Fathers' involvement in early childcare is associated with amygdala resting-state connectivity

Lisa I. Horstman,[1,2] Madelon M.E. Riem, [1,3] Kim Alyousefi-van Dijk,[1,2] Anna M. Lotz,[1,2] and Marian J. Bakermans-Kranenburg[1,2]

[1]Clinical Child and Family Studies, Faculty of Behavioral and Movement Sciences, Vrije Universiteit, Amsterdam 1081 BT, The Netherlands
[2]Leiden Institute for Brain and Cognition, Leiden University Medical Center, Leiden 2300 RC, The Netherlands
[3]Behavioral Science Institute, Radboud University, Nijmegen 6500 HE, The Netherlands
Correspondence should be addressed to Madelon M.E. Riem, Clinical Child and Family Studies, Faculty of Behavioral and Movement Sciences, Vrije Universiteit, Van der Boechorststraat 1, Amsterdam, 1081 BT, The Netherlands. E-mail: madelon.hendricx-riem@ru.nl.

Abstract

Becoming a parent requires new skills and frequent task switching during daily childcare. Little is known about the paternal brain during the transition to fatherhood. The present study examined intrinsic neuronal network connectivity in a group of first-time expectant and new fathers (total $N = 131$) using amygdala seed-based resting-state functional connectivity analysis. Furthermore, we examined the association between paternal involvement (i.e. hours spent in childcare and real-time push notifications on smartphone) and connectivity within the parental brain network in new fathers. There were no significant differences in functional connectivity between expectant and new fathers. However, results show that in new fathers, time spent in childcare was positively related to amygdala connectivity with the supramarginal gyrus, postcentral gyrus and the superior parietal lobule—all regions within the cognition/mentalizing network that have been associated with empathy and social cognition. Our results suggest that fathers' time investment in childcare is related to connectivity networks in the parental brain.

Key words: resting-state functional connectivity; fathers; paternal involvement; amygdala; pregnancy

Becoming a parent requires a range of new skills, such as sensitivity to child signals, emotion recognition and frequent task switching between child-caring practices and other daily activities. Little is known about the paternal brain during the transition to fatherhood. Whereas maternal caregiving is triggered by physiological processes related to pregnancy and labor, the paternal brain is thought to adapt to the parental role through active involvement in childcare (Abraham *et al.*, 2014). Fathers' involvement in direct care of their child has increased during the past decade (Bakermans-Kranenburg *et al.*, 2019) and has been associated with fewer behavior problems, higher intelligence quotient scores, better educational outcomes and positive well-being of the child (Sarkadi *et al.*, 2008; Wilson and Prior, 2011). However, little is known about the neural mechanisms related to early fatherhood and how the paternal brain relates to involvement of fathers in infant care. Examining differences in the paternal brain before and after the transition to fatherhood may shed light on (changes in) neurobiological mechanisms during early fatherhood. In this study, we therefore examined the basic functional connectivity patterns in fathers-to-be and new fathers and explored how fathers' involvement in his child's life relate to these patterns, using resting-state functional magnetic resonance imaging (fMRI).

First-time fatherhood comes with many psychological, emotional and behavioral changes in fathers' lives (Genesoni and Tallandini, 2009). Exposure to a child has been associated with

hormonal changes in men (Rilling and Mascaro, 2017), especially in highly involved fathers (Gettler *et al.*, 2011). More specifically, Gettler *et al.* (2011) report that fathers who were involved in childcare for 3 hours or more a day had lower testosterone levels compared to fathers who were not involved in the caretaking of their child. Another study showed that paternal oxytocin levels increased within the first 6 months of fatherhood (Gordon *et al.*, 2010), and more involved fathers had higher levels of plasma oxytocin and lower levels of plasma testosterone (Mascaro *et al.*, 2014). These studies thus provide evidence that involvement in child-caring activities triggers hormonal changes. In mothers, hormonal changes are considered potential mediators of the morphometric brain changes during the transition to motherhood (Barba-Müller *et al.*, 2019). Previously observed hormonal changes in fathers may also be accompanied by changes in the paternal brain. However, neural changes during the transition to fatherhood remained largely unexplored. There is some evidence that the paternal brain shows structural changes during the transition to fatherhood. In one study with 16 new fathers, gray matter volume in regions involved in parental motivation, such as the hypothalamus and the amygdala, the striatum and the lateral prefrontal cortex, increased within months after the birth of the baby (Kim *et al.*, 2014). Another study found no gray mater volume changes in fathers compared to a male control group who stayed childless during the same period (Hoekzema *et al.*, 2017).

In addition to structural brain changes in the transition to parenthood, functional brain activity may change in the transition to fatherhood. Patterns of functional brain activation in fathers may differ from those in men without children. For example, mothers as well as fathers show increased activity in the amygdala during exposure to infant crying compared to non-parents (Seifritz *et al.*, 2003). The amygdala is one of the principal neural structures for emotional learning (Cardinal *et al.*, 2002), detection of emotionally salient stimuli (Anderson and Phelps, 2001), and a major site of neural plasticity (Pare *et al.*, 2004). It is part of the parental brain network, a network of brain regions that have been implicated in human caregiving (Swain *et al.*, 2014; Feldman, 2015). Non-parents showed lower amygdala reactivity to infant crying compared to parents (Seifritz *et al.*, 2003), and a previous longitudinal neuroimaging study showed heightened amygdala activation in first-time fathers both shortly before and after the birth of their child while watching infant-threatening situations (Van't Veer *et al.*, 2019). Heightened amygdala activity in response to potential threat to the infant may be adaptive as it may promote alertness and protective behaviors toward the child. Interestingly, disruptions of the basolateral amygdala are related to impairment in parental behavior, especially in males (Lee and Brown, 2007), and causes a reduction in paternal care (Kirkpatrick *et al.*, 1994).

The amygdala is a functional connectivity hub with projections to other cortical and subcortical regions that are important for emotion processing (Phelps and LeDoux, 2005). Moreover, it is functionally connected with other brain regions within the parental caregiving network (Abraham *et al.*, 2014). The parental caregiving network consists of a number of sub-networks; frontal brain regions and the anterior cingulate cortex (ACC) that are regions important for emotion regulation; the ventral striatum, a region involved in reward processing and salience; and regions involved in cognition/mentalizing, including the inferior frontal gyrus, orbitofrontal gyrus and the temporoparietal junction (Swain *et al.*, 2014; Witteman *et al.*, 2019). Previous studies have shown that connectivity within the parental caregiving network is related to parenting behaviors and may be flexible according to the demands of different stages of parenting (Kim *et al.*, 2016). For example, Atzil *et al.* (2011) found that synchronous and intrusive patterns of maternal care were related to discrete profiles of maternal brain connectivity during exposure to infant videos. In synchronous mothers who displayed sensitive caregiving behaviors such as coordination of gaze and vocalizations with infants, reactivity in reward areas correlated with activity in the inferior frontal gyrus and the medial frontal gyrus, visual and motor areas, and the parietal cortex. This may indicate that connectivity between reward areas and regions involved in attention and social information processing is distinctive for synchronous mother–infant interaction. In contrast, intrusive mothers showed greater amygdala connectivity with frontal regions, possibly reflecting elevated anxiety.

Other studies indicate that functional connectivity within the parental caregiving network is sensitive to childcare experiences. Dufford *et al.* (2019) showed that the strength of amygdala connectivity in mothers increased linearly in the postpartum period. Resting-state functional connectivity between the amygdala and reward areas was greater during the late postpartum period than in the early postpartum period (Dufford *et al.*, 2019). Notably, functional connectivity was examined at 'rest', in the absence of external stimuli. Hence, the intrinsic functional connectivity in mothers increased during the first months postpartum. It is, however, unknown whether this increase reflects an association with

an increase in caregiving experiences or is related to changes in the infant–caregiver relationship in the first months after birth, when the infant becomes a more active partner in the interaction with the parent. Moreover, it is unknown whether and how childcare experiences relate to functional resting-state connectivity in fathers. The effects of amount of contact and exposure to the child may be particularly important in fathers, who do not directly experience the physiological changes associated with a gestation (Brunton and Russell, 2008; Cardenas *et al.*, 2020). Indeed, fathers' functional connectivity between the amygdala and the superior temporal sulcus when they were exposed to infant stimuli was found to be positively related to the amount of time they spent in direct childcare (Abraham *et al.*, 2014). This suggests that spending time in childcare is related to increased connectivity between parenting-related brain areas. However, no study so far has examined fathers' functional connectivity at rest in the period before and after the birth of their first child.

In order to shed more light on the paternal brain during the transition to fatherhood, the present study will examine the functional connectivity between fathers expecting their first child (during the second half of the pregnancy) and new fathers (after the birth of their first baby). We focused on amygdala connectivity with seed-based correlation analysis because the amygdala has been shown to be a part of the main parental network structures and plays an important role in the perception of infant cues (Swain *et al.*, 2014). Moreover, previous studies found that amygdala connectivity specifically increased in the postpartum months in mothers (Dufford *et al.*, 2019) and was positively related to involvement of fathers (Abraham *et al.*, 2014). We firstly expected to find amygdala connectivity with other parental brain networks in both expectant fathers and new fathers. As parenting behaviors might require increased neural communication within the parental networks, we hypothesized that new fathers would show heightened amygdala connectivity with parental brain regions compared to expectant fathers. Secondly, we examined whether the strength of these parental brain network communications in new fathers would be associated with their level of involvement in childcare activities. We anticipated that higher levels of paternal involvement with daily childcare were related to stronger amygdala resting-state functional connectivity (rsFC) to parental brain networks. To our knowledge, this study is the first to examine rsFC in expectant fathers *vs* new fathers.

Method
Participants

Expectant and new fathers were recruited via online advertisement and through midwife practices. New fathers were also informed about the study by the municipality of a major city in the Netherlands. When fathers showed interest in the study, more detailed information on the study was sent. Participants were screened on inclusion criteria during telephone interviews. To be eligible for participation in the study, participants had to be cohabitating with their partner and (expecting) a healthy infant and able to read and speak Dutch. Exclusion followed when participants had nonremovable metallic parts in their body, self-reported neurological, neuroendocrine and psychiatric disorders, claustrophobia, or alcohol/substance abuse. Expectant fathers were excluded when their partners used tobacco, alcohol or illicit drugs during the pregnancy or had a body mass index over 30 before pregnancy. Partners of expected fathers had to have uncomplicated singleton pregnancies, which was confirmed by a standard 20-week medical ultrasound via their

health-care service. In addition, new fathers with premature babies (born before 37 weeks) were also excluded from participation. One infant was born at 36 weeks and 6 days, but was considered healthy and did not receive medical care. One father was not the biological father of the infant, but had been cohabitating with the mother since mid-pregnancy.

Our study had a between-subject design. A total of 62 expectant and 69 new fathers participated in the study. The measurements reported here were parts of the first assessments of a larger study. Fathers were either expecting their first child or just had their first child. Two expectant fathers dropped out of the MRI session due to dental braces that warmed up and claustrophobic anxiety while lying in the scanner. Four expectant fathers were excluded from analyses due to medication intake on assessment day ($n = 2$) or corrupt resting-state data ($n = 2$). One new father dropped out of the MRI session because of claustrophobic anxiety during scanning and one new father had corrupt data and was therefore excluded from analyses. Thus, a total sample of 56 expectant and 66 new fathers were included in the analyses. Mean age of the expectant fathers was 32.75 years (s.d. = 2.97) and mean age of the new fathers was 33.16 years (s.d. = 4.85). Partners of expectant fathers had a gestational age of 18–31 weeks and new fathers were included when the age of the infant was 7.5–21.5 weeks. The mean gestational age of the child in the group of expectant fathers was 25.58 weeks (s.d. = 4.58) and the mean age of the infant in the group of new father was 11.32 weeks (s.d. = 3.07).

Procedure

Sessions took place at the Leiden University Medical Centre where the participants performed some behavioral tasks, filled out questionnaires and underwent (f)MRI measurements. Participants were asked to refrain from alcohol and caffeine 24 hours prior to the visit. During MRI measurements, participants lay in the supine position where the head was restrained with additional padding to minimize head movement during scanning. During the resting-state task, we asked participants to look at a fixation cross that was shown on the screen which was visible through a mirror on top of the head coil. Participants were instructed to keep their eyes focused on the fixation cross during the entire length of the scan and to not close their eyes or fall asleep. After completion, all participants were asked whether they had not fallen asleep. Additionally, new fathers were instructed to download an app that would deliver week-long notifications and questions about their whereabouts and involvement in childcare, in the week following the lab visit. Lastly, all participants received an online questionnaire at home with items on basic demographics and depressive symptoms. New fathers received additional questions on their direct involvement in caregiving activities.

Participants were reimbursed for their time and travel costs. The study was approved by the Ethics Committees of the Department of Education and Child Studies at Leiden University and the Leiden University Medical Centre. The study was carried out in accordance with the Declaration of Helsinki and all participants gave written informed consent prior to the start of the session.

Measures
Paternal involvement

For the daily real-time assessment of paternal involvement in new fathers, participants received notifications via an app installed on their smartphones for 7 days, starting the day after the lab session. Notifications were sent on six different time points per day.

They were sent at a random moment within time slots (i.e. 9–10 am, 11–12 am, 1–2 pm, 3–4 pm, 7–8 pm and 9–10 pm). Questions were visible for 1 hour before they disappeared from the screen. The notifications started with the question whether the participant had thought about, spoken about or communicated with their baby in the past 15 minutes. The next question was whether he had been near his baby in the past 15 minutes. If yes, the follow-up question was if he had interacted with the child when their child was awake (see Supplementary Figure S1 in Supplementary Material for a flowchart of questions). Scores of 0 were given when participants answered 'no' and 1 when they answered 'yes' on each question. A score for involvement was based on the response to the first question and the number of times they had interacted with their child when they were near their baby and their baby was awake (i.e. when they had the opportunity to interact with their baby). A mean score was calculated in which higher scores indicated more involvement with their child. As missing data are inevitable within daily monitoring, completion rates for the smartphone application data were calculated as the percentage of valid responses to the first question, because participants were likely to complete all questions once they completed the first question (95–100%). Fathers showed a mean response rate of 58.74% (s.d. = 24.78). Nine fathers did not fill out the daily app due to technical problems ($n = 7$), lack of a smartphone ($n = 1$) or drop-out after the first lab session ($n = 1$). Little's missing completely at random (MCAR) test indicated that data were missing completely at random (chi-square = 3257.94, $P = 0.97$). Inspection of skewness and kurtosis showed no deviation from normal score distribution.

Furthermore, hours spent in direct childcare were measured via an online self-reported questionnaire that participants received at home in the week following the lab session. They were asked to indicate the number of hours they spent in direct childcare for all separate days of the week, counting only time that father and child were both awake. Visual inspection of boxplots in combination with corresponding z-values indicated one outlier ($z > 3.29$) that was therefore winsorized (Tabachnick and Fidell, 2007). Mean scores were calculated to indicate the amount of direct childcare per week in hours ($M = 5.29$, s.d. = 2.36). Data were missing for four participants who did not fill out the questionnaire ($n = 3$) or dropped out after the first lab session ($n = 1$), resulting in a sample of 62 fathers for analyses on the involvement in direct childcare.

Self-reported hours spent in direct childcare and involvement as measured with the app were significantly correlated ($r = 0.386$, $P = 0.004$).

Perinatal depression

The Edinburgh Postnatal Depression Scale (EPDS) is a self-reported questionnaire measuring mild postnatal depression (Cox et al., 1987, Dutch version translated by Pop, 1991). It is widely used and well validated to detect depression in mothers during the perinatal period and has also been shown valid for the assessment of depression in fathers (Matthey et al., 2001; Edmondson et al., 2010). It comprises 10 symptoms scored on a scale for severity ranging from 0 (absent) to 4 (severe). A sum of scores was calculated for each participant with higher scores meaning more depressive symptoms. The relevant depression cutoff score for fathers is 10 (Edmondson et al., 2010). Depression has been documented to affect several resting-state networks (Mulders et al., 2015); therefore, we included depression as a covariate in our analyses. Mean scores of the expectant fathers were 4.20 (s.d. = 3.22) and new fathers had a mean score of 3.15 (s.d. = 2.89).

In our sample, Cronbach's alpha of the EPDS was 0.75. Depression scores were not significantly different between the groups [$t(115) = 1.88$, $P = 0.06$].

MRI data acquisition

Whole brain fMRI data were obtained on a 3T Philips Achieva TXMRI system (Philips Medical Systems, Best, the Netherlands) at the Leiden University Medical Centre. Resting-state functional connectivity was obtained with a T2-weighted gradient-echo echo-planar imaging sequence. Functional data were collected using the following sequences: repetition time (TR) = 2200 ms, echo time (TE) = 30 ms, flip angle = 80°, 38 transverse slices and voxel resolution of 2.75 × 2.75 × 3.03 mm (200 volumes). A T1-weighted anatomical scan was obtained with TR = 7.9 ms, TE = 3.5 ms, flip angle = 8°, 155 transverse slices and voxel size 1.0 × 1.0 × 1.1 mm. Preprocessing of the imaging data was performed using fMRIPrep 1.5.2 (Esteban *et al.*, 2019), see Supplementary Material for preprocessing steps.

Statistical analysis

A seed-based correlation approach was used (Lee *et al.*, 2013). We created binary masks of the left and right amygdala using the Harvard–Oxford Subcortical Atlas. Amygdala masks were not thresholded. After transformation to native space, the mean time series for each participant were extracted from the voxels in the seed regions. The times series of the left and right amygdala were then entered as regressors in two separate general linear models within FMRIB Software Library (FSL) FMRI Expert Analysis Tool (FEAT; https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT) to examine amygdala connectivity. In addition, cerebrospinal fluid and white matter signals were added as regressors to the model in order to reduce the influence of artifacts caused by physiological signal sources on the results. The global signal was not added to the model, as there is no consensus on the use of this regressor (Almgren *et al.*, 2020).

The temporal derivative of each regressor was added to the model, resulting in six regressors. Contrasts of interest were the parameter estimates corresponding to the regressor of the left and right amygdala, which represents functional connectivity with that region. First-level analyses were performed in native space. These first-level contrast images and the corresponding variance images of connectivity with each seed region were transformed to standard space and submitted to second-level mixed-effects group analyses using FMRIB's Local Analysis of Mixed Effects. Secondary level analysis was performed on both the expectant group and the new fathers group for left and right amygdala connectivity. Because of the prominence of the parental brain network in previous fMRI studies with parents, region of interest analyses were performed with the arousal/salience network (the nucleus accumbens), emotion regulation network (the medial frontal cortex and the ACC), and the cognition network (the insula, superior frontal gyrus, orbitofrontal gyrus, frontal pole, inferior frontal gyrus, and the temporoparietal junction), based on Swain *et al.* (2014). The temporoparietal junction comprised the supramarginal gyrus, posterior superior temporal gyrus, posterior superior temporal sulcus and angular gyrus, similar to Igelstrom *et al.* (2015). Regions were anatomically defined with the Harvard–Oxford (Sub)cortical Atlas and used as one single inclusive mask.

Group means were tested using one-sample *t*-tests and group differences were tested using two-sample *t*-tests comparing the expectant and new fathers. In addition, in the group of new fathers, the correlation between amygdala connectivity and paternal involvement was assessed. Hours spent in direct child-care and paternal involvement as measured with the app were assessed in separate analyses. Age of the father, educational level and depressive symptoms were added to the model as confound regressors in all higher-level analyses. See Supplementary Table S2 for mean scores of expectant and new fathers on these variables. Educational level was lower in new fathers and was therefore included as covariates in all analyses. Hours of involvement were significantly related to depressive symptoms ($r = -0.26$, $P = 0.04$). We also explored whether involvement was related to quality of sleep, but it was unrelated ($r = 0.11$, $P = 0.52$). Quality of sleep was therefore not included as a covariate. Group comparisons and associations between amygdala connectivity and parental involvement for new fathers were assessed non-parametrically using FSL's Randomize tool, incorporating threshold-free cluster enhancement (TFCE), with 5000 iterations. Statistical maps were thresholded at $P < 0.05$. We used TFCE, embedded in Randomize in FSL, because this method gives generally better sensitivity than cluster-based thresholding over a wide range of test signal shapes and signal-to-noise values (Smith and Nichols, 2019). A mask was created for connectivity regions significantly associated with involvement and used as input for a featquery extracting the individual mean z-values for illustration purposes.

Results

Functional connectivity

The analyses revealed no significant differences in left or right amygdala connectivity with parental brain network regions between expectant and new fathers. Both groups showed significant left and right amygdala connectivity with regions within the emotion regulation network, including the medial frontal cortex and ACC, and the cognition network, including the insula, orbitofrontal gyrus, superior frontal gyrus, frontal pole, inferior frontal gyrus and the temporoparietal junction. Figure 1 shows a trend toward heightened amygdala connectivity with parental brain regions for new fathers compared with expectant fathers, but the difference is not significant. For both expectant and new fathers one large cluster was identified in the analyses with the left and right amygdala with peak z-values in the pre- and post-central gyrus. See Supplementary Table S1 of Supplementary Material for cluster table.

In new fathers, there was no main effect of paternal involvement as measured with the application on amygdala connectivity. However, a main effect of hours spent in direct childcare on amygdala connectivity was found. More hours spent in direct child-care were associated with greater connectivity between the right amygdala and the supramarginal gyrus, postcentral gyrus and the superior parietal lobule ($P < 0.05$, TFCE, family-wise error (FWE) corrected), see Figures 2 and 3. Following a reviewer's suggestion, functional connectivity analyses were repeated with child's age as a covariate. Amygdala connectivity was unrelated to child's age. Analyses were repeated without controlling for depressive symptoms, but the results did not change. In addition, analyses with involvement scores as measured with the application were repeated with missing data imputed based on the regression equation predicting involvement from number of hours spent in childcare. Analyses with imputed data did not show significant associations with the supramarginal gyrus ($r = 0.12$, $P = 0.35$), postcentral gyrus ($r = 0.14$, $P = 0.27$) and the superior parietal lobule ($r = 0.18$, $P = 0.16$).
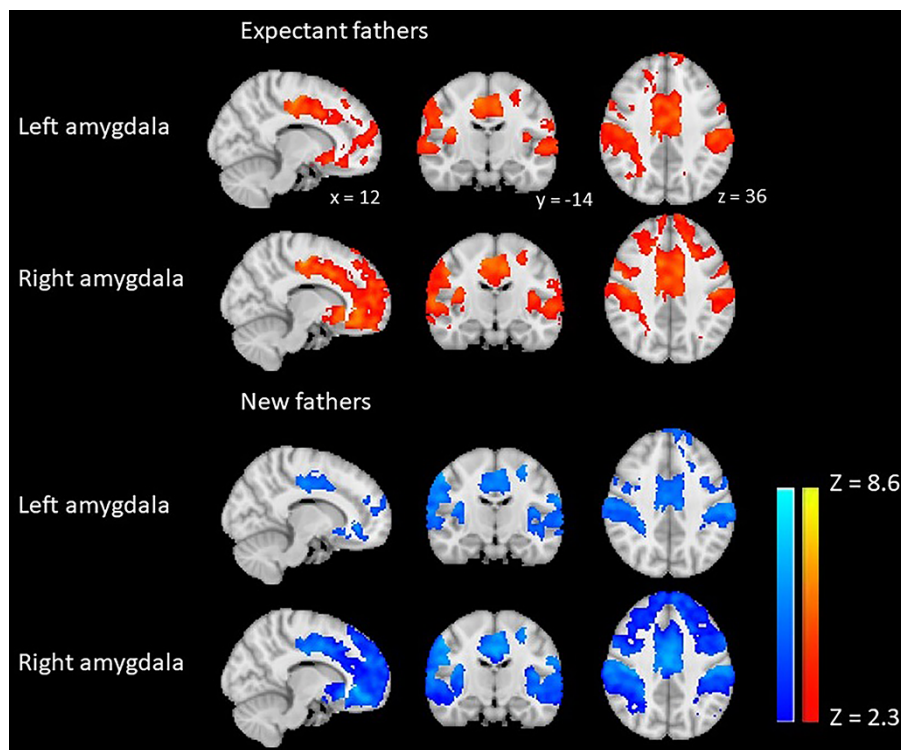
Fig. 1. Right and left amygdala connectivity with parental brain regions in expectant fathers (upper panel/red) and new fathers (lower panel/blue). Images are z-statistics shown at a threshold of $z > 2.3$ and $P < 0.05$ corrected for illustrative purpose, overlaid on the MNI-152 standard brain, controlled for age, educational level and depressive symptoms. The left hemisphere of the brain corresponds to the right side in this image.
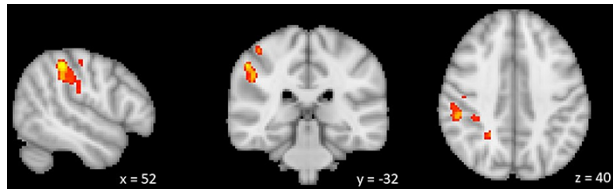

Fig. 2. Significant association between hours spent in childcare by new fathers and right amygdala connectivity with the supramarginal gyrus, postcentral gyrus, and the superior parietal lobule, TFCE, FWE corrected, $P < 0.05$, controlled for age, educational level and depressive symptoms, overlaid on the MNI-152 standard brain. Cluster size $N = 1526$ voxels, MNI coordinates max t: $x = 19$, $y = 46$, $z = 58$. The left hemisphere of the brain corresponds to the right side in this image.

Discussion

The current study is the first to examine resting-state functional connectivity in expectant and new fathers in order to shed more light on neural mechanism underlying early fatherhood. We hypothesized that higher levels of paternal involvement in daily childcare would be related to stronger amygdala rsFC to parental brain networks. We indeed found that time spent in direct childcare was associated with increased connectivity of the right amygdala with the supramarginal gyrus, postcentral gyrus and the superior parietal lobe—structures that previously have been related to recognizing and processing infant cues in fathers (Kuo *et al.*, 2012) and are part of the cognition/mentalizing module of Swain *et al.* (2014)'s model. Moreover, Abraham *et al.* (2014) found that in fathers who were watching videos of their own child, increased amygdala connectivity with the superior temporal sulcus, also part of this cognition/mentalizing network, was related

to increased time spent in childcare. Our study extends the literature by showing that not only task-related connectivity but also resting-state connectivity is related to fathers' time spent in childcare. The amount of child-caring experiences might be especially important for fathers, since mothers are more physiologically prepared to motherhood (Brunton and Russell, 2008).

The other hypothesis of the study was that new fathers compared to expectant fathers would show increased amygdala connectivity with brain regions in the parental brain network. We found that both expectant fathers and new fathers showed significant functional connectivity between the amygdala and emotion regulation and cognition networks that are part of the parental brain, but there were no significant differences between the two groups. There was a trend toward increased connectivity between the amygdala and resting-state networks, especially in frontal areas, in new fathers compared to expectant fathers. This might point to an overall increase in brain activation during a state of rest in new fathers. However, as our design is not longitudinal, future research should explore this observed difference to examine whether it is supported by within-subject changes in the transition to fatherhood.

Contrary to our expectations, paternal involvement, as measured with the smartphone application, was not associated with amygdala connectivity in new fathers. An explanation might be that the application measures a different type of involvement. Whereas hours spent in childcare may reflect quantity of involvement, involvement as measured with the application may be more closely related to quality of involvement as the questions assessed cognitive/affective involvement and engagement with the child. It is possible that brain connectivity after the transition to fatherhood is more related to fathers' intensity of childcare
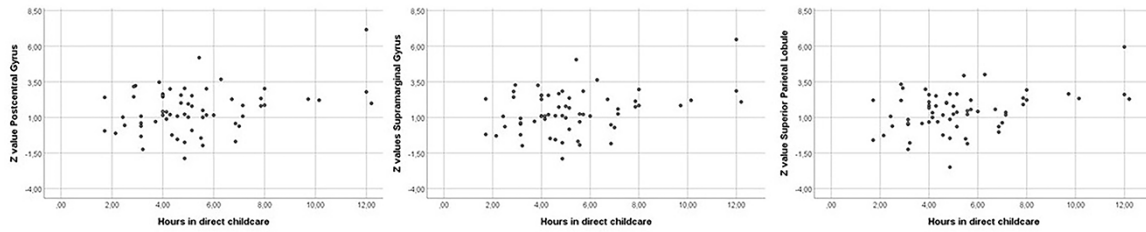
Fig. 3. Mean z-values of the supramarginal gyrus, superior parietal lobule and the postcentral gyrus (extracted using featquery) and hours spent in direct childcare. More time spent in direct childcare was associated with increased connectivity between the right amygdala and the right supramarginal gyrus ($r = 0.34$, $P < 0.01$), superior parietal lobule ($r = 0.39$, $P < 0.01$) and postcentral gyrus ($r = 0.34$, $P < 0.01$).

experiences rather than their quality. Indeed, time spent in direct childcare was only weakly related to involvement as measured with the smartphone application. The fact that the push notifications were mainly given throughout the day may also play a role here: it is possible that fathers were involved at other moments, for example during the night.

Parents need to recognize the emotions of the child to be able to respond appropriately and provide adequate care. The supramarginal gyrus, together with the postcentral gyrus, is an important hub in social cognition (Silani *et al.*, 2013) and emotional empathy (Hooker *et al.*, 2008; Nummenmaa *et al.*, 2008; Hoffmann *et al.*, 2016; Seehausen *et al.*, 2016), which are both crucial for providing adequate parental care. Increased connectivity between the amygdala and the mentalizing/cognition network may facilitate emotion processing, thereby promoting sensitive fathering. However, deficits in emotion regulation increase the risk of psychopathology (McLaughlin *et al.*, 2011) and are associated with negative parenting behaviors (Lovejoy *et al.*, 2000; Wilson and Durbin, 2010). Divergent amygdala–supramarginal gyrus connectivity has been linked to both general anxiety and social anxiety disorders (Pannekoek *et al.*, 2013; Makovac *et al.*, 2016; Jung *et al.*, 2018), and increased connectivity between the postcentral gyrus and the emotional network was related to heightened anxiety level (Yin *et al.*, 2018). This coupling may be associated with an increased need to downregulate emotions. The need to downregulate intensified and worrying emotions may indeed occur in fathers during the first weeks and months of new fatherhood. An important task for new fathers is effectively managing emotional and potentially distressing situations, for example when calming a crying infant. Identifying potential threats for the child's safety has been found to trigger brain activity in the amygdala in expectant fathers (Van't Veer *et al.*, 2019) and new fathers (Lotz *et al.*, 2020) when they were exposed to infant-threatening videos. Interestingly, a recent meta-analysis reports right lateralization for infant cry perception (Witteman *et al.*, 2019), which is in line with our finding of right lateralization of the effect of hours in direct childcare. Increased coupling between the cognition and emotion networks in fathers spending more time in childcare may suggest a heightened state of alertness, promoting accurate perception of infant signals.

It is currently unclear whether this heightened connectivity is related to positive or negative parental outcomes. It is tempting to think that parents who spend more time with their child will be more aware of the needs and emotions of their child and as a result will show more adequate or sensitive care than parents who are less involved in childcare activities. Indeed, previous research has shown that fathers who engaged in more caregiving activities are more likely to have securely attached infants (Fuertes *et al.*, 2016). It is important to understand the link between paternal involvement and the neurobiology of fatherhood, because of the known positive effects of father involvement in the development of their child (Sarkadi *et al.*, 2008; Wilson and Prior, 2011). This paper is the first study exploring resting-state networks connectivity related to fatherhood. In future studies, other parental regions need to be examined to get more insight into the overall resting-state connectivity in the male brain during the first phase of fatherhood. A major strength of the current study is the relatively large group size, limiting power problems that are often observed in neuroimaging studies (Button *et al.*, 2013). Another strength of the study is the extensive assessment of paternal involvement using two types of measurements: online questionnaire and real-time push notifications on a smartphone. Real-time measurements through app notifications are considered to reflect real-time feelings and behaviors at the time of assessment (Sonck and Fernee, 2013), avoiding recall problems. This may provide more reliable insights into parental thoughts and behaviors than standard questionnaires. Further validation of the application to measure parental involvement is however necessary. For the measurement of different types of paternal involvement, further research could examine more closely differences between quantity and quality of paternal involvement, which can also have divergent effects on child development (Moroni *et al.*, 2015).

Some limitations should be noted. The between-subject design of the study implies the risk of differences between the two groups, hampering the comparison. Definitive conclusions about the direction of the association between hours spent in child care and amygdala connectivity cannot be drawn. Longitudinal studies are required to further examine neuronal changes in the transition to fatherhood. Second, the amount of missing data in the app measurement of father involvement may be an explanation for the absence of an effect with this measure. Furthermore, we did not include men without children, and new fathers participated in the first 4 months after the child's birth, which is a relatively short period of time to adjust to fatherhood. A longitudinal study, starting before pregnancy, during pregnancy and following fathers over the first year after the birth of their first child, including measures of both quality and quantity of paternal involvement, would be optimal to examine the effects of fatherhood on new fathers' brains. In addition, future research should include other regions that are part of the parental brain network, for a better overview of brain connectivity during the early stages of fatherhood. Our findings do however suggest that fathers' time investment in caregiving is related to brain malleability in parental brain networks.

Conflict of interest

The author declared that they had no conflict of interest with respect to their authorship or the publication of this article.

Author contributions

L.H.: conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, visualization and project administration. M.R.: conceptualization, methodology, formal analysis, investigation, writing—review and editing, visualization and supervision. K.A-v.D: investigation, data curation, review and editing, and project administration. A.L.: investigation, data curation, review and editing, and project administration. M.J.B-K.: conceptualization, methodology, writing—review and editing, formal analysis, supervision and funding acquisition.

Supplementary data

Supplementary data are available at *SCAN* online.

References

Abraham, E., Hendler, T., Shapira-Lichter, I., Kanat-Maymon, Y., Zagoory-Sharon, O., Feldman, R. (2014). Father's brain is sensitive to childcare experiences. *Proceedings of the National Academy of Sciences of the United States of America*, **111**(27), 9792–7.

Almgren, H., Van de Steen, F., Razi, A., Friston, K., Marinazzo, D. (2020). The effect of global signal regression on DCM estimates of noise and effective connectivity from resting state fMRI. *NeuroImage*, **208**, 116435.

Anderson, A.K., Phelps, E.A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, **411**(6835), 305–9.

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.

Bakermans-Kranenburg, M.J., Lotz, A., Alyousefi-van Dijk, K., Van, I.M. (2019). Birth of a father: fathering in the first 1,000 days. *Child Development Perspectives*, **13**(4), 247–53.

Barba-Müller, B., Craddock, S., Carmona, S., Hoekzema, E. (2019). Brain plasticity in pregnancy and the postpartum period: links to maternal caregiving and mental health. *Archives of Women's Mental Health*, **22**, 289–99.

Brunton, P.J., Russell, J.A. (2008). The expectant brain: adapting for motherhood. *Nature Reviews: Neuroscience*, **9**(1), 11–25.

Button, K.S., Ioannidis, J.P., Mokrysz, C., *et al.* (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nature Reviews: Neuroscience*, **14**(5), 365–76.

Cardenas, E.F., Kujawa, A., Humphreys, K.L. (2020). Neurobiological changes during the peripartum period: implications for health and behavior. *Social Cognitive and Affective Neuroscience*, **15**, 1097–1010.

Cardinal, R.N., Parkinson, J.A., Hall, J., Everitt, B.J. (2002). Emotion and motivation: the role of the amygdala, ventral striatum, and prefrontal cortex. *Neuroscience and Biobehavioral Reviews*, **26**(3), 321–52.

Cox, J.L., Holden, J.M., Sagovsky, R. (1987). Detection of postnatal depression: development of the 10-item Edinburgh Postnatal Depression Scale. *The British Journal of Psychiatry*, **150**(6), 782–6.

Dufford, A.J., Erhart, A., Kim, P. (2019). Maternal brain resting-state connectivity in the postpartum period. *Journal of Neuroendocrinology*, **31**(9), e12737.

Edmondson, O.J., Psychogiou, L., Vlachos, H., Netsi, E., Ramchandani, P.G. (2010). Depression in fathers in the postnatal period: assessment of the Edinburgh Postnatal Depression Scale as a screening measure. *Journal of Affective Disorders*, **125**(1–3), 365–8.

Esteban, O., Markiewicz, C.J., Blair, R.W., *et al.* (2019). fMRIPrep: a robust preprocessing pipeline for functional MRI. *Nature Methods*, **16**(1), 111–6.

Feldman, R. (2015). The adaptive human parental brain: implications for children's social development. *Trends in Neurosciences*, **38**(6), 387–99.

Fuertes, M., Faria, A., Beeghly, M., Lopes-dos-santos, P. (2016). The effects of parental sensitivity and involvement in caregiving on mother-infant and father-infant attachment in a Portuguese sample. *Journal of Family Psychology*, **30**(1), 147–56.

Genesoni, L., Tallandini, M.A. (2009). Men's psychological transition to fatherhood: an analysis of the literature, 1989–2008. *Birth*, **36**(4), 305–18.

Gettler, L.T., McDade, T.W., Feranil, A.B., Kuzawa, C.W. (2011). Longitudinal evidence that fatherhood decreases testosterone in human males. *Proceedings of the National Academy of Sciences*, **108**(39), 16194–9.

Gordon, I., Zagoory-Sharon, O., Leckman, J.F., Feldman, R. (2010). Oxytocin and the development of parenting in humans. *Biological Psychiatry*, **68**(4), 377–82.

Hoekzema, E., Barba-Muller, E., Pozzobon, C., *et al.* (2017). Pregnancy leads to long-lasting changes in human brain structure. *Nature Neuroscience*, **20**(2), 287–96.

Hoffmann, F., Koehne, S., Steinbeis, N., Dziobek, I., Singer, T. (2016). Preserved self-other distinction during empathy in autism is linked to network integrity of right supramarginal gyrus. *Journal of Autism and Developmental Disorders*, **46**(2), 637–48.

Hooker, C.I., Verosky, S.C., Germine, L.T., Knight, R.T., D'Esposito, M. (2008). Mentalizing about emotion and its relationship to empathy. *Social Cognitive and Affective Neuroscience*, **3**(3), 204–17.

Igelstrom, K.M., Webb, T.W., Graziano, M.S. (2015). Neural processes in the human temporoparietal cortex separated by localized independent component analysis. *The Journal of Neuroscience*, **35**(25), 9432–45.

Jung, Y.H., Shin, J.E., Lee, Y.I., Jang, J.H., Jo, H.J., Choi, S.H. (2018). Altered amygdala resting-state functional connectivity and hemispheric asymmetry in patients with social anxiety disorder. *Frontiers in Psychiatry*, **9**, 164.

Kim, P., Rigo, P., Mayes, L.C., Feldman, R., Leckman, J.F., Swian, J.E. (2014). Neural plasticity in fathers of human infants. *Social Neuroscience*, **9**(5), 522–35.

Kim, P., Strathearn, L., Swain, J.E. (2016). The maternal brain and its plasticity in humans. *Hormones and Behavior*, **77**, 113–23.

Kirkpatrick, B., Carter, C.S., Newman, S.W., Insel, T.R. (1994). Axon-sparing lesions of the medial nucleus of the amygdala decrease affiliative behaviors in the prairie vole (Microtus ochrogaster):

behavioral and anatomical specificity. *Behavioral Neuroscience*, **108**(3), 501–13.

Kuo, P.X., Carp, J., Light, K.C., Grewen, K.M. (2012). Neural responses to infants linked with behavioral interactions and testosterone in fathers. *Biological Psychology*, **91**(2), 302–6.

Lee, A.W., Brown, R.E. (2007). Comparison of medial preoptic, amygdala, and nucleus accumbens lesions on parental behavior in California mice (Peromyscus californicus). *Physiology and Behavior*, **92**(4), 617–28.

Lee, M.H., Smyser, C.D., Shimony, J.S. (2013). Resting-state fMRI: a review of methods and clinical applications. *American Journal of Neuroradiology*, **34**(10), 1866–72.

Lotz, A.M., Verhees, M., Horstman, L.I., *et al.* (2020). Exploring the hormonal and neural correlates of paternal protective behavior to their infants. *Developmental Psychobiology*, **63**, 1358–69.

Lovejoy, M.C., Graczyk, P.A., O'Hare, E., Neuman, G. (2000). Maternal depression and parenting behavior: a meta-analytic review. *Clinical Psychology Review*, **20**(5), 561–92.

Makovac, E., Meeten, F., Watson, D.R., *et al.* (2016). Alterations in amygdala-prefrontal functional connectivity account for excessive worry and autonomic dysregulation in generalized anxiety disorder. *Biological Psychiatry*, **80**(10), 786–95.

Mascaro, J.S., Hackett, P.D., Rilling, J.K. (2014). Differential neural responses to child and sexual stimuli in human fathers and nonfathers and their hormonal correlates. *Psychoneuroendocrinology*, **46**, 153–63.

Matthey, S., Barnett, B., Kavanagh, D.J., Howie, P. (2001). Validation of the Edinburgh Postnatal Depression Scale for men, and comparison of item endorsement with their partners. *Journal of Affective Disorders*, **64**(2–3), 175–84.

McLaughlin, K.A., Hatzenbuehler, M.L., Mennin, D.S., Nolen-Hoeksema, S. (2011). Emotion dysregulation and adolescent psychopathology: a prospective study. *Behaviour Research and Therapy*, **49**(9), 544–54.

Moroni, S., Dumont, H., Trautwein, U., Niggli, A., Baeriswyl, F. (2015). The need to distinguish between quantity and quality in research on parental involvement: the example of parental help with homework. *The Journal of Educational Research*, **108**(5), 417–31.

Mulders, P.C., van Eijndhoven, P.F., Schene, A.H., Beckmann, C.F., Tendolkar, I. (2015). Resting-state functional connectivity in major depressive disorder: a review. *Neuroscience and Biobehavioral Reviews*, **56**, 330–44.

Nummenmaa, L., Hirvonen, J., Parkkola, R., Hietanen, J.K. (2008). Is emotional contagion special? An fMRI study on neural systems for affective and cognitive empathy. *NeuroImage*, **43**(3), 571–80.

Pannekoek, J.N., Veer, I.M., van Tol, M.J., *et al.* (2013). Resting-state functional connectivity abnormalities in limbic and salience networks in social anxiety disorder without comorbidity. *European Neuropsychopharmacology*, **23**(3), 186–95.

Pare, D., Quirk, G.J., Ledoux, J.E. (2004). New vistas on amygdala networks in conditioned fear. *Journal of Neurophysiology*, **92**(1), 1–9.

Phelps, E.A., LeDoux, J.E. (2005). Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron*, **48**(2), 175–87.

Rilling, J.K., Mascaro, J.S. (2017). The neurobiology of fatherhood. *Current Opinion in Psychology*, **15**, 26–32.

Sarkadi, A., Kristiansson, R., Oberklaid, F., Bremberg, S. (2008). Fathers' involvement and children's developmental outcomes: a systematic review of longitudinal studies. *Acta Paediatrica*, **97**(2), 153–8.

Seehausen, M., Kazzer, P., Bajbouj, M., *et al.* (2016). Effects of empathic social responses on the emotions of the recipient. *Brain and Cognition*, **103**, 50–61.

Seifritz, E., Esposito, F., Neuhoff, J.G., *et al.* (2003). Differential sex-independent amygdala response to infant crying and laughing in parents versus nonparents. *Biological Psychiatry*, **54**(12), 1367–75.

Silani, G., Lamm, C., Ruff, C.C., Singer, T. (2013). Right supramarginal gyrus is crucial to overcome emotional egocentricity bias in social judgments. *The Journal of Neuroscience*, **33**(39), 15466–76.

Smith, S.M., Nichols, T.E. (2019). Threshold-free cluster enhancement: addressing problems of smoothing, threshold dependence and localisation in cluster inference. *NeuroImage*, **44**, 83–98.

Sonck, N., Fernee, H. (2013). Using smartphones in survey research: a multifunctional tool. *Institute for Social Research*.

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.

Tabachnick, B.G., Fidell, L.S. (2007). *Using Multivariate Statistics*. 5th edn, New York: Pearson/Allyn and Bacon.

Van't Veer, A.E., Thijssen, S., Witteman, J., van Ijzendoorn, M.H., Bakermans-Kranenburg, M.J. (2019). Exploring the neural basis for paternal protection: an investigation of the neural response to infants in danger. *Social Cognitive and Affective Neuroscience*, **14**(4), 447–57.

Wilson, K.R., Prior, M.R. (2011). Father involvement and child well-being. *Journal of Paediatrics and Child Health*, **47**(7), 405–7.

Wilson, S., Durbin, C.E. (2010). Effects of paternal depression on fathers' parenting behaviors: a meta-analytic review. *Clinical Psychology Review*, **30**(2), 167–80.

Witteman, J., Van, I.M.H., Rilling, J.K., Bos, P.A., Schiller, N.O., Bakermans-Kranenburg, M.J. (2019). Towards a neural model of infant cry perception. *Neuroscience and Biobehavioral Reviews*, **99**, 23–32.

Yin, Z., Chang, M., Wei, S., *et al.* (2018). Decreased functional connectivity in insular subregions in depressive episodes of bipolar disorder and major depressive disorder. *Frontiers in Neuroscience*, **12**, 842.