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First-time fathers show longitudinal gray matter cortical volume reductions: evidence from two international samples

Magdalena Martínez-García^{1,2,*}, María Paternina-Die^{1,2}, Sofia I. Cardenas³, Oscar Vilarroya^{4,5}, Manuel Desco^{1,2,6,7}, Susanna Carmona^{1,2}, Darby E. Saxbe³

¹Instituto de Investigación Sanitaria Gregorio Marañón, Madrid, Spain,

²Centro de Investigación Biomédica en Red de Salud Mental, Instituto de Salud Carlos III, Madrid, Spain,

³Department of Psychology, University of Southern California, Los Angeles, California, USA,

⁴Department of Psychiatry and Legal Medicine, Autonomous University of Barcelona, Barcelona, Spain,

⁵Hospital del Mar Medical Research Institute, Barcelona, Spain,

⁶Departamento de Bioingeniería e Ingeniería Aeroespacial, Universidad Carlos III de Madrid, Madrid, Spain,

⁷Centro Nacional de Investigaciones Cardiovasculares (CNIC), Madrid, Spain

*Corresponding author: Fundación para la Investigación Biomédica del Hospital Gregorio Marañón (FIBHGM), C/Doctor Esquerdo, 46 – Pabellón de Gobierno, planta baja, 28007 Madrid, Spain. Email: mmartinez@hggm.es

Emerging evidence points to the transition to parenthood as a critical window for adult neural plasticity. Studying fathers offers a unique opportunity to explore how parenting experience can shape the human brain when pregnancy is not directly experienced. Yet very few studies have examined the neuroanatomic adaptations of men transitioning into fatherhood. The present study reports on an international collaboration between two laboratories, one in Spain and the other in California (United States), that have prospectively collected structural neuroimaging data in 20 expectant fathers before and after the birth of their first child. The Spanish sample also included a control group of 17 childless men. We tested whether the transition into fatherhood entailed anatomical changes in brain cortical volume, thickness, and area, and subcortical volumes. We found overlapping trends of cortical volume reductions within the default mode network and visual networks and preservation of subcortical structures across both samples of first-time fathers, which persisted after controlling for fathers' and children's age at the postnatal scan. This study provides convergent evidence for cortical structural changes in fathers, supporting the possibility that the transition to fatherhood may represent a meaningful window of experience-induced structural neuroplasticity in males.

Key words: brain plasticity; fatherhood; longitudinal; parental brain; structural MRI.

Introduction

Modern societies are witnessing increasing father involvement in childcare (Dermott and Millar 2015), with positive potential impacts on a child's social, emotional, and cognitive functioning (Cardenas et al. 2022). The transition to parenthood is a critical period of enhanced neural plasticity in adulthood (Been et al. 2021). During the past decade, researchers have discovered a global human “parental caregiving brain network” that is sensitive to pregnancy-induced factors and sensory cues from the child (Feldman 2015; Abraham and Feldman 2018; Rogers and Bales 2019). This research has advanced a conceptualization of the postpartum period as a crucial life window to study experience-dependent neural plasticity (Abraham and Feldman 2022). Fathers participating in parenting are ideal targets for study, since they experience the cognitive, physical, and emotional demands of caring for a newborn without going through pregnancy.

To date, most of the research on the brain changes associated with the parenthood transition has focused exclusively on mothers, while the neural substrates of human paternal care have been much less explored. In terms of structural magnetic resonance imaging (MRI), we are aware of 12 longitudinal studies reporting brain changes in biological mothers (Martínez-García et al. 2021).

In contrast, only two studies have prospectively followed the structure of the human paternal brain (Kim et al. 2014; Paternina-Die et al. 2020). Fathers are underrepresented in structural MRI studies because researchers have prioritized characterizing the pregnancy-induced neuroadaptations in moms, a crucial milestone in women's health research. However, identifying the typical trajectories of brain change in fathers can contribute to this goal by helping to better discern the intrinsic pregnancy-related and the extrinsic experiential factors that shape the parental brain.

In mothers, the literature has consistently reported structural changes in subcortical brain areas such as the hippocampus, amygdala, thalamus, caudate, pallidum, putamen, and nucleus accumbens, as well as in cortical areas of the default mode mentalizing network, such as the superior temporal sulcus, pre-cuneus, posterior cingulate cortex, and medial prefrontal cortex (Martínez-García et al. 2021). Researchers have described these two networks as part of the global human “parental caregiving network,” a system of functionally interconnected brain regions that underpin different aspects of human parental care (Feldman 2015; Feldman et al. 2019). Functioning of the subcortical structures may maintain aspects of parental behavior conserved among mammals, such as vigilance of infant signals and

reward from the parent-to-infant attachment, while the default mode network is a later-evolving and higher-order system that may be responsible for identifying infants' needs and responding appropriately.

Over the last decade, new evidence for maternal brain plasticity has led to a growing interest in paternal neural plasticity. The few human studies assessing the paternal brain have reported brain structural changes that are less pronounced and affect fewer regions than those reported in biological mothers. This finding dovetails with the high levels of inter-subject variability seen in human paternal behavior and suggests that pregnancy-related factors contribute more strongly to brain plasticity than parental experience. For example, a unique longitudinal study that examined the effects of pregnancy and new parenthood on the mother's brain and included two male control groups (20 first-time Spanish fathers scanned before and after their partners' pregnancies and 17 childless men scanned at a comparable time interval) detected no significant whole-brain anatomical differences in first-time fathers compared to the childless men (Hoekzema et al. 2017). These two male groups were then re-analyzed using surface-based methods, and statistical differences were determined based on threshold-free cluster enhancement (TFCE) and permutation testing to improve the balance between the specificity and the sensitivity. Results revealed a decrease in the fathers' precuneus, a core region of the default mode network (Paternina-Die et al. 2020). Another longitudinal study investigated structural changes in 16 fathers' brains during the first four months postpartum, including both first-time fathers and experienced fathers, and found mixed gray matter volume increases and decreases (Kim et al. 2014). Both studies converged in finding gray matter volume reductions in the precuneus (Kim et al. 2014; Paternina-Die et al. 2020), and Kim et al. (2014) also found gray matter changes in additional default mode regions such as the cingulate cortex, superior temporal, and medial frontal gyri. Therefore, there is preliminary evidence that cortical mentalizing regions may be dynamic during men's neuroanatomical transition to parenthood.

Human fathers, like mothers, also engage subcortical circuits when performing functional tasks related to parenting (Horrell et al. 2021), which may translate to neuroanatomic traits. However, the few neuroimaging studies of fatherhood-induced brain subcortical changes have led to conflicting and mixed results. Kim et al. (2014) found volume increases within parenting-related subcortical structures such as the amygdala, the hypothalamus, the pallidum, the putamen, and the caudate. Also, the higher the gray matter volume increase in striatal and amygdala regions, the fewer depressive symptoms, fatigue, and sleep disturbance at the follow-up postpartum visit (Kim et al. 2014). However, one cross-sectional study of the hypothalamus in first-time fathers whose children were 5–6 years old did not find significant differences in hypothalamic volume between the fathers and non-fathers groups (Long et al. 2021). Notably, the Kim et al. (2014) sample had a mix of first-time and experienced parents and did not include a comparison control group, which may explain the differences across studies. To date, it is still unclear whether first-time fatherhood involves brain changes specific to the later-evolved cortical circuits of parenting or if they also affect the ancient subcortical regions -as is the case with pregnancy-induced brain changes in mothers-.

The current study reflects the first international collaboration between two neuroimaging groups that have prospectively scanned males before and after the transition to fatherhood. One group, based in Spain, scanned the fathers described in Hoekzema

et al. (2017) and Paternina-Die et al. (2020) before their partners' pregnancies and then again at 2–3 months postpartum, together with a control group of childless men. Another group, based in California, United States, recruited cohabiting male partners of pregnant females and scanned them in mid-to-late pregnancy and then again at 7–8 months postpartum. We quantified the change in the cortical and subcortical volumes, and changes in cortical thickness and pial surface area, structural properties of the cortical mantle that contribute to cortical volume. To further explore the localization of the structural changes in the brain, we divided the cortex into the main functional networks and the subcortex into its compound subcortical structures. Keeping with the small extant literature, we hypothesize that both groups of fathers will show comparable neuroanatomic changes that affect the cortex more than the subcortex. Based on previous structural findings of the human maternal and paternal brains (Kim et al. 2014; Hoekzema et al. 2017; Paternina-Die et al. 2020), we expect the default mode network to display structural changes among both groups of fathers.

Methods

Participants

The present study analyzed the MR structural images of two unique prospective datasets of men transitioning to first-time fatherhood, one acquired by the Hospital del Mar in Barcelona, Spain, and one by the University of Southern California in Los Angeles, California (United States). Both datasets were restricted to right-handed first-time fathers who were cohabitating with their pregnant partners. Both collected a structural MR image of the dads before the birth of their first child and then again during the postpartum. Males with a history of neurological or psychiatric illness and substance abuse disorders were excluded from both samples.

The first sample was acquired in Barcelona, Spain, and comprised 20 first-time fathers [mean age (standard deviation (SD)) = 35.60 (4.25) years] scanned before their partners' pregnancies and again at around two months postpartum [mean (SD) = 2.31 (1.62) months between childbirth and postnatal MRI scan]. Seventeen childless men [mean age (SD) = 32.07 (6.32) years] without plans of becoming fathers in the next year were also scanned at a time interval comparable with that of the fathers-to-be group. For further details about these samples see Hoekzema et al. (2017) and Paternina-Die et al. (2020).

The second sample was acquired in Los Angeles, California (United States), and included 20 first-time fathers [mean age (SD) = 31.1 (3.42) years] scanned during the third trimester of their partners' pregnancies [mean pregnancy weeks (SD) = 30.26 (4.67)] and again at 7–9 months following their infants' birth [mean (SD) = 8.93 (4.19) months between childbirth and postnatal MRI scan]. These participants were drawn from a larger longitudinal Hormones and Attachment across the Transition to Childrearing (HATCH) study, which follows opposite sex, cohabitating couples expecting their first child from the mothers' mid-to-late pregnancy through the first year postpartum. Follow-up data collection was impacted by COVID-19 pandemic lockdowns starting in spring 2020. Specifically, four fathers (20% of the California sample) had to complete their postnatal MRI scans more than one year after the birth of their child due to COVID-19 related scanner shutdowns. To err on the side of caution, we repeated the within-group and general linear models analyses in cortical volume, thickness and area, and subcortical volume, excluding fathers who completed their postnatal scan more than one year

Table 1. Demographic table.

	Californian fathers	Spanish fathers	Control men	Statistic
Sample size [number of subjects]	20	20	17	
Age at prenatal session [years]				F(2,54) = 4.99; P-value = 0.01
Mean (SD)	31.1(3.42)	35.6(4.25)	32.06(6.32)	
Median (IQR)	31.5(3.5)	35.33(2.8)	29.56(8.46)	
Range	25–37	27–46	24–44	
Scan interval time (days)				F(2,54) = 5.12; P-value < 0.001
Mean (SD)	336.95(137.36)	453.75(116.72)	419.18(93.18)	
Median (IQR)	283(116)	472.5(167.75)	430(161)	
Range	220–700	287–700	252–546	
Parturition-to-post time (months)				F(1,38) = 43.36; P-value < 0.001
Mean (SD)	8.93(4.19)	2.31(1.62)		
Median (IQR)	6.97(2.56)	1.74(0.99)		
Range	5.79–20.38	0.76–7.3		
ICV at prenatal session (mm ³)				F(2,54) = 3.71; P-value = 0.03
Mean (SD)	1538008.31(125713.64)	1642675.38(101908.01)	1585419.19(137340.15)	
Median (IQR)	1507435.01(208257.03)	1638626.48(148597.31)	1588072.91(213938.16)	
Range	1398260.20–1835271.66	1820621.79–354068.60	1844299.76–474151.66	
Education (%)				$\chi^2 = 4.97$, P-value = 0.55
Middle School	0	10	5,88	
High School	5	15	0	
College	20	5	17,65	
University	75	70	76,47	

Spanish and Californian fathers differ in age at the prenatal scan (P-value = 0.01, Tukey's honest significant difference (HSD) corrected), scan interval days (P-value < 0.001, Tukey's HSD corrected), parturition-to-post months (P-value < 0.001, Tukey's HSD corrected) and intracranial volume (ICV) at the prenatal session (P-value = 0.02, Tukey's HSD corrected). Pearson's chi-squared test did not show any significant group difference in education ($\chi^2 = 4.97$, P-value = 0.55). SD = standard deviation. IQR = interquartile range.

after the birth of their child ($n = 4$) and fathers who completed their postnatal scan after the pandemic (March 2020) ($n = 5$), which rendered comparable results.

Table 1 provides a general description of the groups at baseline. Figure 1 depicts the MRI timelines in the Californian and Spanish fathers' samples, highlighting the periods exclusive to each sample, and the perinatal period captured by both samples.

The studies from which the data were obtained were approved by their corresponding local ethics committees, that is, the Clinical Research Ethical Committee of the Hospital del Mar Research Institute for the Spanish sample and the Institutional Review Board (IRB) of the University of Southern California for the Californian sample.

MRI acquisition

For the two Spanish samples (fathers and childless control men), two prospective structural MRI images were acquired on a 3 Tesla Philips scanner using a T1-weighted gradient echo pulse sequence in the axial plane. The image acquisition parameters were as follows: repetition time = 8.2 ms, echo time = 3.7 ms, voxel size = 0.9375 × 0.9375 × 1 mm, field of view = 240 × 240 × 180 mm, matrix size = 256 × 256 × 180 voxels, no gap, and a flip angle = 8°.

For the Californian sample, two prospective structural MRI images were acquired on a Siemens 3 Tesla MAGNETOM Prisma System using a T1-weighted 3D Magnetization Prepared Rapid Acquisition Gradient Echo (MP-RAGE) sequence in the coronal plane. The image acquisition parameters were as follows: repetition time = 2530 ms, echo time = 3130 ms, size = 1 × 0.9 × 1 mm, field of view = 256 × 207.9 × 256 mm, matrix size = 256 × 208 × 256 voxels, no gap, and a flip angle = 10°.

Image Processing

For every participant, MR T1-weighted structural images were processed using the *FreeSurfer* longitudinal stream (version 7.1.1) (Reuter et al. 2012). This workflow starts with cross-sectional processing of each prenatal and postpartum image to later create an unbiased within-subject template space using information from both MR. The within-subject template serves as an initialization point to produce longitudinal series with higher reliability and statistical power. This stream includes motion and intensity correction, skull removal, transformation into stereotaxic (MNI) space, white matter segmentation, and reconstruction of the inner (white matter) and outer (pial) cortical surfaces. *FreeSurfer* reconstructions of inner and outer cortical surfaces were visually inspected and manually corrected where needed as per *FreeSurfer*'s guidelines.

We extracted from *FreeSurfer* the cortical volume, calculated as the sum of voxels belonging to the cortical gray matter segmentation. We also extracted two structural properties of the cortical mantle that contribute to the cortical volume: the mean cortical thickness, calculated as the Euclidean distance between the outer and inner cortical surfaces, and the pial cortical surface area, calculated as the sum of the areas of the triangles that compose the outer cortical surface (the interface between the CSF and the gray matter). Figure 2 displays a schematic representation of the different brain cortical measurements that were examined in the present study. Additionally, we computed the global subcortical gray matter volume, and the volume of its compounding subcortical structures: the thalamus, putamen, pallidum, hippocampus, amygdala, nucleus accumbens, and the hypothalamus. The hippocampus, amygdala and hypothalamus were segmented using the Iglesias et al. (2015), Saygin et al. (2017) and Billot et al.

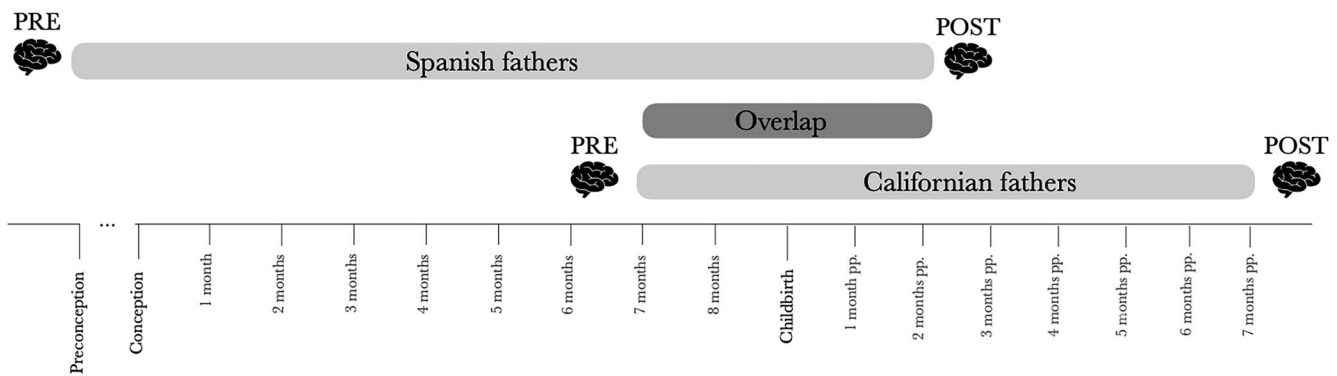


Fig. 1. MRI timelines in the Californian and Spanish fathers' samples. PRE = prenatal MRI scan. POST = postnatal MRI scan. Prenatal scans took place at 6.96 (1.07) mean pregnancy months in the Californian fathers. The time elapsed between childbirth and the postnatal MRI scan was not normally distributed in the fathers' groups, and therefore median values are represented. Californian fathers' postnatal scan took place at a median value of 6.97 (range: 5.78–20.38) postpartum months, and Spanish fathers' postnatal scan took place at a median value of 1.74 (range: 0.7–7.29) postpartum months.

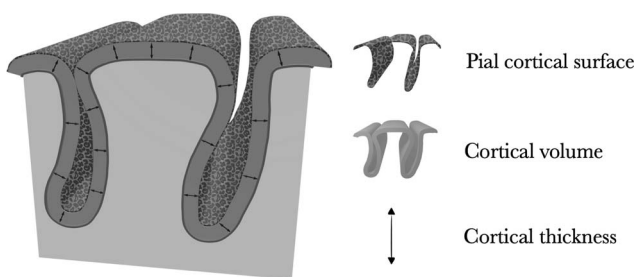


Fig. 2. Schematic representation of a gyrus and sulci displaying different cortical morphological measures used in the current study.

(2020) ex-vivo atlases, which provide more informative volume estimates than *FreeSurfer's* default segmentation.

We also aimed to identify which large-scale functional networks, as defined by *Yeo et al. (2011)*, were specifically affected by the cortical volume changes. We applied a 7-network cortical parcellation, which comprises the visual, somatomotor, limbic, dorsal, and ventral attention, frontoparietal, and default mode networks, using the parcellation atlas obtained from *FreeSurfer*.

Statistical Analyses

All the analyses were performed using RStudio version 1.4.1717 (R version 4.1.0). For each brain morphological measure (cortical volume, cortical thickness, pial surface area, and subcortical volume), we estimated the percentage of change relative to the baseline level (the prenatal session) by employing the following formula:

$$\text{Percentage of change measure} = \frac{\text{Post measure} - \text{Pre measure}}{\text{Pre measure}} * 100$$

Percentage of change was calculated both at a whole-brain level (Fig. 3A, Supplementary Table 1), at a functional cortical networks level (Fig. 3C, Supplementary Table 2) and at the subcortical structures level (Supplementary Table 3).

The statistical tests were performed with the R package *rstatix*, a pipe-friendly framework. Two-tailed within-sample parametric *t*-tests were used as the primary analysis to assess if the groups' percentage of change differed significantly from zero. As a confirmatory analysis, between-group comparisons were applied to the percentage of change employing two-tailed pairwise *t*-tests. To correct for multiple testing, we applied a false discovery

rate (FDR) adjustment across measures and groups. Uncorrected *P*-values, FDR-adjusted *P*-values, and effect sizes, measured as Cohen's *d*, are reported. Those variables that were not normally distributed as per Shapiro–Wilk tests were also assessed using non-parametric Wilcoxon tests, which rendered comparable statistical results.

We performed additional supplementary analyses to examine the robustness of our findings. Specifically, we checked if the participant's age at the prenatal session and the time between the childbirth and the postnatal MRI (which can indirectly reflect paternal experience), were associated with the brain changes detected by the current study. For that purpose, we fitted within-group general linear models using the age at the prenatal session (mean-centered to zero) and the child's age at the postnatal scan (mean-centered to zero) as predictor variables and examined the significance of the models' intercepts. General Linear Models were complemented with post hoc two-tailed *Spearman* correlations.

Results

Figure 3A displays the percentage of change of each group and brain metric—cortical volume, cortical thickness, pial surface area, and subcortical volume. The descriptive and inferential statistics of the percentage of change are displayed in Supplementary Table 1.

Spanish and Californian first-time fathers exhibited mean cortical volume reductions of 1.14 (1.91) % mm³ (Cohen's *D* = 0.60, uncorrected *P*-value = 0.01, FDR-adjusted *P*-value = 0.06) and 0.76 (1.58) % mm³ (Cohen's *D* = 0.48, uncorrected *P*-value = 0.04, FDR-adjusted *P*-value = 0.13), respectively.

The cortical volume decreases decomposed into a 1.10 (1.85) % cortical thickness reduction in Spanish fathers (Cohen's *D* = 0.59, uncorrected *P*-value = 0.02, FDR-adjusted *P*-value = 0.06), and a 0.52 (0.60) pial surface area reduction in Californian fathers (Cohen's *D* = 0.86, uncorrected *P*-value = 0.001, FDR-adjusted *P*-value = 0.01). No significant changes were detected in the control group of childless men (all Cohen's *D* < 0.40, all uncorrected *P*-values > 0.12). Subcortical volume did not significantly change within groups (all Cohen's *D* < 0.41, all uncorrected *P*-values > 0.08). When subcortical structures were examined individually (Supplementary Table 3), no significant within-group significant changes were observed (all Cohen's *D* < 0.45, all uncorrected *P*-values > 0.06), except for a reduction of the

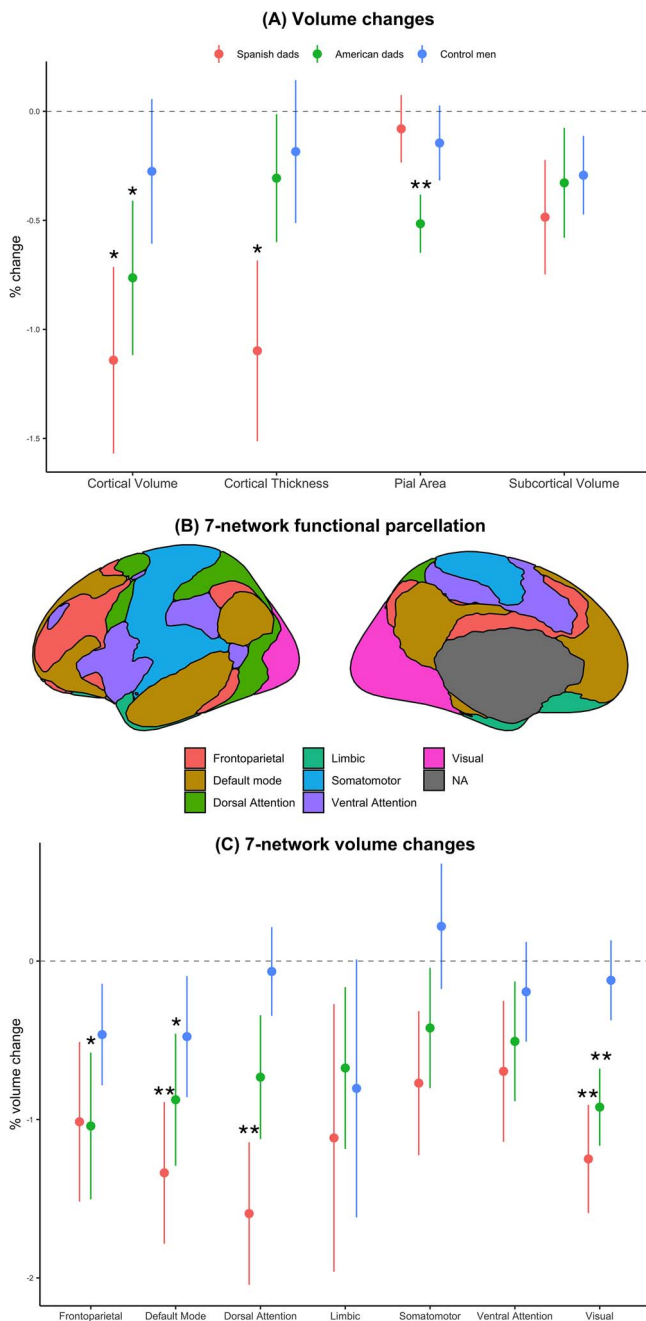


Fig. 3. One-sample t-tests analyses of the percentage of change (y-axis) between prenatal and postnatal MRI scans for each metric. A) Percentage of volume change for each brain measure. B) 7-network functional cortical parcellation of Yeo et al. 2011. C) Percentage of volume change within the seven functional cortical networks described by Yeo et al. 2011. Results have different colours for each sample group (Spanish fathers, Californian fathers, and childless control men). Circles indicate the means, and scatter bars indicate the standard errors of the means. One asterisk highlights the t-tests analyses that survive an uncorrected P-value of 0.05 and two asterisks denote the t-tests that survive and FDR-adjusted threshold a $q < 0.05$.

caudate volume in the childless control group (Cohen's $D = 0.74$, uncorrected P -values = 0.007, FDR-adjusted P -values = 0.17). Pairwise group comparisons indicated that fathers' percentage of change did not differ from childless men in any of the cortical (Supplementary Table 1; all uncorrected P -values > 0.09)

or subcortical (Supplementary Table 3; all uncorrected P -values > 0.16) brain measures, except for a difference in the pial surface area change between the Californian and Spanish fathers (uncorrected P -value = 0.04, FDR-adjusted P -value = 0.12).

We calculated the cortical volume changes within each of the seven functional networks described by Yeo et al. (2011). Figure 3C displays the percentage of cortical volume change for each functional network, and Supplementary Table 2 includes the descriptive and inferential statistics of the percentage of change. Spanish fathers displayed significant volume reductions within the visual (Cohen's $D = 0.82$, uncorrected P -value = 0.002, FDR-adjusted P -value = 0.01), dorsal attention (Cohen's $D = 0.79$, uncorrected P -value = 0.002, FDR-adjusted P -value = 0.01) and default mode networks (Cohen's $D = 0.67$, uncorrected P -value = 0.008, FDR-adjusted P -value = 0.04). Californian fathers showed significant volume reductions within the visual network (Cohen's $D = 0.85$, uncorrected P -value = 0.001, FDR-adjusted P -value = 0.015), the frontoparietal (Cohen's $D = 0.50$, uncorrected P -value = 0.04, FDR-adjusted P -value = 0.15) and default mode (Cohen's $D = 0.47$, uncorrected P -value = 0.05, FDR-adjusted P -value = 0.17) networks. Pairwise group comparisons indicated that the Spanish (uncorrected P -value = 0.01, FDR-adjusted P -value = 0.04) and Californian (uncorrected P -value = 0.03, FDR-adjusted P -value = 0.04) fathers' volume reductions within the visual network, and the Spanish fathers' dorsal attention network reductions (uncorrected P -value = 0.007, FDR-adjusted P -value = 0.02), significantly differed from those of the control men.

Results from the supplementary analyses are summarized below. General linear models were fitted to those within-group significant percentages of change to investigate any potential predictor variables further. Fathers' age at the prenatal scan, and the child's age at the postnatal scan, were not significantly associated with the percentage of change in cortical volume, thickness and area and subcortical volumes, and the intercept of the models remained significant after controlling for these two variables (P -values > 0.034). Regarding the 7-network functional parcellations, Californian fathers' age at the prenatal scan was significantly associated with the percentage of change in the visual network (Spearman correlation; $r = 0.49$, P -value = 0.028), but the intercept of the linear model remained significant (P -value = 0.0006, estimate = -0.922). Finally, excluding fathers who completed their postnatal scan more than one year after the birth of their child ($n = 4$) and fathers who completed their postnatal scan after the pandemic (March 2020) ($n = 5$) rendered similar statistical trends in the t-tests and general linear model analyses.

Discussion

The present study examined changes in the brain cortex and subcortex of two independent samples of first-time fathers drawn from two countries. Both groups of fathers showed cortical volume reductions, which did not depend on the fathers' age at the prenatal scan and their child's age at the postnatal scan. Although subcortical structures have been classically involved in the conserved aspects of mammalian mothering (Feldman 2015), fathers did not exhibit significant volume changes in any subcortical structure that we measured. Instead, as predicted, both fathers' groups showed volume reductions within the default mode network, a later-evolved cortical network that may support parents' ability to mentalize with their infants. Fathers also revealed unexpected, pronounced volume reductions within the visual system, a network where structural changes and functional activations

have been occasionally reported, but traditionally overlooked in the parental brain literature, rarely being explored or discussed (Swain 2011; Atzil et al. 2012; Kim et al. 2018; Luders et al. 2020). One study that investigated the association between parity and middle-age cognitive function in both sexes using UK Biobank data found that fathers performed better in visual memory tasks compared with childless participants, an effect that appeared to be larger in male subjects than female subjects (Ning et al. 2020). These findings may suggest a unique role of the visual system in helping fathers to recognize their infants and respond accordingly, a hypothesis to be confirmed by future studies.

This study is the first to identify structural brain changes in first-time fathers that mostly affect cortical circuits, involved in social understanding, and not subcortical circuits, associated with reward processing and motivational approach. An earlier study by our group that includes the present Spanish sample focused on the cortical circuits of fatherhood (Paternina-Die et al. 2020). The only other longitudinal structural MRI study that explored fathers' brains at a global level found brain changes in both cortical and subcortical structures, including the putamen, caudate, pallidum, amygdala, and hypothalamus (Kim et al. 2014). However, participants in that study included both first-time fathers (44%) and more experienced fathers, which may explain the discrepancy with the subcortical null findings of the present study, since the number of offspring has been linked to less apparent brain aging in several limbic subcortical structures including the putamen and the amygdala (de Lange et al. 2019). Our findings of more pronounced changes in cortical versus subcortical areas are in line with several functional MRI studies with parents. The preserved limbic subcortical network, which is particularly sensitive to pregnancy hormones, appears to play a more central role in maternal behavior, while fathers rely more on cortical networks that may engage to facilitate the cognitive and emotional demands of parenting (Atzil et al. 2012; Abraham et al. 2014; Feldman 2015; Feldman et al. 2019; Grande et al. 2020). Our study provides preliminary evidence that these distinct neural pathways to maternal and paternal care in humans might be reflected in brain structure. Interestingly, among homosexual male fathers who are primary caregivers, the subcortical and cortical circuits of the global human caregiving system appear to show greater coherence (Abraham et al. 2014). However, our study only focused on fathers who were heterosexual males partnered with pregnant females. Further work with primary-caregiver fathers and non-heterosexual fathers can continue to illuminate how different components of the parental brain may be tied to different types of parenting experiences.

All the brain changes we found in first-time fathers pointed in the same direction of reductions in brain volume. Although cortical reductions sometimes reflect a process of neurodegeneration, they can also be a sign of refinement and specialization of neural circuits. Adolescence, for instance, is a life period characterized by the continued elimination of redundant synapses (i.e. synaptic pruning) which parallels cognitive and emotional development (Selemon 2013). In the context of the transition to parenthood, several examples across human and non-human mammals show functional improvements after reductions in brain markers (Pawluski et al. 2022). In human mothers, brain volume reductions have been found coupled with greater neural activations toward the newborns and greater mother-infant attachment (Hoekzema et al. 2017, 2020). In the two studies tracking brain changes in human fathers, brain volume decreases were also associated with positive adaptations to parenthood. According to Paternina-Die et al. (2020), volume reductions were positively correlated with

the father's brain response to his infant's cues, and (Kim et al. 2014) reported structural reductions in the orbitofrontal cortex correlated with increasing paternal stimulation behavior, which is considered a sign of sensitive parenting (Feldman et al. 2019; Rajhans et al. 2019). Because of different measures collected by the two research groups, the current study lacked overlapping assessments of the fathers' relationship with their child, or their parenting beliefs or behaviors, which hindered us from evaluating the adaptive significance of the observed results. Understanding how the structural changes associated with fatherhood translate into parenting and child outcomes is a largely unexplored topic, providing exciting avenues for future research.

Compared to the consistent and prominent pregnancy-induced changes reported in human mothers (Hoekzema et al. 2017; Carmona et al. 2019), the changes we detected in fathers were less pronounced and uniform. For instance, volume reductions were significantly different from zero, but did not differ from the childless men, and several findings did not survive a multiple testing threshold. Conversely, our previous studies have found significant differences between the brains of mothers and non-mothers, and brain changes in mothers were so pronounced that a classification algorithm could correctly classify all women's parity status based on the GM changes in the brain (Hoekzema et al. 2017). The human parental brain is especially sensitive to pregnancy-related hormones but also responds to parenting experience. Biological mothers, who experience striking hormonal shifts during pregnancy and childbirth, may show larger and more consistent brain changes than fathers, who do not experience pregnancy directly, and whose caregiving practices range more widely from providing no direct infant care to being the primary caregiver. Among fathers, brain plasticity may depend more on behavior and individual differences, rendering less uniform and pronounced changes. For instance, the amount of time fathers spend in direct childcare is associated with the degree of functional brain change (Abraham et al. 2014). In trying to assess this, we did not find larger volume reductions in the fathers' sample that captured a more extended postpartum period (i.e. Californian fathers), nor any association between the cortical volume changes and the baby's age at the postnatal session. However, the postpartum time does not accurately indicate how much a father has interacted with his infant after birth: a father may have been absent during most of the postpartum period or vice versa. Future studies with more accurate quantitative and qualitative measures of paternal investment will shed light on the amount of brain plasticity induced by parenting experience or other mediating factors such as partner effects on male hormones or sleep quality.

Although we found converging evidence of cortical reductions across the two samples, a number of divergent findings also emerged. First, when disentangling the cortical volume reductions, Californian fathers displayed significant reductions in area and Spanish fathers in thickness. Changes in the area may reflect changes in the number of cells located between radial columns of the brain, while changes in thickness may reflect changes in the number of cells within ontogenic columns (Petanjek et al. 2011). Secondly, the volume of the dorsal attentional network, which supports goal-directed attention, was significantly reduced in Spanish fathers, while it did not show significant changes in Californian fathers. Combined with the default mode network, this network may control sustained attention (Spreng et al. 2010, 2013), a behavior that is often required during childrearing. It is possible that these inconsistent results at the statistical level may be due to the different scan timing windows or to cultural

or behavioral differences. For example, due to more generous paternity leave policies in Spain, Spanish fathers may spend more time engaging directly in infant care in the early postpartum period, which may help to explain the more pronounced dorsal attentional volume changes in the Spanish sample. However, given that this is the first study to compare fathers from these two countries, more cross-cultural research is needed to elucidate these distinct findings.

The present study represents a unique collaboration to analyze two longitudinal samples of first-time fathers. However, some caveats need to be considered when interpreting the results. The main limitation of the study is that the two fathers' samples were acquired independently from each other and thus differed in culture, language, demographics, and scanning environment. The mismatched scan interval times between samples capture different stages of paternal transition, which may be associated with unique parental experiences and hormone correlates (Sobral et al. 2022). Nevertheless, this limitation can also be considered a strength since we replicated GM cortical reductions within the default mode and visual systems regardless of the above-mentioned sample differences. Furthermore, we were unable to evaluate the adaptive significance and the hormonal correlates of the brain changes associated with fatherhood, since there were no overlapping assessments of perinatal hormonal levels, parenting behaviors and practices, amount and quality of parental investment in child-rearing, or father-child relationship. By including a childless group, we were also able to control for age-related brain changes (Bethlehem et al. 2021), and other potential confounding factors. However, the control group was designed to match the Spanish fathers' sample, while there was no specific control group for the Californian fathers. This should not be of major concern since between-group comparisons were conducted to confirm the within-group analyses. Our sample size of 57 men (20 in each sample and 17 in the childless sample) is relatively small, although larger than many other prospective, longitudinal studies of parental brain structure. Larger samples could increase the sensitivity to detect meaningful changes in the paternal brain not captured by the current study. Another limitation is that the Spanish sample has already been explored in previous studies (Hoekzema et al. 2017, Paternina-Die et al. 2020). However, the current article is novel in focusing on both cortical and subcortical structures and calculating the overlap with Yeo's brain functional parcellation. Finally, one of the main contributions of this study was to compare the paternal brain structure across two different countries, but both Spain and the United States represent Western industrialized democracies. We encourage future research to examine a broader range of fathers from more diverse backgrounds and cultures to challenge the current status quo of Western-centric research.

Conclusion

This paper reports on an international collaboration between two laboratories that have prospectively collected structural neuroimaging data from men before and after the birth of their first child. In both samples, we found structural cortical reductions, specifically within the default mode and visual perception networks, along with the preservation of subcortical structures. This study advances knowledge about structural neuroplasticity related to the paternal experience and suggests the need for further research on the specific timing and predictors of brain changes in fathers. In isolating and describing the experience-dependent brain plasticity of fathers, we will gain a better

understanding of how a father successfully adapts to parenting, which has a direct impact on public policies that support father involvement.

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Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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Data sharing plan

The R code that supports the findings of this study is available on request from the corresponding author, Magdalena Martínez-García. The neuroimaging data are not publicly available due to their containing information that could compromise the privacy of the research participants.

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