapping 8 (SPM8) (Wellcome Department of Neurology, London, UK). The VBM analysis is an automated approach to brain structure. Using the default preprocessing approach of the VBM8 toolbox for a longitudinal data analysis, the two time point data were first realigned (from T2 to T1) for each subject separately. Next, intrasubject bias was corrected for signal inhomogeneity. The bias-corrected images were then segmented into GM, white matter, and cerebrospinal fluid, using the segmentation algorithm in SPM8. Both linear registration, using affine, and nonlinear registration, using a diffeomorphic image registration algorithm (DARTEL), were performed. The segmentation procedure was further refined by accounting for partial volume effects (i.e., mixed voxels with two tissue types) (Tohka, Zijdenbos, & Evans, 2004), applying adaptive maximum a posteriori estimations (Rajapakse, Giedd, & Rapoport, 1997) and a hidden Markov random field model (Cuadra, Cammoun, Butz, Cuisenaire, & Thiran, 2005). The different tissue segments were modulated by the nonlinear normalization parameters to account for individual brain size differences. Finally, the warped images were then smoothed with an isotropic Gaussian kernel of 8-mm full-width at half-maximum. The resulting images were normalized to a standard template brain [the Montreal Neurological Institute (MNI) template] and voxel size of 1.5 $mm^3$. All images were checked for scanner artifacts and anatomical anomalies that would affect the image analyses.

At the whole-brain level analysis, in SPM, the processed images were analyzed with a repeated-measure analysis of variance to test changes in GM between T1 and T2, controlling for ages of fathers, parenting experience (primiparous or multiparous status), and scan intervals. First, the suprathreshold clusters were identified at $p$ < .005 (uncorrected), and then, the results at $q$ < 0.05, false discovery rate (FDR)-corrected at the cluster level, were reported. Additional detail regarding breakdown of the clusters into the proportions of voxels in specific anatomical regions was obtained via the MNI Space utility, as visualized and reported through xjView (http://www.alivelearn.net/).

Estimates of gray volume change averaged across the entire suprathreshold region were extracted for each participant using MarsBaR (MARSeille Boîte À Région d'Intérêt) (65) and were then entered into Statistical Package for the Social Sciences (SPSS, Inc.) for additional analyses. Pearson's bivariate correlations were performed to test the associations among GM changes and paternal behavioral measures. Differences in depressive symptoms from T1 to T2 as well as depressive symptoms at T2 were used for correlation analyses with GM changes from T1 to T2.

# RESULTS

## Longitudinal changes in gray matter volume during the first 4 months postpartum

The longitudinal VBM analyses revealed that from T1 (2-4 weeks postpartum) to T2 (12-16 weeks postpartum), fathers showed an increase in GM volume in the striatum (as well as amygdala, hypothalamus, and subgenual cortex), lateral PFC, and superior temporal gyrus, $p < .05$, FDR-corrected (Table 1, Figure 1). In contrast, several brain regions showed decrease in GM volume from T1 to T2 including the OFC, posterior cingulate cortex (PCC), insula, and fusiform gyrus, $p < .05$, FDR-corrected (Table 1, Figure 1).

## Correlations among gray matter changes, depressive symptoms, and parenting behaviors

We first examined zero-order correlations among depressive symptoms, parental sensitivity, and intrusiveness, but all correlations were nonsignificant. For parenting behaviors, a decrease in GM volume in the OFC was correlated with higher levels of intrusive parenting behaviors during interactions with infants, $r(14) = -0.55$, $p < .05$ (Figure 2). In the post hoc analysis, the correlations among five subscales of paternal intrusiveness (i.e., forcing, overriding, anger, hostility, and anxiety) and the OFC change were explored. The only significant correlation was with forcing (e.g., parent's physical manipulation of infant's body), $r(14) = 0.65$, $p < .05$. No other region was associated with paternal intrusiveness or sensitivity.

Differences in depressive symptoms between T1 and T2 were not correlated with GM changes. However, an increase in GM volume in a cluster that included part of the striatum, amygdala, and subgenual cortex was negatively correlated with depressive symptoms assessed at T2, $r(15) = -0.55$, $p < .05$ (Figure 3). A decrease in the PCC and fusiform gyrus [$r(15) = 0.54$, $p < .05$; $r(15) = 0.60$, $p < .05$, respectively] was also associated with lower levels of depressive symptoms at T2. In the post hoc analysis, we explored the correlations among individual items of the Beck Depression Inventory and GM changes in the cluster including the striatum and subgenual cortex, which includes regions involved in parental motivations. The increase in GM volume was negatively correlated with predominantly physical items such as an item on sleep (i.e., I wake up several hours earlier than I used to and cannot get back to sleep) [$r(15) = -0.55$, $p < .05$] and an item on fatigue (i.e., I am too tired to do anything) [$r(15) = -0.64$, $p < .05$].

**TABLE 1**
Brain regions showing gray matter changes from 2–4 weeks to 12–16 weeks postpartum in fathers

| *Regions* | *BA* | *Side* | *MNI coordinates (peak within a cluster)* *x* | *y* | *z* | *Cluster size* | *z-Value* | *Contrast of parameter estimates (90% confidence intervals)* | |
|---|---|---|---|---|---|---|---|---|---|
| Grey matter increase from 2–4 weeks to 3–4 months postpartum | | | | | | | | | |
| Putamen, caudate, subgenual cingulate, pallidum, globus pallidus, amygdala, hypothalamus | 13,25,34 | L | −15 | 19 | −10 | 2591 | 6.53 | 0.05 | (0.04; 0.06) |
| Superior, middle, and inferior frontal gyrus, superior and middle temporal gyrus, temporal pole, precentral gyrus | 9,10,21,22,38,44,45,46,47 | R | 51 | 33 | 34 | 2758 | 3.70 | 0.02 | (0.01; 0.02) |
| Grey matter decrease from 2–4 weeks to 3–4 months postpartum | | | | | | | | | |
| Orbitofrontal cortex, inferior, medial, and middle frontal gyrus | 11,25,47 | R | 9 | 39 | −22 | 2065 | 5.28 | −0.04 | (−0.05; −0.03) |
| Posterior and middle cingulate gyrus, precuneus | 23,29,30,31 | L | −3 | −52 | 21 | 790 | 4.27 | −0.03 | (−0.04; −0.02) |
| Inferior and middle frontal gyrus, insula | 11,13,44,45,47 | L | −42 | 25 | 12 | 733 | 4.05 | −0.02 | (−0.03; −0.01) |
| Inferior temporal gyrus, fusiform gyrus | 20,37 | L | −52 | −27 | −22 | 646 | 3.87 | −0.05 | (−0.07; −0.03) |
| Cerebellum | | R | 31 | −63 | −37 | 685 | 3.65 | −0.05 | (−0.07; −0.03) |

*Note*: $q < 0.05$, false discovery rate (FDR)-corrected; BA = brodmann area.

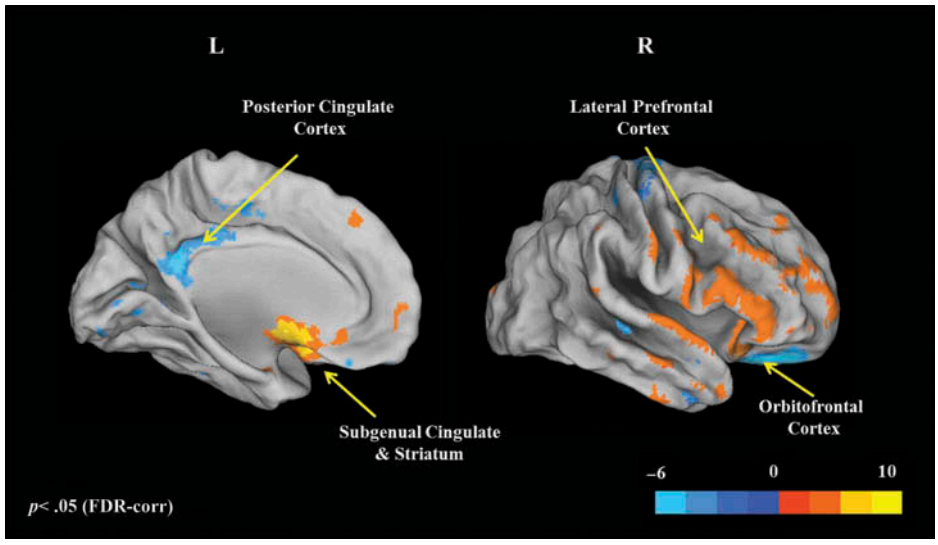


**Figure 1.** Gray matter (GM) increase (red) and decrease (blue) from 2–4 weeks to 12–16 weeks postpartum in fathers. $q < 0.05$, false discovery rate (FDR)-corrected.



## DISCUSSION

The current study is the first to examine anatomical changes in human fathers' brains from 2-4 weeks to 12-16 weeks postpartum. On one hand, we found GM volume increases in the striatum/subgenual anterior cingulate cortex (ACC) and lateral PFC. On the other hand, the OFC, PCC, insula, and fusiform gyrus show GM volume decreases over time. In addition, lower levels of depressive symptoms, particularly physical depressive symptom items, at 12-16 weeks postpartum were associated with GM volume increases in the striatum/subgenual ACC over the first few months postpartum. Structural decreases in the OFC were associated with higher levels of paternal intrusiveness, particularly physical plays during father–infant interactions. The findings may shed light on the brain regions that adopt structural changes in concert with the human father's transition to parenthood and regulate each father's ability to develop appropriate parental behaviors and regulate postpartum mood.

Consistent with the key brain regions involved in the expression of parenting behaviors in animals, we report that the striatum, amygdala, and hypothalamus show increases in GM volume from 2-4 weeks to 12-16 weeks postpartum in fathers. Nonhuman studies have underlined the importance of these regions as regulators of behavioral reactivity and salience of infant stimuli (De Jong et al., 2009; Kenkel et al., 2014; Kentner et al., 2010; Storey & Walsh, 2013). The regions also play a critical role in the rewarding experience of attachment and the expression of affiliative behaviors (Lee & Brown, 2007; Moll et al., 2012). Studies with animal males found high levels of oxytocin and vasopressin receptors in these regions and increased bindings during the postpartum period (Loup, Tribollet, Dubois-Dauphin, & Dreifuss, 1991). In human fathers, watching video clips of own (vs. control) baby activated the caudate, a part of the striatum, at 2-4 months postpartum (Kuo et al., 2012). Therefore, the volume increase in the striatum, amygdala, and hypothalamus that we report in fathers may constitute a mechanism for the functional adaptations that fathers display some months into the postpartum period for parental motivation and detection of salient infant cues.

Our findings on the increased GM volumes in the lateral PFC are consistent with data from the biparental primate marmoset males, whose parenting experience was associated with higher density of pyramidal cells in the dendritic spines of the PFC (Kozorovitskiy et al., 2006). In human fathers, the lateral PFC is activated while viewing own vs. control infants at 2-4 months postpartum (Kuo et al., 2012). Literature on the maternal brain consistently suggests that the lateral PFC plays a role for the complex decision processes involved in parental behaviors (Numan & Insel, 2003). Superior temporal regions may perform sensory information processing (Nishitani, Doi, Koyama, & Shinohara, 2011). Indeed, greater responses in lateral prefrontal and superior temporal regions to own vs. control infant-related stimuli have been consistently detected across the neuroimaging studies of human mothers (reviewed in Barrett & Fleming, 2011; Landi et al., 2011;

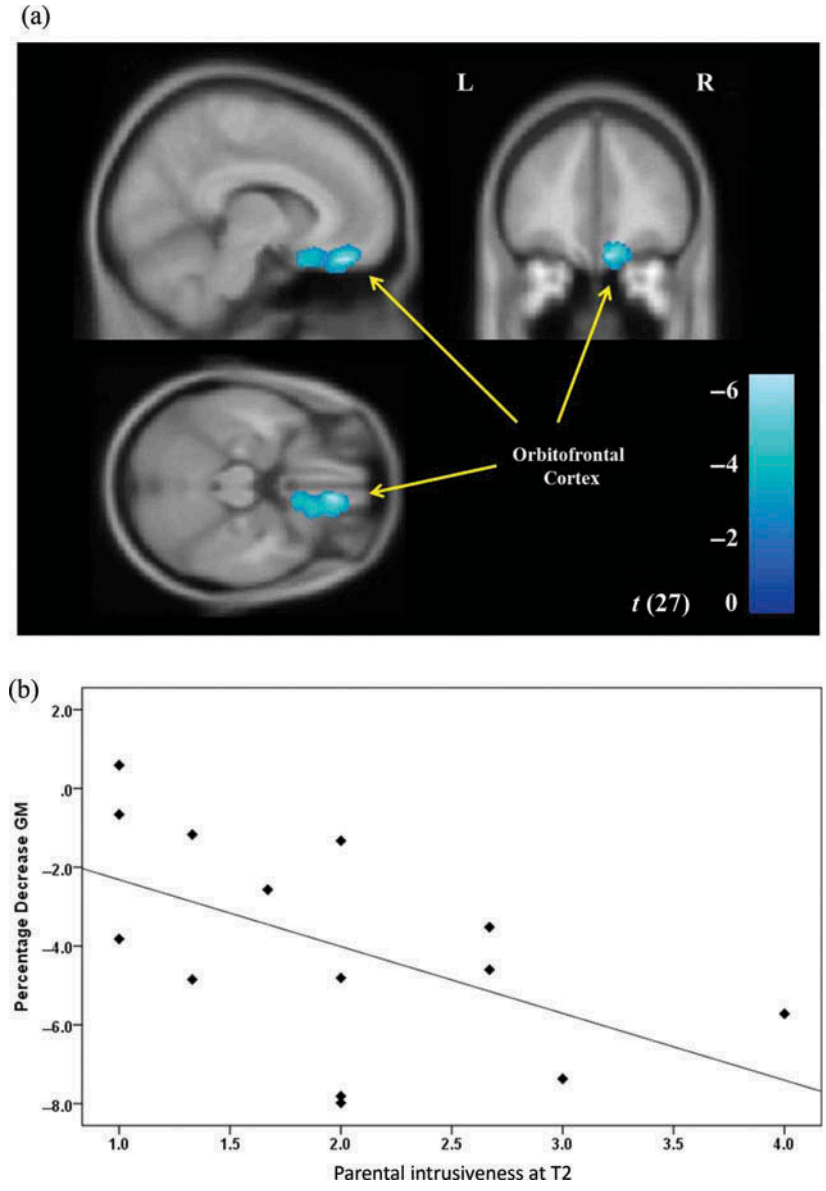


**Figure 2.** (a) Gray matter (GM) volume decrease in right orbitofrontal cortex in fathers from 2-4 weeks [time 1 (T1)] to 12-16 weeks postpartum [time 2 (T2)], $q < 0.05$, false discovery rate-corrected. (b) Correlation between GM volume increases in this region and paternal intrusive parenting behaviors at 12-16 weeks postpartum.

Parsons et al., 2013; Swain, 2010; Swain et al., in press, 2007). Furthermore, in a study comparing fathers' and mothers' neural responses to infant video clips at 4-6 months postpartum, fathers showed greater activation in the lateral PFC and superior temporal regions than mothers (Atzil et al., 2012), highlighting the role of the lateral PFC and superior temporal regions in fathering. Our findings of increased lateral PFC and superior temporal gyrus volume in human fathers may support the conclusion that these regions serve an important function for the initiation of parenting behaviors in fathers during the early postpartum period.

While increases in the GM volumes in the midbrain, lateral PFC, and superior temporal regions in fathers were consistent with those of mothers (Supplementary Table 1), the current study also revealed neural regions showing several areas of decreased volume over time in fathers. This was different from mothers (Kim et al., 2010) for whom we found no regions with structural decrease over the same postpartum periods (Supplementary Table 1).

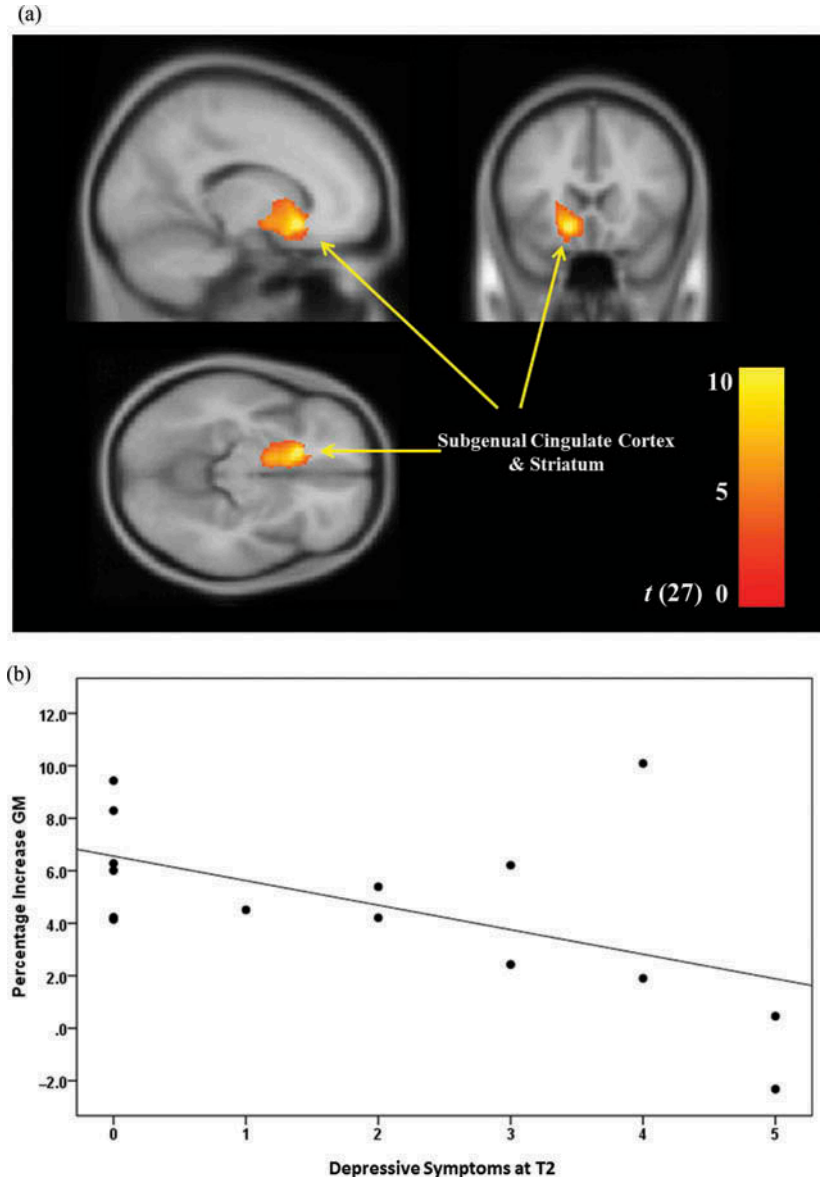


**Figure 3.** (a) Gray matter (GM) volume increase in left striatum, hypothalamus, amygdala, and subgenual anterior cingulate cortex (ACC) in fathers from 2-4 weeks [time 1 (T1)] to 12-16 weeks postpartum [time 2 (T2)], $q < 0.05$, false discovery rate (FDR)-corrected. (b) Correlation between GM volume increase in this region and depressive symptoms at 12-16 weeks postpartum.

The regions that showed a decrease in GM volumes, including medial PFC, PCC, precuneus, and inferior parietal cortex, comprise key regions of the default-mode network (Buckner, Andrews-Hanna, & Schacter, 2008; Fransson & Marrelec, 2008). In a study including both parents of children older than 4 years and nonparents, men showed less deactivation in parts of the default-mode network compared to women while listening to infant cry sounds (De Pisapia et al., 2013). Deactivations in the default-mode network are associated with increased attention to a task (Greicius & Menon, 2004). Thus, a decrease in GM volumes among fathers during the early postpartum period may indicate a shift of resources to other regions, such as lateral PFC and striatal regions, as attention to parenting increases.

The other regions that exhibited GM decrease among fathers are right OFC and left insula. The OFC is involved in learning the emotional value of information, and the insula receives signals from the amygdala and OFC for further processing of emotional relevance. Both regions are particularly active under the context of threats and stress (Morris & Dolan, 2004; Paulus & Stein, 2006). For example,

hyperactivity in the insula and OFC has been implicated in anxiety (Milad & Rauch, 2007; Stein, Simmons, Feinstein, & Paulus, 2007). Both the insula and OFC have also been implicated in processing uncertainty and ambiguous information (Bach & Dolan, 2012; Simmons, Matthews, Paulus, & Stein, 2008). Therefore, it is possible that reductions in structural volume over time reflect reduced levels of ambiguity and stress during the first 3–4 months postpartum, as the amount of experience and interaction time increases between fathers and their infants.

This may be supported by the finding that a decrease in the OFC volume was associated with higher paternal intrusiveness, particularly the physical manipulation of the infant's body during play. Although maternal intrusiveness tends to be considered negative for infants, paternal intrusiveness, particularly paternal stimulatory behavior with infants, has been characterized as sensitive parenting (Volling, Mcelwain, Notaro, & Herrera, 2002). Maternal sensitivity is expressed by emotional warmth and support, whereas paternal sensitivity is expressed by providing stimulating interactions (Feldman, 2003; Grossmann, Grossmann, Kindler, & Zimmermann, 2008; Volling et al., 2002). In a previous study with fathers, stimulatory contact (i.e., proprioceptive and stimulatory touch and exploratory play), but not affectionate contact, was positively associated with an increase in peripheral levels of oxytocin, a hormone important for parental motivation (Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010). Therefore, among healthy fathers, physical manipulation of the infant's body and the parent leading the interaction may capture the typical paternal parenting style more accurately than paternal sensitivity during the early postpartum period.

Interestingly, at 4-6 months postpartum, while parents are viewing their own baby's pictures, plasma oxytocin and vasopressin levels were negatively associated with OFC and insular activity among fathers (Atzil et al., 2012). No lateral PFC region has been associated with oxytocin, vasopressin, or parenting behaviors in fathers (Atzil et al., 2012; Kuo et al., 2012). In mothers, maternal sensitivity was positively associated with lateral PFC activity during the 18 months postpartum (Musser, Kaiser-Laurent, & Ablow, 2012), whereas in fathers, paternal sensitivity was negatively associated with the right OFC activity during the 2-4 weeks postpartum (Kuo et al., 2012). Therefore, parenting behaviors may be positively associated with the lateral PFC activity more strongly in mothers, while an opposite pattern in the OFC activity is characteristic of fathers. However, it should be noted that the right OFC is also involved in processing angry expressions and regulating aggression (Blair, 2001) and the lesion in the right OFC increases antisocial behaviors (Yang & Raine, 2009). Therefore, future research should examine the role of the reduced right OFC volumes in fathers may also be associated with parental aggression and processing of social threats to better characterize the right OFC plasticity in fathers.

We also explored relationships between paternal brain structural changes and depressive symptoms. In fathers, volume increases in the striatum and subgenual ACC were correlated with lower depressive symptoms at 12-16 weeks postpartum. This is similar to maternal brain activation findings in the caudate in response to baby cries being inversely associated with depressive symptoms at 18 months postpartum (Laurent & Ablow, 2012). A meta-analysis of structural brain imaging studies also indicates that decreases in the striatum and subgenual ACC volume are related to depression (Kirkpatrick et al., 1994). GM increases in these regions may be associated not only with parental motivations but also with the father's ability to regulate his emotions during the first 4 months postpartum. The correlations were driven by two of the physical depressive symptoms: difficulties in falling asleep and feeling tried. These physical symptoms may lead to depression if symptoms are chronic. However, it should be noted that all fathers in the current study reported none to a few symptoms of depression and no evidence of chronicity of these symptoms; thus, the generalization of the current finding to clinical depression is limited. Future work to compare clinically depressed and healthy fathers is needed.

There may be several factors that are related to changes in fathers' brains. Although endocrine regulation of human paternal behaviors is not well understood, there is evidence that a hormone, vasopressin, may be related to fathers' parenting motivation and changes in brain structure. Male prairie voles, a biparental species, have AVP receptors in brain regions including the olfactory bulb, hypothalamus, amygdala, and thalamus. Binding of AVP to vasopressin V1a receptors is critical for parenting behaviors including grooming, crouching over young, contacting, and retrieving pups (Seifritz et al., 2003). In biparental primates, parenting experience was associated with increased V1a receptors in fathers' brains (Kozorovitskiy et al., 2006). The increase in V1a receptors in the PFC, not in oxytocin or prolactin receptors, drove the enhanced density of dendritic spines on pyramidal neurons of the PFC in the marmoset fathers. Thus, vasopressin may contribute to structural changes in fathers' brains during the early postpartum period. The structural changes may also

be linked to individual differences in parenting experience. We have controlled for previous parenting experience, first-time vs. experienced father, in our analysis; however, we do not have information on how actively fathers were involved in their child's care throughout the first months. There may have been a wide range of parental involvement among fathers during this period, and future work is needed to examine the associations between individual parenting experiences and neural plasticity in fathers.

The findings should be considered in light of the following limitations. First, the GM changes in the current study have been compared with findings in neural activity among mothers and fathers in other studies. Training-included increases in GM volumes have been associated with increased levels of activations in the same regions (Hamzei, Glauche, Schwarzwald, & May, 2012; Ilg et al., 2008; Taubert, Lohmann, Margulies, Villringer, & Ragert, 2011). However, such an approach requires caution because increases in the neural activity in a particular region have not always been associated with the same trend with respect to volume. For instance, hyperactivation in the amygdala but decreased amygdala volumes have been observed in patients with major depressive disorders (Hamilton, Siemer, & Gotlib, 2008; Savitz et al., 2013) and posttraumatic stress disorders (Ganzel, Kim, Glover, & Temple, 2008; Shin, Rauch, & Pitman, 2006). Changes in functional activity but not in structure after learning have also been reported (Thomas et al., 2009). More studies with combined functional and morphometric MRI methods are needed to further investigate the associations between anatomical and functional changes in fathers during the early postpartum period. Second, the study has a relatively small sample size, which may have contributed to differences in findings between fathers and mothers. The study also includes a homogenous sample of Caucasian and middle- to high-socioeconomic status background. Therefore, the findings of the associations among neural changes and parental mood symptoms and behaviors need to be replicated in a larger sample of subjects with diverse backgrounds. Third, because our study is limited to changes during the first few months postpartum, it is unclear whether the structural changes may last beyond that period. In marmoset fathers, the structural increase in the PFC came back to the baseline as the offspring got older and fathers were less involved in parenting (Kozorovitskiy et al., 2006). Thus, it is possible that the structural changes we observed may be limited to the early postpartum period, but structural plasticity may also follow individual circumstances. Future studies may examine whether structures are maintained, or if other changes occur according to the level of fathers' parenting involvement over many years of a child's life. Last, although our findings suggest longitudinal changes in fathers' brains over the first few months, we must underline that the causal relations between the structural changes and these factors are still unclear. The structural changes may have reciprocal relations with mood regulation, increased experience of interacting with infants, and hormonal changes or other issues such as early life experience and poverty.

In the current study, we found longitudinal changes in GM over the first 4 months postpartum in human fathers. This postpartum period is critical for fathers to develop an emotional bond with their infants through their intense interactions. Indeed, these early father–infant interactions and emotional bonding become the basis of the fatherinfant attachment, which has a long-lasting impact on cognitive functions and social attachment for offspring (Feldman, Bamberger, et al., 2013; Parke, 2002; Ramchandani et al., 2011; van Ijzendoorn & Dewolff, 1997). The findings may thus lead to the identification of specific brain regions of potential importance for early father–infant attachment and mood symptoms. Further research is thus required to identify distinct changes in the parental brain among at-risk fathers in order to construct more specific and early interventions (Panter-Brick et al., in press) to prevent the onset of postpartum mood disorders and to optimize environments for child development.

## Supplementary material

Supplementary Table 1 is available via the 'Supplementary' tab on the article's online page (http://dx.doi.org/10.1080/17470919.2014.933713).

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