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The Behavioral, Hormonal, and Neural Correlates of Cognitive Control in Response to Sexual Interference Stimuli in Fathers and Non-fathers

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Abstract

The Behavioral, Hormonal, and Neural Correlates of Cognitive Control in Response to Sexual Interference Stimuli in Fathers and Non-fathers
By Julia A. Saltalamacchia

Despite the fact that there is great variation in human paternal care, its benefits to children are immense and well documented. Life History Theory suggests that men pursue a reproductive strategy on a spectrum from mating effort to parenting effort. The purpose of this study is to investigate behavioral, hormonal and neurobiological differences between fathers and non-fathers through four aims. We use a choice reaction time task with sexual interference in fMRI to investigate brain and behavioral differences in reaction to sexual stimuli. Additionally, we investigate differences in testosterone levels and differences in brain structure. We found that fathers are less distracted by sexual interference stimuli than non-fathers, as measured by reaction time. Those with the slowest reaction times engaged the cognitive and emotional control areas of their prefrontal cortex less than those with faster reaction times. Fathers have lower baseline levels of testosterone than non-fathers, and those with higher baseline levels of testosterone engage their prefrontal cortex less during the reaction time task. Our results also suggest that fathers have greater gray matter density than non-fathers in the medial oribital frontal cortex and rostral ACC. These results suggest that differences between fathers and non-fathers manifest themselves in differences in behavior, brain structure and function, and hormones.

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Introduction

Sherman made the terrible discovery that men make about their fathers sooner or later... that the man before him was not an aging father but a boy, a boy much like himself, a boy who grew up and had a child of his own and, as best he could, out of a sense of duty and, perhaps love, adopted a role called Being a Father so that his child would have something mythical and infinitely important: a Protector, who would keep a lid on all the chaotic and catastrophic possibilities of life. ~Tom Wolfe, The Bonfire of the Vanities

Paternal care is relatively rare among mammals, and humans are among the few species that exhibit biparental care (Paquette 2004). The benefits of paternal care for human children are well documented and include higher IQs at age 3, increased social competence, and increased popularity (Bogels and Phares 2008; Konner 2010). The role of the father in child development is complex, has changed over the course of history, and is varied across cultures. However, despite such variation, paternal involvement is highly beneficial for children (Lamb 2004). Paquette (2004) describes the father-child activation relationship, in which the father is responsible for showing the child new things and peaking curiosity about the outside world. Children who grow up without a father in their home do worse than their biparental counterparts on almost all measures of social capital and welfare. Children living in father-absent homes are 54% more liking to be living below the poverty line, and single mothers have higher infant mortality and morbidity rates than their married counterparts (US Census). Children that grow up in father-absent homes are more likely to suffer injury, are more likely to be incarcerated as an adult, and are more likely to become pregnant as a teenager (Harper 2004; Teachman 2004). Despite the clear benefit of paternal presence and care, there is great variation in paternal care and nurturance among human males (Hrdy 2009). Differences in paternal behavior in human males likely stem from a variety of genetic and environmental factors, and manifest themselves as differences in brain structure and brain function.

The purpose of this study is to investigate behavioral, hormonal and neurobiological differences between fathers and non-fathers. There are several specific aims: the first aim is to explore behavioral differences between fathers and non-fathers on a choice reaction time task with sexual interference stimuli, the second aim is to analyze differences in plasma testosterone levels of fathers and non-fathers at baseline and after viewing child stimuli and sexual stimuli. The third aim is to use fMRI to investigate differences in brain function between fathers and non-fathers, as well as correlations between reaction time and brain function. The final aim is to investigate differences in brain structure between fathers and non-fathers using voxel-based morphometry.

While there is relatively little research on the neural correlates of paternal behavior, there is a wealth of research on human maternal behavior. Studies have shown that mothers activate the ventral striatum, a part of the mesolimbic dopamine reward system, the ventral ACC, and the insula when looking at pictures of their own children compared with other children they were acquainted with, suggesting that mothers likely find viewing pictures of their child rewarding (Bartels and Zeki 2004). Additionally, Lenzi et al. (2009) showed that mothers activate areas of the mirror neuron system more strongly when viewing pictures of their own infant as opposed to an unknown infant. The mirror neuron system is implicated in empathy and emotion, implying that women may feel more empathy toward their own child. Interestingly, women with secure attachment styles more strongly activate the ventral striatum when viewing images of their child with a happy or sad expression than mothers with an insecure attachment style (Strathearn, Fonagy et al. 2009). Women who become mothers have increased gray matter volumes in their prefrontal cortex and hypothalamus (Kim, Leckman et al.).

Behavioral ecologists have proposed a theory that attempts to explain individual differences in human reproductive strategies. Life History Theory posits that men adopt a reproductive strategy somewhere on a spectrum from "dad to cad." A "dad" or parental effort reproductive strategy would invest more energy in ensuring the health and well-being of offspring and thus increase fitness by ensuring that offspring thrive, while a "cad" or mating effort reproductive strategy would invest more energy in seeking out mating partners, and thus increase his fitness from having many mates. Absence of a father figure in early childhood leads to a cad-like strategy, characterized by exaggeration of masculinity and viewing sexual contact as a conquest, because the child does not grow up with the example of a stable pair bond and continued parental investment. Conversely, children that grow up with a father figure view stable pair bonds as the model relationship, and therefore are more likely to pursue a pair bond (Draper and Harpending 1982). Interestingly, in a study that used characters from 19th century novels to assess Life History Theory, women tended to prefer the "dad" characters, those who were compassionate, caring, and industrious, for long term relationships, but preferred "cads," characters that were competitive, dominant, and brave, for short term affairs (Kruger and Fisher 2005). Because women may choose to mate with men pursuing both types of strategies, both strategies persist across generations (Kruger and Fisher 2005). Life History Theory also argues that a variety of genetic and environmental factors impact men's reproductive strategies and, in turn, their sexual behavior. It argues that individuals who are high K-selected, a measure of life history, are more likely to have high parental investment, monogamy, and lower birth rates and may be characterized by "long-term thinking, substantial social support structures, adherence to social rules, and careful

consideration of risks," whereas those who are low K-selected are more likely to have many offspring with low parental investment, and may be characterized by "impulsivity, short-term thinking, promiscuity, little social support, disregard for social rules, and extensive risk-taking" (Figueredo, Jossquez et al. 2006).

Given the theory that men choose between a parental effort reproductive strategy and a mating effort reproductive strategy, we postulated that men who choose to become fathers would be less distracted by sexual stimuli than non-fathers in a choice reaction time task because non-fathers invest more energy in mating and would therefore focus more on sexual stimuli than fathers who have chosen to pair bond and therefore are less interested in sexual stimuli. To investigate these differences, we compared fathers and non-fathers on a choice reaction time test with sexual interference stimuli. Wright and Adams (1994) created a task in which subjects had to press a button corresponding to the location of a dot overlaid on different types of sexual and nonsexual stimuli, to measure the degree of sexual interference of each of the stimuli. They showed that subjects had longer reaction times when the images were sexualized pictures of the sex that the subject was attracted to, and were therefore able to predict the subjects' sexual orientation.

Hypothesis 1: Fathers will have faster choice reaction times than non-fathers in response to a dot task with sexual interference stimuli as compared to neutral interference stimuli, indicating greater ability to override sexual impulses.

A reaction time task with visual sexual stimuli has not yet been investigated using fMRI. However, there is a wealth of information from fMRI on both visual sexual stimuli and other types of emotional reaction time tasks. In response to visual sexual stimuli, men show activation in the amygdala, the hypothalamus, the visual cortex, the insula, and a

variety of other regions (Mouras, Stoléru et al. 2003; Hamann, Herman et al. 2004; Ferretti, Caulo et al. 2005). A variety of different studies using different methods have investigated the cognitive control over emotions or impulses, in order to perform a task. The rostral anterior cingulate cortex and prefrontal cortex appear to play an important role in the cognitive control of emotion (Bush, Luu et al. 2000; Ochsner and Gross 2005; Volman, Roelofs et al. 2011). There is evidence to suggest that such areas have a modulatory effect on "emotional areas" such as the amygdala and the mOFC (Ridderinkhof, Ullsperger et al. 2004; Koch, Pauly et al. 2007). It has also been suggested that the lateral areas of the prefrontal cortex are involved in the cognitive processing and cognitive control of emotion, and the medial areas of the PFC are involved in emotional processing (Kouneiher, Charron et al. 2009).

Hypothesis 2: Men with faster reaction time will have greater activation in the prefrontal cortex, indicating great cognitive control of emotion, and that those with slower reaction times would have greater activation in the areas associated with visual sexual stimuli.

Data on paternal hormone levels suggests that the effect of fatherhood on testosterone may play an important role in the development of paternal behavior in men. Fatherhood in humans decreases testosterone levels over time (Gettler, McDade et al. 2011). Exposure to infant scent decreases testosterone levels in marmoset monkeys (Prudom, Broz et al. 2008). Fathers with lower testosterone levels report greater sympathy in response to infant cry stimuli, suggesting that a decrease in testosterone levels may signal a channeling of energy and resources away from mating and toward parenting (Fleming, Corter et al. 2002). Testosterone levels in fathers in polygynous

societies predict paternal efforts, as measured by both direct care and economic support, in that high-investing fathers had lower testosterone levels, and low-investing fathers had higher levels of testosterone (Alvergne, Faurie et al. 2009). Interestingly, such changes in testosterone levels are not seen in cultures with little or no paternal care (Kuzawa, Gettler et al. 2009; Muller, Marlowe et al. 2009).

Hypothesis 3a: Fathers will have lower baseline testosterone than non-fathers, and that the men's testosterone levels would decrease after viewing pictures of children, and would be more pronounced in fathers and the men's testosterone levels would increase after viewing pictures of sexual stimuli and would be more pronounced in non-fathers.

Hypothesis 3b: Additionally, we hypothesized that men with higher levels of baseline testosterone would have slower sexual-nonsexual reaction times, and less activation in the prefrontal cortex during the choice reaction time task.

To investigate structural differences in the brain between fathers and non-fathers, we conducted voxel-based morphometry (VBM) analysis. VBM is the preferred structural image analysis method for comparing gray matter volume in the brain, and allows the user to make whole brain voxel-wise comparisons between two groups, or as a covariate with a variable of interest (Mechelli, Price et al. 2005). While this method has never been used to compare fathers and non-fathers, a longitudinal VBM study on mothers found that motherhood increased gray matter densities in the prefrontal cortex, the amygdala, the hypothalamus, and other areas associated with maternal motivation (Kim, Leckman et al. 2010). Additionally, a study in marmosets found that fathers have

increased density of dendritic spines and vasopressin receptors in the prefrontal cortex compared to monkeys that had never been fathers (Kozorovitskiy, Hughes et al. 2006).

Hypothesis 4: We hypothesized that fathers would have greater gray matter density in the prefrontal cortex compared to non-fathers.

By investigating these four aims, we hope to gain a clearer understanding of brain and biological differences between fathers and non-fathers in reacting to sexual stimuli, which can be used to inform future research on paternal behavior.

Methods

This study was conducted as part of a larger study on the biological basis of individual differences in paternal nurturance. The study is being conducted in accordance with the Emory Institutional Review Board.

Subjects

Twenty-five heterosexual fathers with a child between the ages of 1-3 who were living with the child's mother were recruited from the Emory University community. Twenty-five heterosexual single men living without a female partner were recruited from the Emory University community as "non-fathers." Groups were matched for age and years of education.

Behavioral Procedures and Task

Prior to scanning, subjects completed two reproductive attitude scales: a sociosexual orientation inventory (Simpson and Gangestad, 1991) and a mini-k life history scale (Figueredo, Jossquez et al. 2006). The sociosexual orientation inventory measures an individual's willingness to participate in uncommitted sexual behavior, while the mini-k life history scale is a broad scale that measures individuals' attitudes toward a variety of social relationships and situations. A high score on the sociosexual orientation inventory indicates greater "openness" and less commitment in sexual relationships. A high score on the mini-k is correlated with positive friend and romantic relationships, and negatively correlated with neuroticism, and avoidance of romantic partner attachment. Additionally, fathers and mothers completed a parental responsibility

measure, which measures the degree of parenting behavior the father takes on (Sheryl Goodman, Emory University) and a modified Block Child Rearing Practices Report to measure paternal warmth or nurturance and paternal restrictiveness (Rickel and Biasatti 1982). Data on the sex of the child and years of fatherhood were also collected from the fathers.

While in the scanner, subjects performed a choice reaction time task, modeled after Wright and Adams (1994), in which subjects must push a button on the button box corresponding to the horizontal quadrant in which a yellow dot is located on top of a photo. The task consists of 4 conditions with different photo content: sexual, nonsexual, male, and blank. The task consists of 160 trials, 40 images of each condition displayed for two seconds in pseudorandom order, with a three second inter-trial fixation cross display. The sexual, nonsexual, and male conditions used the images taken from stock internet photos. The blank condition consisted of a dark blue background. The yellow dots were superimposed on four horizontal quadrants (far left, left-middle, right-middle, and far right) in pseudorandom order over the 160 trials (Figure 1). Stimuli were presented and reaction time data collected using E-prime software (Psychology Software Tools).

Sexual and nonsexual images were piloted for sexual arousal and sexual attraction. 10 pilot subjects rated the sexual images significantly higher on attractiveness (sexual mean = 5.7, nonsexual mean = 3.7, $t(78) = -13.4$, $p<0.001$) and arousal (sexual mean = 5.9, nonsexual mean = 2.9, $t(78) = -21.4$, $p<0.001$) as compared to nonsexual images on a 1-7 likert scale.

Behavioral and Demographic Analyses

Fathers' and non-fathers' age was compared using an independent samples t-test. Levels of education were converted to years of education and then compared between fathers and non-fathers using an independent samples t-test. Sexual – Nonsexual change in reaction time (S-NS Reaction time) between conditions was found by subtracting the average reaction time of the non-sexual condition from the sexual condition reaction time for each subject. Reaction time differences between fathers and non-fathers were analyzed using an independent samples t-test. The same analysis was carried out for the Sexual – Male change in reaction time (S-M reaction time). Bivariate correlations were carried out to test for a correlation between life history and behavioral surveys and reaction time, and between testosterone levels and S-NS Reaction time

Plasma Collection and Hormone Analysis

Blood samples were collected from 20 fathers and 20 non-fathers. All subjects were fitted with an indwelling catheter. 16 mL of blood were drawn before the start of the scan. Another 16 mL of blood were drawn after approximately 25 minutes of scanning, and then again approximately 66 minutes after the start of scanning. The second and third blood draws correspond to 20 minutes after the men see child images, and 20 minutes after the men see sexual images, in order to assess peak plasma hormone levels in response to these visual stimuli (Figure 2). The blood samples were centrifuged at 4C within 20 minutes of the draw. Plasma was harvested and frozen until assay.

Plasma samples were assayed for testosterone in the Clinical Pathology Translational Research Laboratory at Emory University using a standard protocol.

fMRI Image Acquisition

Imaging was conducted on a Siemens Trio 3T MRI scanner with padded head restraint. A T1-weighted MPRAGE anatomical scan (TR= 2300 ms, TE = 4 ms, matrix = 256x256, FOV=256, slice thickness = 1.00 mm, gap = 0 mm) and a field map were acquired. Functional data were acquired with an EPI sequence of the following parameters: TR = 2000 ms, TE = 28 ms, matrix = 64 x 64, FOV = 192 mm, slice thickness = 3.0 mm, and 32 axial slices.

fMRI Image Analysis

All image analysis and preprocessing was conducted with Brain Voyager QX (version 2.0.8) software (Brain Innovation, Maastricht, The Netherlands). Functional images were realigned by six-parameter 3-D motion correction. Functional images were co-registered with their high-resolution 3-D anatomical scan. Images were normalized into Talairach space (Talairach J 1988). Images were then smoothed at 8-mm FWHM. A separate general linear model was defined for each subject for the time before they pressed the button indicating their choice and for the time after they reacted while they were passively viewing the stimuli for the remainder of the two seconds. Four regressors were defined for each subject: sexual, nonsexual, male, and blank. Each regressor was convolved with a standardized model of the hemodynamic response. For each subject contrasts of parameter estimates of interest (e.g. S-NS) were computed at every voxel of the brain. A random effects analysis was used to compare individual subject values between fathers and non-fathers across the four conditions for both the reaction time epoch and the post-reaction time epoch. The resulting t-statistic maps were thresholded at

an uncorrected p value less than 0.001, with a spatial extend threshold of 20 voxels. Covariate analysis for S-NS reaction time and baseline testosterone was conducted using random effects ANCOVA. The resulting correlation maps were thresholded at an uncorrected p value less than 0.01, with a 10-voxel spatial extent threshold.

VBM Analysis

Voxel-based morphometry (VBM) allows for detailed analysis of differences in gray matter density between two groups of subjects or in correlation to a variable of interest. Structural data was analyzed with FSL-VBM (Ashburner and Friston 2000; Good, Johnsrude et al. 2001) carried out with FSL tools (S.M. Smith 2004). First, to remove the skull and neck from the images, structural images were brain-extracted using BET (Smith 2002). Next, tissue-type segmentation was carried out using FAST4 (Y. Zhang 2001). The resulting grey-matter partial volume images were then aligned to MNI152 standard space using the affine registration tool FLIRT (Smith 2001; Jenkinson, Bannister et al. 2002), followed by nonlinear registration using FNIRT (Andersson, Jenkinson et al. 2007; Andersson, Jenkinson et al. 2007), which uses a b-spine representation of the registration warp field (Rueckert, Sonoda et al. 1999). The resulting images were averaged to create a study-specific template, to which the native grey matter images were then non-linearly re-registered. The registered partial volume images were then modulated (to correct for local expansion or contraction) by dividing by the Jacobian of the warp field. The modulated segmented images were then smoothed with an isotropic Gaussian kernel with a sigma of 3 mm. Finally, voxelwise GLMs for both the main contrast of Fathers > Non-father and correlations with testosterone and reaction

time were applied using permutation-based non-parametric testing. The resulting maps were visualized in FSL-VIEW and thresholded at a $p < 0.005$ (Douand and Smith 2008).

Results

Demographic

The average age of all subjects combined was 32.8 years old, and they had an average of 17.0 years of education. Fathers and non-fathers did not differ from each other in age (Father mean = 33.4 years, Non-father mean = 32.2 years, $p>0.05$) or education (Father mean = 17.5 years, Non-father mean = 16.3 years, $p>0.05$), though there was a trend for fathers to have more years of education.

Behavioral

The average accuracy on the choice reaction time task for all subjects combined was 96.1%. Two subjects had accuracy scores more than three standard errors below the mean, and were therefore excluded from all analyses. During the dot task, the men reacted slowest, on average, in the sexual condition (801.0 ms), followed by the nonsexual condition (741.2 ms), and the male condition (712.4 ms). All subjects took on average 59.8 milliseconds longer to react during the sexual condition as compared with the nonsexual condition, and non-fathers were significantly slower than fathers (Fathers=54.4 ms, non-fathers=93.8 ms, $t(54) = -1.744$, one-tailed $p < 0.05$)(Figure 3). The same pattern held true for the sexual – male data. Across all subjects, the men were 88.9 milliseconds slower in the sexual condition than the male condition. Non-fathers were 109.6 milliseconds slower in the sexual condition, whereas fathers were only 68.22 milliseconds slower ($t (54) = -1.69$, one-tailed $p <0.05$). There was no significant difference between fathers and non-fathers on their nonsexual – male reaction time. The difference in reaction time between the sexual condition and nonsexual condition was the

main variable of interest, and will thus be referred to as "S-NS Reaction time" in the remainder of the paper.

In order to determine if reproductive strategies and paternal behavior were related to reaction time delays, we tested the correlation between S-NS Reaction time and Sociosexual Orientation, Mini-k score, and Beck Depression index, and found no significant correlation. Additionally, there was no significant correlation between fathers' S-NS Reaction time and paternal responsibility or warmth. We also considered the possibility that years of fatherhood and the sex of their child could affect reaction time delays and paternal behaviors. Among fathers, there was no difference on scores of parental warmth or responsibility, or S-NS reaction time between fathers with female children and fathers with male children, nor did years of fatherhood have a significant effect on such measures.

Hormones

Fathers' mean baseline testosterone of 4.0 ng/mL was significantly lower than non-fathers' mean baseline testosterone, 5.0 ng/mL ($t(40) = -2.18$, $p < 0.05$). However, there was no significant difference in testosterone levels between fathers (mean = 4.4 ng/mL) and non-fathers (mean = 4.5 ng/mL) at the time of the second draw. Fathers had a markedly lower level of testosterone at draw 3 than non-fathers (father mean = 2.7 ng/mL, Non-father mean = 4.6 ng/mL, $t(38) = -4.65$, $p < 0.001$). Non-fathers showed no significant change in testosterone levels across all three draws ($F(2, 60) = 0.63$, $p = 0.54$). Fathers showed a significant change in testosterone levels across three draws ($F(2,57) = 11.17$, $p<0.001$). Fathers had significantly lower testosterone at draw 3 than at

baseline (Tukey's HSD = 1.3046, $p<0.01$) and at draw 2 (Tukey's HSD = 1.68789, $p<0.001$) (Figure 4). Fathers showed markedly similar testosterone increases and decreases across the three draws, whereas non-fathers had a large amount of variation among the subjects across the three draws (Figure 5). There was no difference in the change in testosterone levels across draws between fathers with female children and fathers with male children. There was no significant correlation between S-NS Reaction time and baseline testosterone, however, there was a trend in the positive direction ($r = .252$, $p = 0.132$).

Functional MRI data

Two general linear models were created to analyze fMRI data: one model taking into account only the time while subjects were reacting, i.e. before they pressed a button, and one model taking into account the time after the subjects reacted until the onset of the next fixation cross.

Reaction time epoch: The main effect of sexual condition – nonsexual condition showed large activations in the visual cortex, the fusiform gyrus, bilateral insula, the lateral hypothalamus, the extrastriate body area and the caudate nucleus, among other regions (Table 1, Figure 6).

There were no significant activations for the Non-father (sexual – nonsexual) > Fathers (sexual-nonsexual) contrast or vice-versa.

Post reaction time epoch: The main effect of the sexual condition – nonsexual condition during the time after the subject reacts showed large activations in the left fusiform gyrus, the right precentral gyrus, right superior frontal gyrus, left inferior frontal gyrus, and the insula. A full list of activations is in Table 2. The t statistic maps for the time during reaction and the time after reaction were very similar (Figure 7).

Covariates: When sexual-nonsexual reaction time was entered as covariate with the sexual-nonsexual neuroimaging data, there were negative correlations in the medial orbital frontal cortex and the ventral lateral prefrontal cortex (Table 3, Figure 8), indicating as S-NS Reaction time increases, i.e. men take longer on sexual pictures, mOFC and vlPFC activation decrease. When baseline testosterone was entered as a covariate, there were negative correlations in the dorsal lateral prefrontal cortex, and the ventral lateral prefrontal cortex in the sexual > nonsexual contrast (Table 4, Figure 9), indicating that as baseline testosterone levels increase, there is less brain activity in those regions during the dot task.

Structural

Main effect: Fathers showed greater gray matter density in the premotor cortex, and in the tail of the caudate at an uncorrected p value less than 0.005 (Table 5, Figure 10). Fathers showed greater gray matter density in the rostral anterior cingulate cortex (rACC) and the dorsal lateral prefrontal cortex (dlPFC) at a more liberal uncorrected p value less than 0.05 (Figure 11). Non-fathers showed greater gray matter density in the temporal

pole, the superior temporal sulcus, and the precuneus at an uncorrected p value less than 0.005 (Table 6, Figure 12).

Correlations: There were no significant correlations between S-NS Reaction time and gray matter density, nor were there any significant correlations between gray matter density and baseline testosterone levels at an uncorrected p value less than 0.005.

Discussion

The aim of this study was to investigate differences between fathers and non-fathers in reaction time and brain function during a choice reaction time task with sexual interference stimuli, and to investigate differences between fathers and non-fathers in brain structure and plasma testosterone levels. Our hypotheses were four-fold: 1) Fathers will have faster sexual-nonsexual reaction times than non-fathers, 2) Those with faster S-NS reaction times will have greater activation in the cognitive control areas of the prefrontal cortex, and those with slower reaction time would have greater activation in the amygdala and hypothalamus, 3) Fathers will have lower baseline testosterone than non-fathers, and the men's testosterone levels would decrease after viewing pictures of children, and would be more pronounced in fathers and the men's testosterone levels would increase after viewing pictures of sexual stimuli and would be more pronounced in non-fathers, and those with higher baseline testosterone would have less activation in the prefrontal cortex during the reaction time task, and 4) Fathers would have greater gray matter density in the prefrontal cortex than non-fathers.

Reaction time

The men reacted slowest to sexual stimuli, followed by nonsexual stimuli, and then male and blank stimuli. These findings are consistent with findings from other studies using a choice reaction time with interference task that found that people react slowest to arousing pictures of the sex of their preferred partner (Wright and Adams 1994). Santtila et al. (2009) found that the choice reaction time with interference task could be used to measure sexual interest. Non-fathers had a larger sexual – nonsexual

reaction time than fathers, a finding consistent with our hypothesis that non-fathers would be more distracted by sexual stimuli than fathers. We did not see this difference in the nonsexual-male reaction time data, suggesting that non-fathers' slower reaction time was due to the arousing nature of the sexual stimuli, rather than the female nature of the stimuli. Given these studies, our findings suggest that non-fathers are more sexually interested in the arousing stimuli than fathers because they took a significantly longer time to react to them than the nonsexual women.

Although we expected reaction time to correlate with the life history inventories, the mini-K and the sociosexual orientation inventory, we found no such correlations. These finding suggest that factors other than reproductive strategy are mediating differences in reaction time in the men, or that our measures of reproductive strategy (i.e. the SSOI and the mini-K Life History Scale) are not an accurate representation of actual reproductive strategy. Among fathers, paternal warmth and responsibility were not correlated with reaction time, indicating that the amount and quality of paternal care has no further effect on reaction time other than that of fatherhood status. Additionally, we tested for a correlation between years of fatherhood, number of children, and reaction time, in case newer fathers were more likely to be distracted by sexual stimuli, and again found no significant correlation. However, considerations for sample size should be taken into account, and a larger sample may reveal significant correlations in this data, and thus the analyses should be repeated when more data is available. Taken together, these findings suggest that fathers are less distracted than non-fathers by sexual stimuli, but that this difference in reaction time is not necessarily mediated by reproductive strategy as measured by the mini-K and SSOI past the grouping effect of fatherhood.

Brain Function

The sexual-nonsexual reaction time epoch main effect contrast showed activations in several areas characteristic of viewing visual sexual stimuli. Hamann et al. (2004) showed the amygdala and hypothalamus to be consistently active in males while viewing sexual stimuli as compared to neutral stimuli. The visual processing areas of the cortex, including the fusiform face processing area, are also active in response to visual sexual stimuli (Mouras, Stoléru et al. 2003). Consistent with previous findings, we found activations in the visual cortex, the fusiform gyrus, the extrastriate body area, the insula, the hypothalamus, and the amygdala. The visual cortex is more active when subjects view emotionally arousing stimuli compared with neutral stimuli, and more active the more subjects attend to stimuli (Lang, Bradley et al. 1998). The fusiform gyrus is involved in face processing, and is also more active to emotional stimuli, so it follows that the visual cortex and fusiform gyrus are more active in the sexual condition compared with the nonsexual condition (Vuilleumier, Armony et al. 2001). The extrastriate body area is a lateral occipitotemporal region that has been found to be selectively active in response to images of the human body (Downing, Jiang et al. 2001). Greater activation of the extrastriate body implied that the men attended more to the bodies of the women in the sexual condition compared to those of the women in the non-sexual condition. The amygdala and hypothalamus are both involved in sexual arousal and functionally connected (Ferretti, Caulo et al. 2005; Kilpatrick, Zald et al. 2006). The insula is involved in tracking the autonomic and visceral arousal states of the body, including sexual arousal (Arnow, Desmond et al. 2002). Taken together these finding

support previous research using fMRI and visual sexual stimuli, and suggest that the men attended to and were aroused by the faces and bodies of the sexual stimuli more than those of the nonsexual stimuli during the choice reaction time task.

In addition to areas activated by visual sexual stimuli, the sexual-nonsexual contrast showed activations in the rostral anterior cingulate cortex and the ventral lateral prefrontal cortex. The anterior cingulate cortex is associated with a variety of functions including error prediction, emotional control, and cognitive control. The ventral-rostral aspect of the ACC is specifically involved in error tracking and attention during emotional tasks (Bush, Luu et al. 2000). While many different areas of the prefrontal cortex have been implicated in cognitive and emotional control, the ventral lateral prefrontal cortex has been associated specifically with the cognitive control of emotion, and the ability to override emotion and focus on a task (Ochsner and Gross 2005). Additionally, ventral lateral PFC engagement has been associated with amygdala deactivation during cognitive control tasks (Ochsner and Gross 2005). This vlPFC-amygdala connection could explain why there was a smaller area of activation in the amygdala in this contrast than in previous studies using visual sexual stimuli. Overall, our findings suggest that the men were aroused by the visual sexual stimuli and had to exert a degree of cognitive control to focus on the choice reaction time task.

The covariate map of reaction time correlated with sexual-nonsexual brain activity showed a negative correlation between brain activity in the medial orbitofrontal cortex and the ventral lateral prefrontal cortex and reaction time. This finding indicates that the less activation subjects have in those areas, the slower their reaction time, and supports our second hypothesis. As previously mentioned, the vlPFC is involved in the

cognitive control of emotion and the ability to override or filter out emotionally salient stimuli (Ochsner and Gross 2005). The mOFC is also implicated in emotional processing, specifically in regulating the affective quality of stimuli and executive functioning and planning, in particular, the ability to analyze risk and override impulse (Ochsner, Bunge et al. 2002). When baseline testosterone level was entered as a covariate for the sexual – nonsexual contrast, we found a negative correlation in the dorsal lateral prefrontal cortex and again, the ventral lateral prefrontal cortex. The dlPFC is frequently associated with working-memory and top-down task-oriented behavior (Wagner, Maril et al. 2001), suggesting that men with higher baseline T were less able to engage task-performance and cognitive control areas of their brain during the choice reaction time task. Thus, men with less activation in these cognitive control regions likely have less control over their sexual impulses when confronted with sexual stimuli, which slows their reaction time.

We saw no significant activations in the Father (sexual-nonsexual) > Non-father (sexual-nonsexual), despite seeing a significant behavioral difference in that condition. This result could be caused by the small sample size, given that the behavioral difference is significant only at the $p<0.05$ level. The analyses should be repeated with a larger sample size to determine if the behavioral data becomes more significant and if any functional activation in this contrast becomes significant. Overall, our findings were partially consistent with our hypothesis, and indicate that the men with the slowest sexual-nonsexual reaction time activated areas of their brain involved in cognitive control of emotion and executive functioning less than men with faster sexual-nonsexual reaction times. We did not see any positive correlations of brain activation with reaction time in the amygdala, as we had hypothesized, but this could be due to the relatively small

amygdala activation in the sexual > nonsexual main effect contrast. Additionally, consistent with our hypotheses, the testosterone correlation results suggest that men with high baseline testosterone activated working-memory and task performance areas less than men with low baseline testosterone. Thus, men with higher baseline testosterone are less able to engage cognitive control areas of their brain while reacting to sexual stimuli.

Testosterone

As expected, non-fathers had higher baseline testosterone levels than fathers, supporting our hypothesis that fathers have lower testosterone levels than non-fathers. These findings are consistent with previous research that men who are fathers have lower testosterone levels than men who are not fathers (Alvergne, Faurie et al. 2009; Muller, Marlowe et al. 2009). Although our results are cross-sectional, a recent longitudinal study showed that fatherhood decreases men's testosterone over time (Gettler, McDade et al. 2011). There are a variety of reasons why fathers have lower levels of testosterone than non-fathers. Testosterone has been shown to increase both aggressive and sexual behavior in men, neither of which is beneficial to parenting behavior or maintaining pair bonds (John 2006). Fleming et al. (2002) found that fathers with lower testosterone felt more sympathy and need to respond to infant cry stimuli than those with higher testosterone, and interestingly, that exposure to infant cry stimuli increased testosterone levels, which may be associated with increased alertness and action.

The men's change in testosterone levels in response to child stimuli and sexual stimuli differed greatly from what was expected. We expected all men to have a decrease in testosterone in response to child pictures, and for the difference to be more pronounced

in fathers. We expected all men to have an increase in testosterone levels after viewing sexual stimuli, and for the increase to be most pronounced in non-fathers. Non-fathers show no significant change across all three conditions. Fathers' testosterone increased slightly, but not significantly in response to viewing happy, sad, and neutral pictures of their child. This trend could be due to a similar mechanism as in the infant cry findings, such that fathers experience an increase in testosterone level that calls them to "alertness" (Fleming, Corter et al. 2002). Additionally, higher testosterone is associated with increased paternal care in monogamous mice (Trainor and Marler 2002). However, this increase was only a trend and should therefore be reconsidered with a larger sample size. On the other hand, the decrease in paternal testosterone in response to visual sexual stimuli was dramatic. Previous findings have shown testosterone levels to be correlated with interest and viewing time in visual sexual stimuli (Rupp and Wallen 2007). It's possible that the drop in testosterone caused fathers to be disinterested in the sexual stimuli. We also considered the possibility that seeing sexual stimuli so soon after seeing pictures of their own child was uncomfortable to the men. Similarly, it is possible that babies have evolved to manipulate paternal physiology, such that fathers are disinterested in sexual stimuli, and therefore do not divide resources between parenting and mating. It is also possible that because the men see sexual, nonsexual, and male pictures, the effect of the sexual pictures was diluted by the other conditions. However, much more information would need to be obtained before any conclusions could be drawn. In order to understand more about the decrease in testosterone levels, post-scan questionnaires could include questions about how the men felt in response to viewing the sexual stimuli.

Testosterone and S-NS reaction time were not significantly correlated but trended in the positive direction, indicating that the higher baseline testosterone tends to be associated with longer S-NS reaction time. If this trend were to become significant with more subjects, analyses could be done to determine if the correlation was mediated by brain activity in the vlPFC, which is negatively correlated with both reaction time and testosterone levels.

Brain Structure

VBM analyses revealed that fathers have greater gray matter volume in the tail of the caudate and in the premotor cortex compared with non-fathers. The premotor cortex is associated with anticipation of objects and movement and observation of movement (Buccino, Binkofski et al. 2001). The caudate is involved in a variety of functions including visual learning and movement (Schendan, Searl et al. 2003; Tricomi, Delgado et al. 2004). However, it is unclear why either of these areas should necessarily be larger in fathers than non-fathers. It is possibly that these results are false positives; due to the more liberal statistical threshold ($p<0.005$) than is traditionally used with VBM analyses. Interestingly, at a threshold of 0.05, we found results that supported our initial hypotheses. At this lower threshold, we found that fathers had greater gray matter density in the rACC and dorsal lateral prefrontal cortex. As mentioned above the dlPFC is involved in top-down decision-making and cortical control of action and emotion, and these results could indicate that fathers are better at such task-oriented behavior (Wagner, Maril et al. 2001). The rACC is involved in emotional control and attention during emotional tasks (Bush, Luu et al. 2000). The Meyer-Lindenberg group has done

extensive research showing the function connectivity and volume of the rostral (or supragenual) cingulated cortex and the amygdala and prefrontal regions to be important for normal emotional processing, especially emotional regulation (Pezawas, Meyer-Lindenberg et al. 2005; Stein, Wiedholz et al. 2007). Given their work, it is possible that fathers have larger rACC volumes, and are thus better able to regulate emotion and override and suppress amygdala activity. One should be cautious in interpreting these results, however, given the low threshold and high possibility of false positive results.

Non-fathers showed greater gray matter density than fathers in the superior temporal sulcus, the temporal pole, and areas of the visual cortex. The STS is important for biological motion, especially movement of the face, lips, and eyes, and is thus also important for social interaction and cognition (Pelphrey, Morris et al. 2004). The temporal pole is also associated with face processing, specifically emotional face processing (Olson, Plotzker et al. 2007). Our results were somewhat unexpected, given that it seems important for fathers to be able to interpret the emotions of their child's face, and to select that face out of a group of unknown faces. However, it is possible that non-fathers with a mating reproductive strategy may be better able to interpret social cues and perceptions and thus acquire more mates through apt social interaction. Again, it is important to take caution in interpreting these results because they are at a lower threshold than what is typically used, and thus may be showing false positive data. These analyses should be conducted again with a larger sample size to determine which results are truly gray matter differences and which are false positives.

Overall, several of our results supported our hypotheses, while others differed substantially from what we expected. There is still much to be determined about the data,

especially with the full sample size of 50 fathers and 50 non-fathers. The full study also includes genetic analyses of vasopressin and oxytocin genes, two neuropeptides that have been implicated in parenting and mating behavior in both humans and other mammals. Future research could focus on the effect of visual sexual stimuli on fathers' testosterone levels, and compare those levels to the men's subjective reporting of their experience. It would be expected that subjective reports of arousal would be correlated with changes in testosterone level. Post-scan questionnaires could also be amended to include the men's perception of the difficulty of the choice reaction time task to determine whether perceived difficulty is correlated with reaction time, brain activity, and hormone level. Additionally, the study could be expanded to a longitudinal design in which both non-fathers' and fathers' marital and parental status is tracked, to determine which, if any, non-fathers become fathers, and if their marital/parental status correlates with Life History Theory surveys. The longitudinal study could also investigate differences in brain structure over time in fathers, or as men become fathers, as has already been done in women (Kim, Leckman et al. 2010). The future results and directions of this study will do much to further the understanding of the underlying brain structures and mechanisms of paternal behavior.

Tables and Figures

Table 1: Brain Regions activated during reaction time epoch, p<0.001

Brain Region **S > NS**	**Voxels**	**Peak X**	**Peak Y**	**Peak Z**	**Peak t**	**p**
R Fusiform gyrus	2675	29	-50	-9	8.37	1.1 e -6
Occipital Lobe Extrastriate Body Thalamus Lateral Hypothalamus Amygdala						
R Planum Polare	390	35	7	-12	5.42	0.000003
R Insula R Ventral Lateral PFC R Posterior Oribital Gyrus						
R Medial Frontal Gyrus	91	41	-2	27	4.76	0.000022
R Precentral Gyrus	93	5	4	57	4.55	0.000044
R Cingulate Gyrus, BA 31	135	5	-35	30	4.79	0.00002
L Anterior Cingulate	96	-7	25	15	5.46	0.000002
L Occipital lobe	1846	-43	-62	-9	7.74	0.000001
Extrastriate Body						
NS > S						
L Cuneus	31	-4	-92	6	-4.77	0.000022

Table 2: Brain regions activated post-reaction time epoch, p<0.001

Brain Region **S>NS**	**Voxels**	**Peak X**	**Peak Y**	**Peak Z**	**Peak t**	**p**
L Fusiform Gyrus	9078	-37	-71	-12	11.48	1.6 e -6
R Post central gyrus	24	53	-29	42	4.18	0.000142
R Precental gyrus	887	41	-2	30	6.26	0.000001
R Superior Frontal Gyrus	781	2	7	57	5.75	0.000001
L Uncus	26	-22	7	-24	4.22	0.000125
L Inferior Frontal Gyrus	163	-43	1	24	5.37	0.000003
L Superior Frontal Gyrus	73	-28	43	27	5.10	0.000007
L Insula	301	-37	16	-9	5.61	0.000001

Table 3: Correlation of S-NS reaction time with brain activity in the S-NS contrast, p<0.01

Brain Region	Voxels	Peak X	Peak Y	Peak Z	Peak r	p
Precuneus L	260	-49	-77	39	-0.55	0.000099
Middle Frontal Gyrus L	95	-31	13	45	-0.55	0.000093
Inferior Frontal Gyrus L	53	-46	40	12	-0.46	0.00159

Table 4: Correlation of baseline testosterone with brain activity in the S-NS contrast, p<0.01

Brain Region	Voxels	Peak X	Peak Y	Peak Z	Peak t	p
L Fusiform Gyrus	9078	-37	-71	-12	11.48	1.6 e -6
R Post central gyrus	24	53	-29	42	4.18	0.000142
R Precental gyrus	887	41	-2	30	6.26	0.000001
R Superior Frontal Gyrus	780	2	7	57	5.75	0.000001
L Uncus	26	-22	7	-24	4.21	0.000125
L Inferior Frontal Gyrus	163	-43	1	24	5.37	0.000003
L Superior Frontal Gyrus	73	-28	43	27	5.09	0.000007
L Insula	301	-37	16	-9	5.61	0.000001

Table 5: Non-fathers > fathers VBM, p<0.005

Brain Region	Voxels	Z-MAX	Z-MAX X (vox)	Z-MAX Y (vox)	Z-MAX Z (vox)
Superior Temporal Sulcus L	450	1	74	53	34
Precuneus R, Occipital lobe L	432	1	37	24	54
lateral occipital cortex L	317	1	70	32	32
Temporal pole L	227	1	61	71	21
Middle Temporal gyrus R	72	0.999	15	36	39
Supramarginal gyrus L	57	1	75	40	59
Lateral Occipital Cortex L	49	0.999	67	30	61
Medial Orbital Frontal Cortex L	30	1	55	75	29
Middle Temporal Gyrus L	29	0.999	77	37	33
Inferior Temporal Gyrus R	28	0.999	18	40	28

Table 6: Fathers > Non-fathers VBM, p<0.005

Brain Region	Voxels	Z-MAX	Z-MAX X	Z-MAX Y	Z-MAX Z
Cerebellum	256	1	27	22	15
Premotor cortex BA 6 L	116	0.999	56	64	70
Caudate L	76	1	55	54	48
Middle Frontal Gyrus BA45 L	36	1	73	76	50
Frontal Pole R	33	0.999	37	91	54
Paracingulate/cingulate gyrus R	20	0.999	39	87	44

a b c d

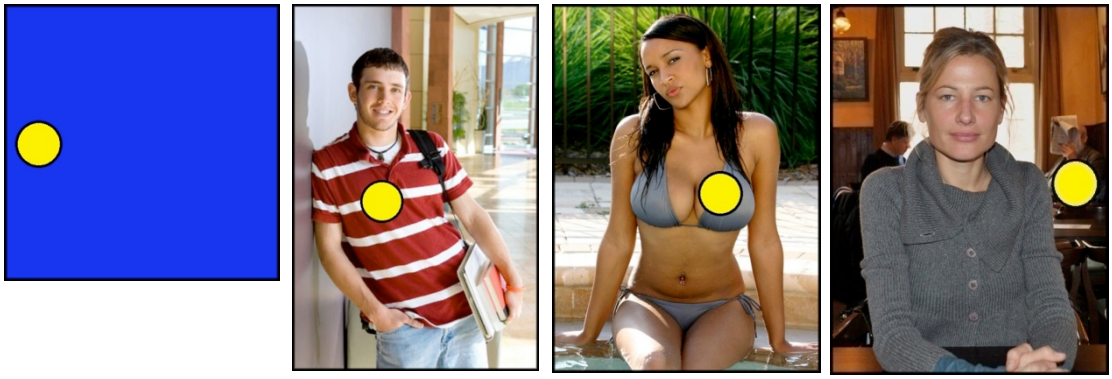
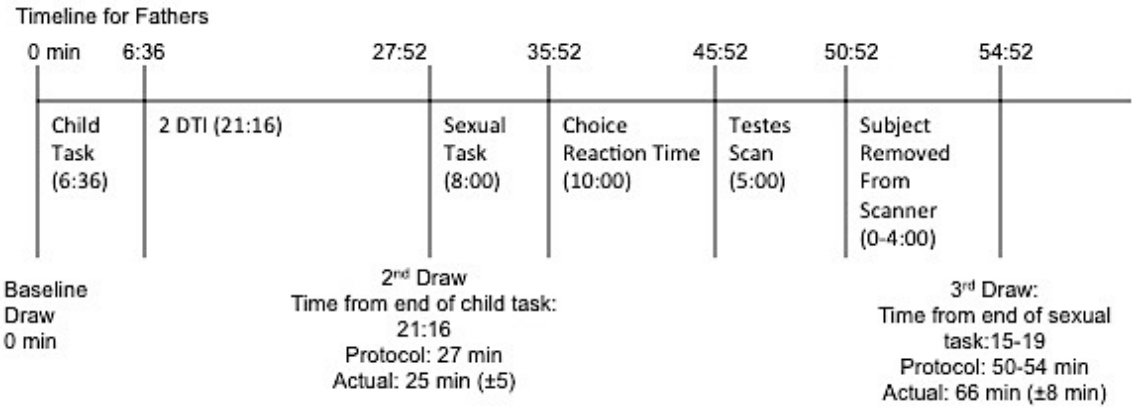


Figure 1: Example images from the choice reaction time task: a) blank b) male c) sexual d) nonsexual

Figure 2: Scan and Blood draw Timeline for a: fathers and b: non-fathers

a



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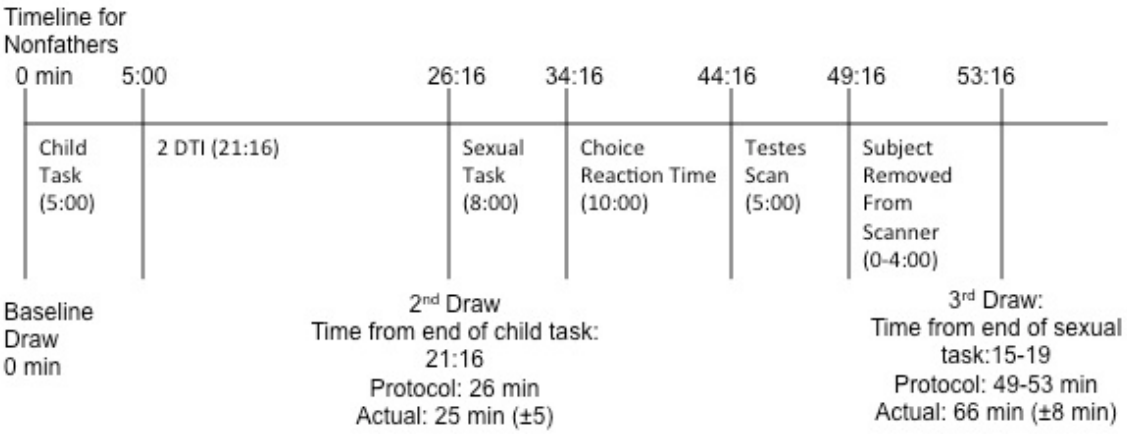

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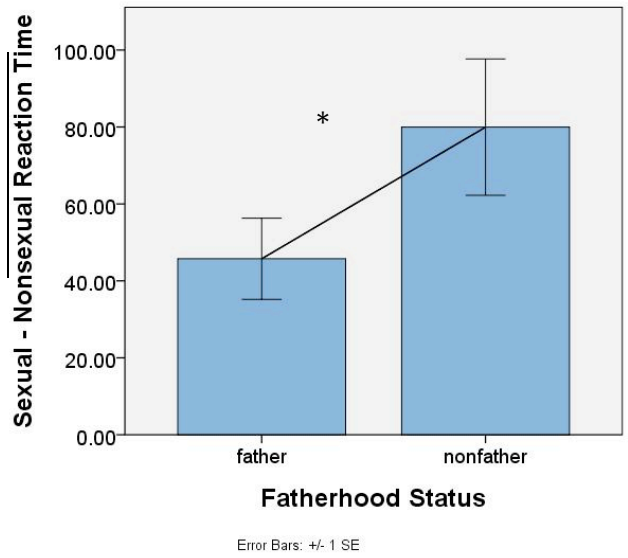

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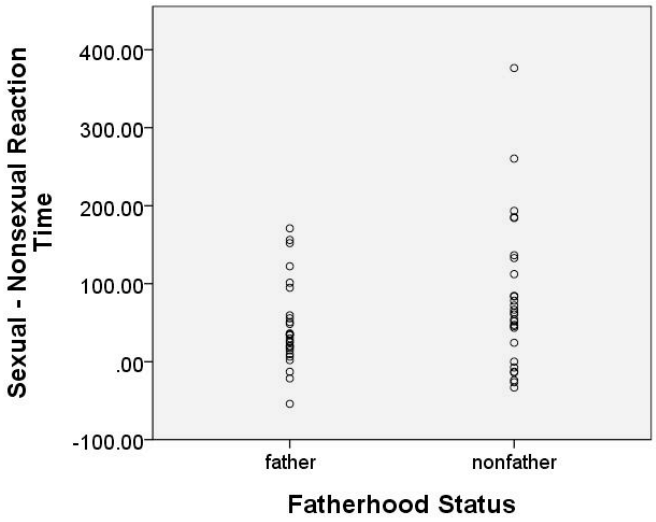


Figure 3: Dot task reaction time as a function of fatherhood status. a) group mean ± 1 S.E., b) individual subject data.

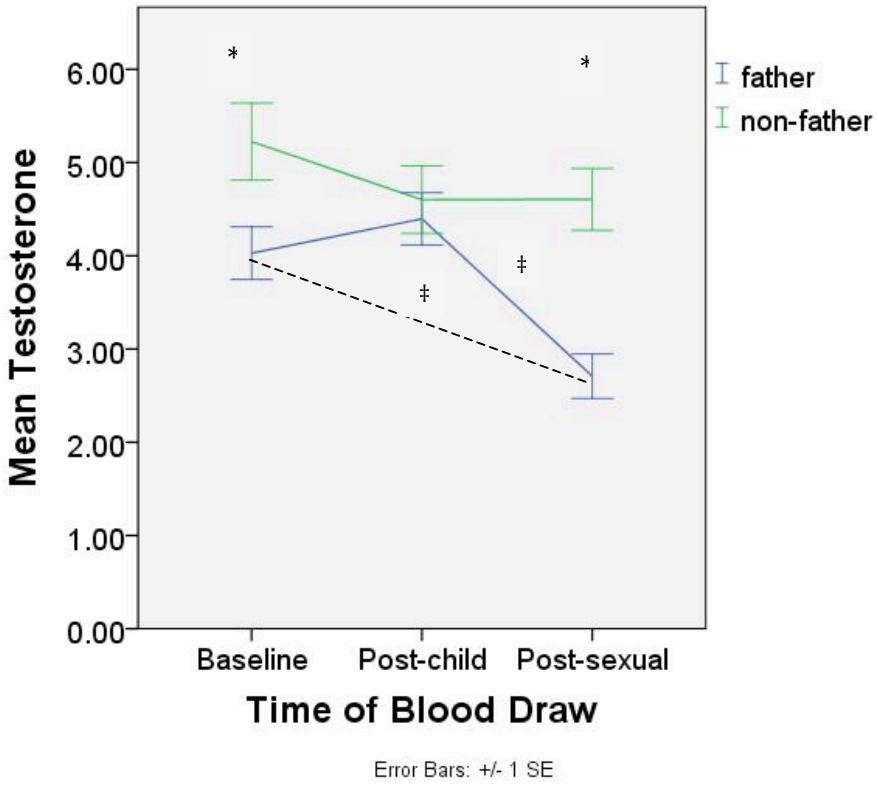


Figure 4: Testosterone levels (mean ± 1 SEM) for fathers and non-fathers at baseline (left), after child stimuli (middle) and after sexual stimuli (right). *: significant difference between fathers and non-fathers at time 1 and time 3, ‡: significant difference among fathers between draw 3 and draws 2 and 1

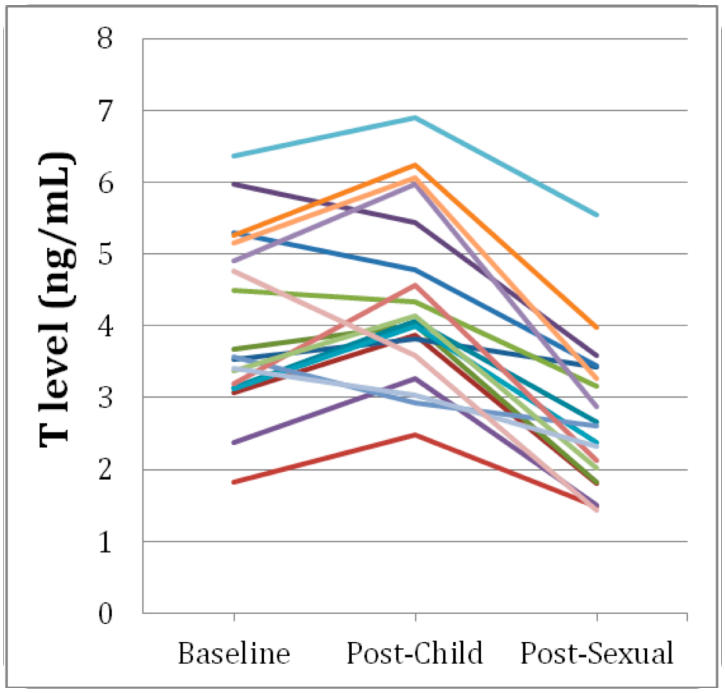


Figure 5a: Individual Testosterone Data – Fathers: Each line represents testosterone levels in ng/mL at each of the three blood draws for one father.

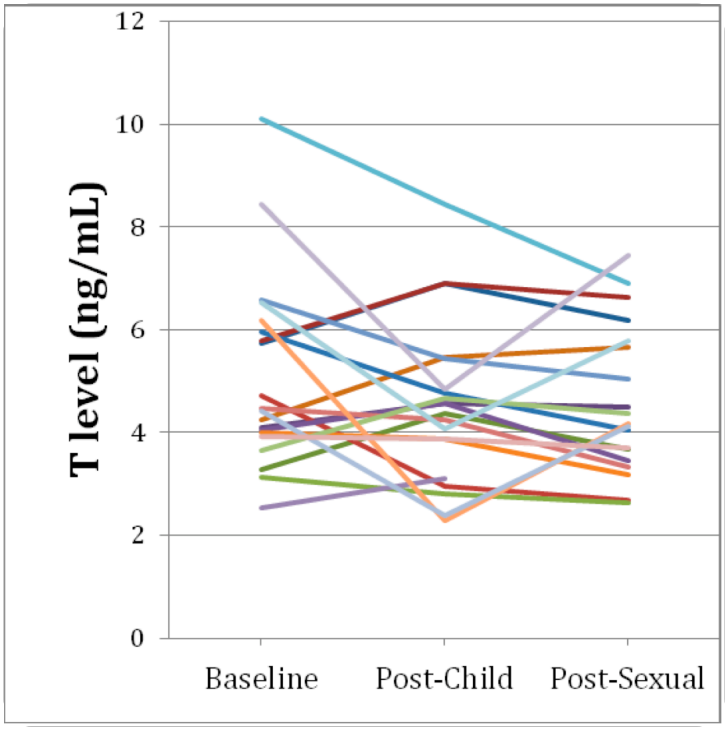


Figure 5b: Individual Testosterone Data – Non-fathers: Each line represents testosterone levels in ng/mL at each of the three blood draws for one Non-father.

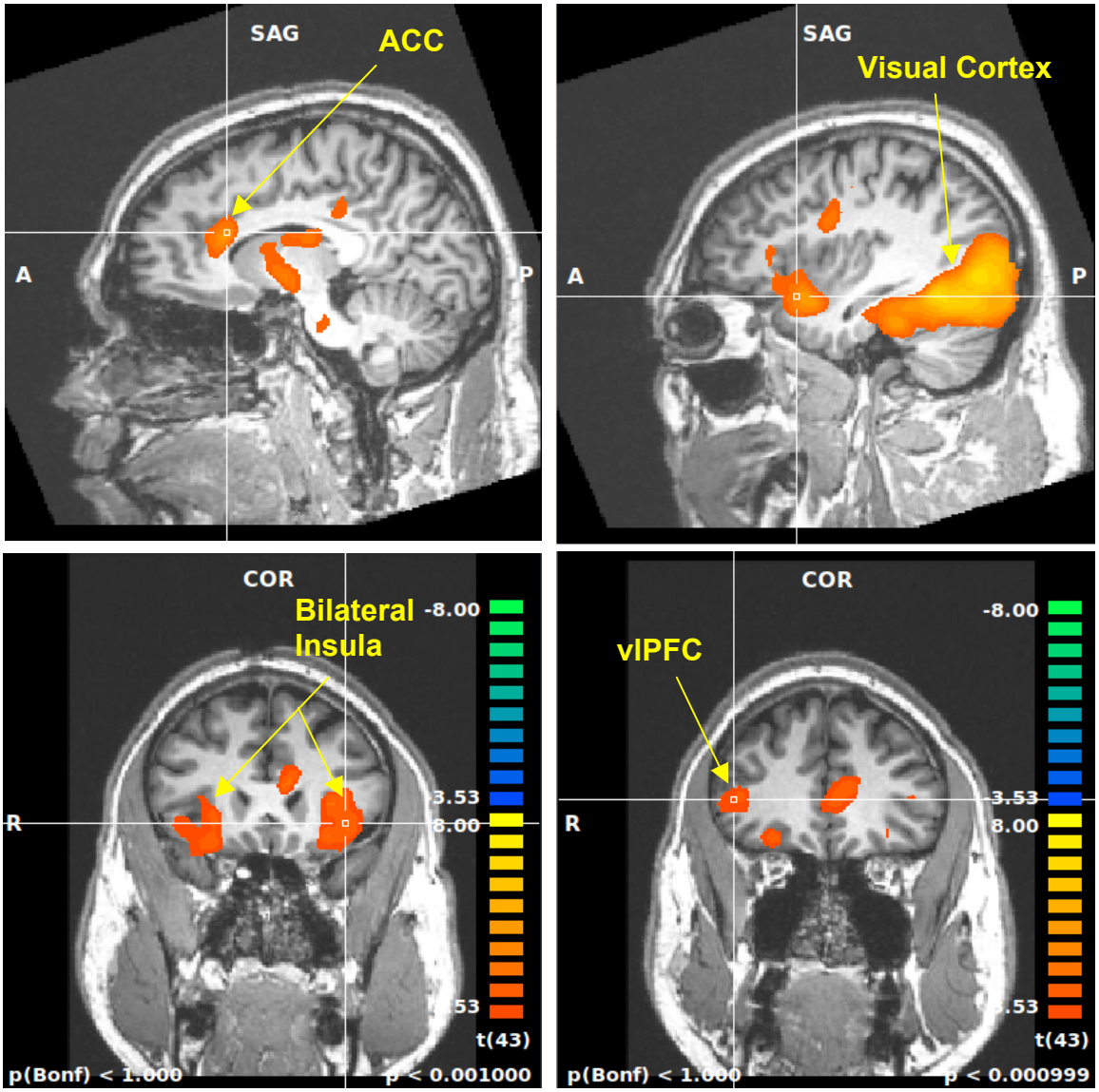


Figure 6: S>NS contrast during reaction epoch. Areas in orange are more active in the sexual condition as compared to the non-sexual condition. Areas in blue are less active in the sexual condition than the non-sexual condition. T statistic map is thresholded at $p<0.001$, uncorrected, with a 20 voxel spatial extent threshold.

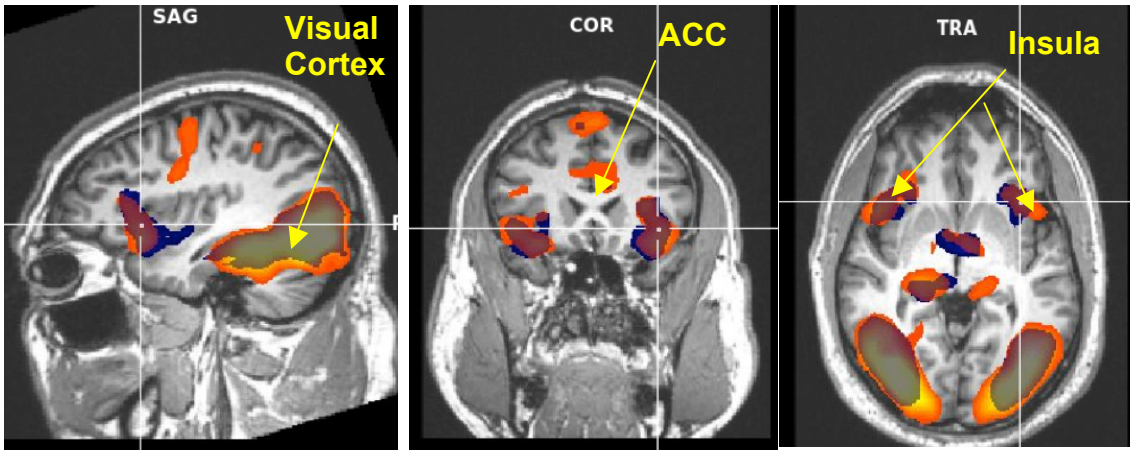
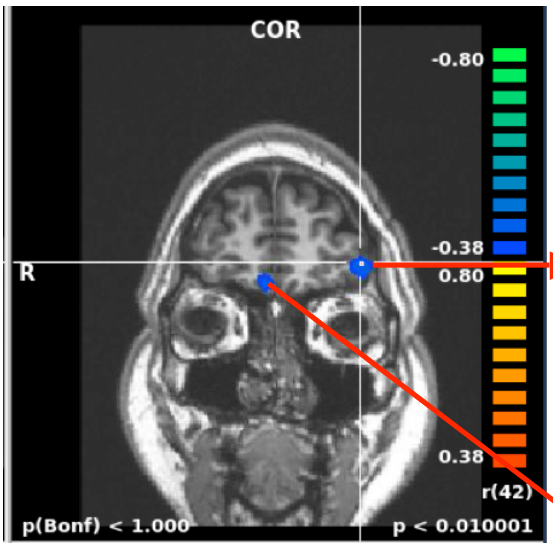


Figure 7: Overlap of S>NS contrast during and after the reaction time epoch. Areas in blue show the time before reaction, areas in orange show the time after reaction. T statistic map is thresholded at $p<0.001$, uncorrected, with a 20 voxel spatial extent threshold.

a



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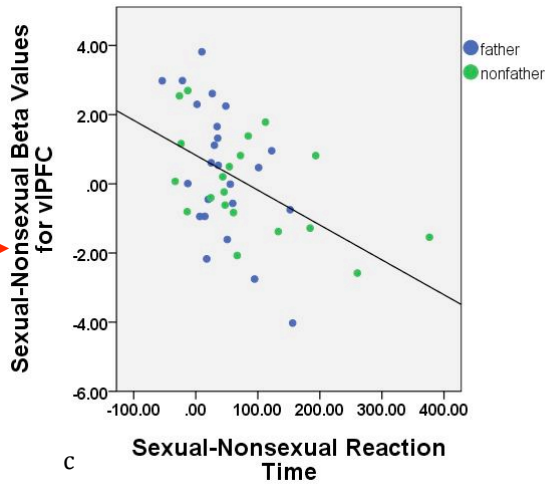

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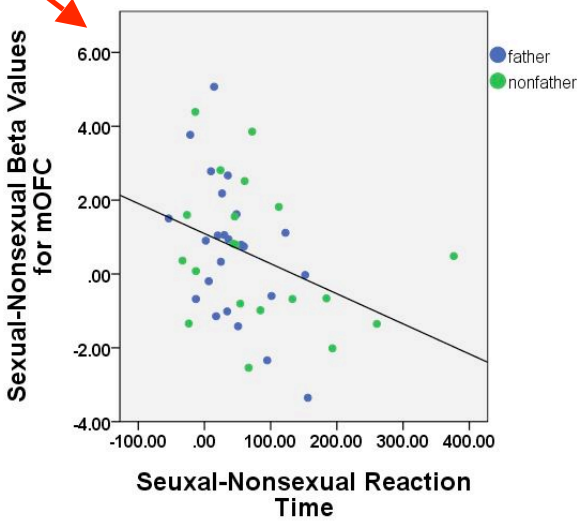


Figure 8: (a) Negative correlation of Reaction Time with Brain activity in the Sexual-Nonsexual Condition in the prefrontal regions (b) vlPFC (r=-0.475, p=0.01) and (c) mOFC (r=-0.354, p=0.018). The covariate map is thresholded at $p < 0.01$, with a 10 voxel spatial extent threshold.

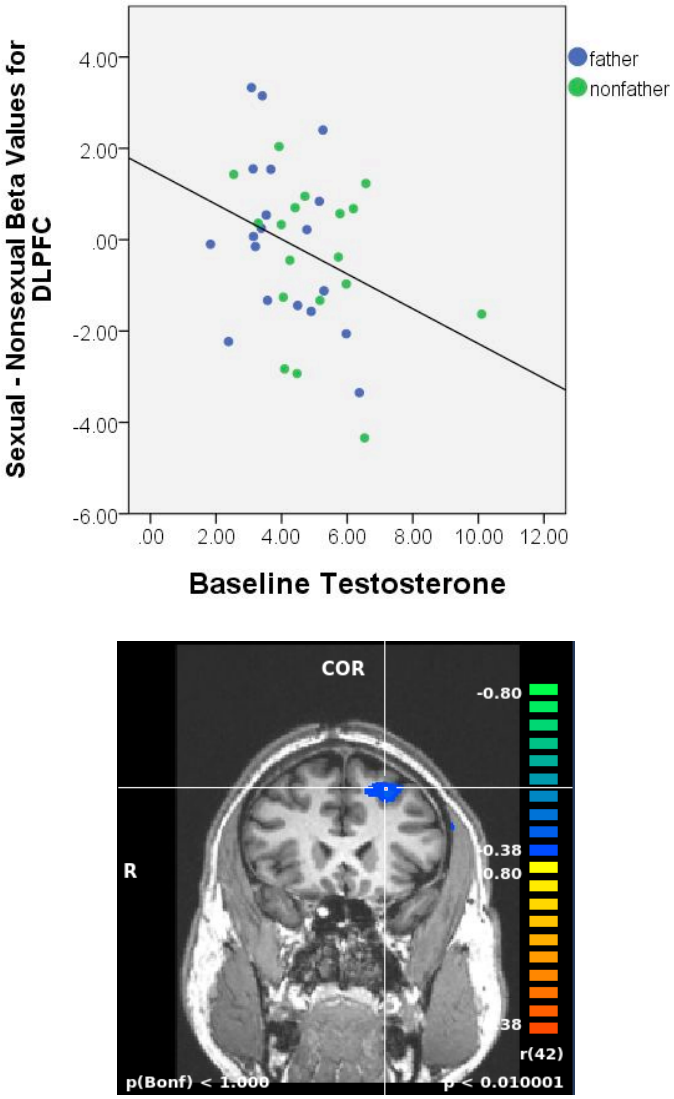


Figure 9: Correlation of Baseline Testosterone with Brain Activity in the Sexual-Nonsexual Condition in the dlPFC

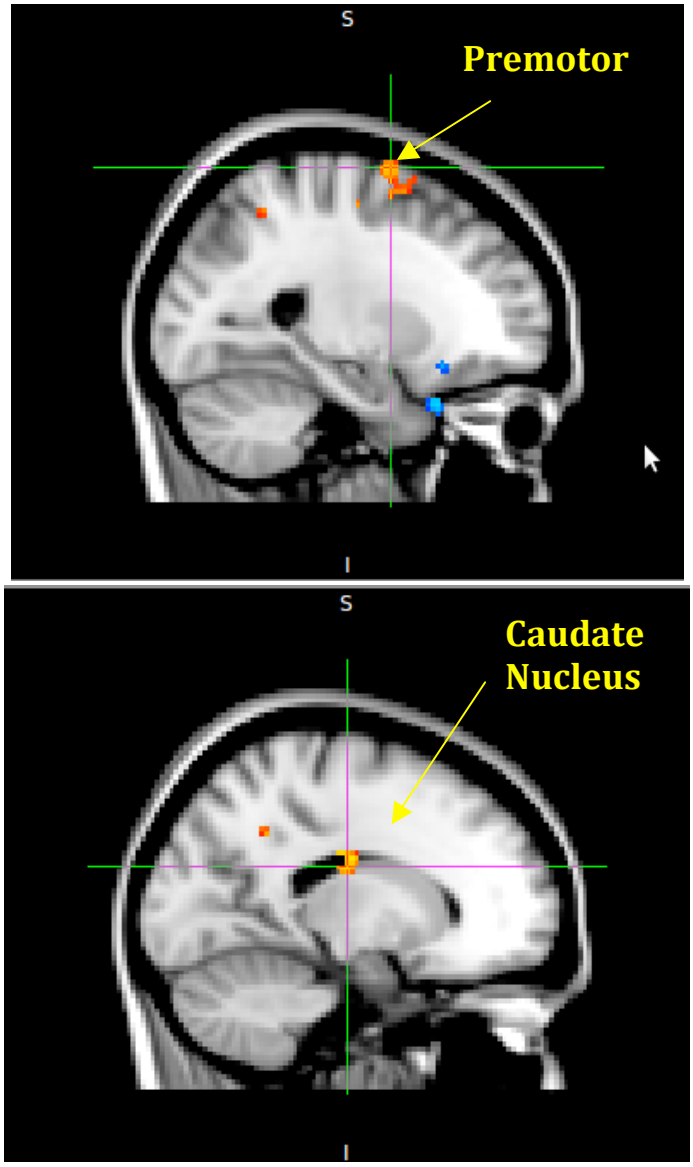
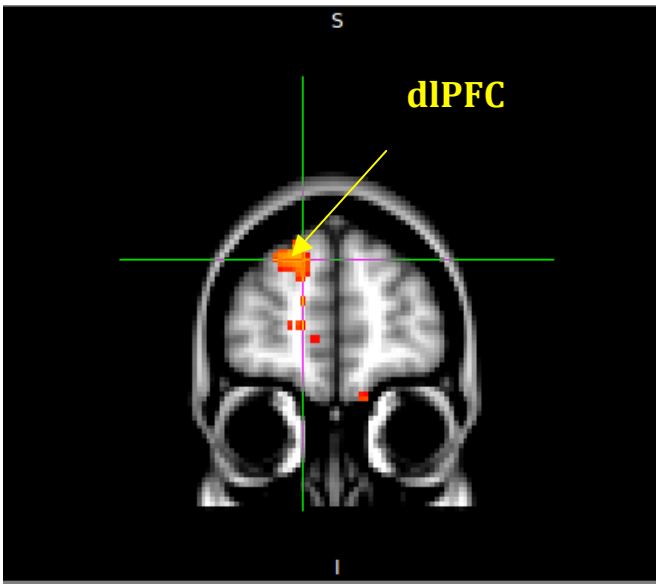


Figure 10: Structural differences of fathers v. non-fathers. Areas in orange are areas where fathers have more gray matter density than non-fathers. T statistic map is thresholded at $p<0.005$, uncorrected.



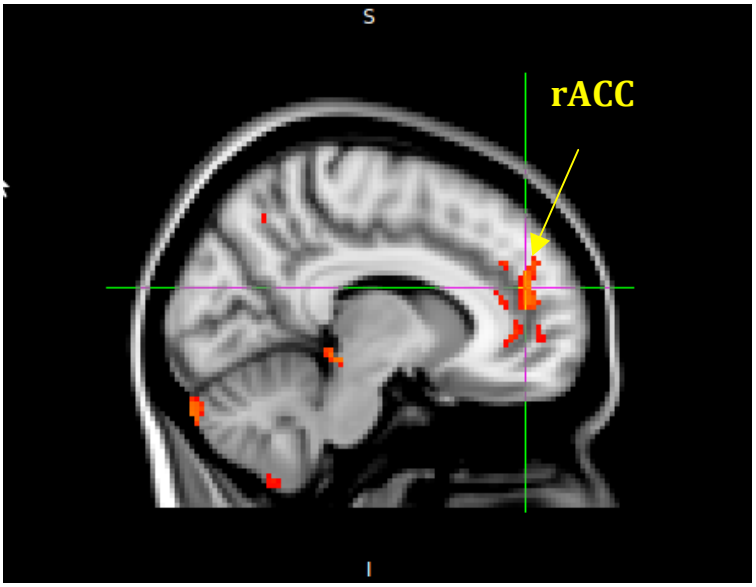


Figure 11: Areas of greater gray matter density in fathers than non-fathers in the (a) dlPFC and (b) rACC. T statistic map is thresholded at $p<0.05$, uncorrected.

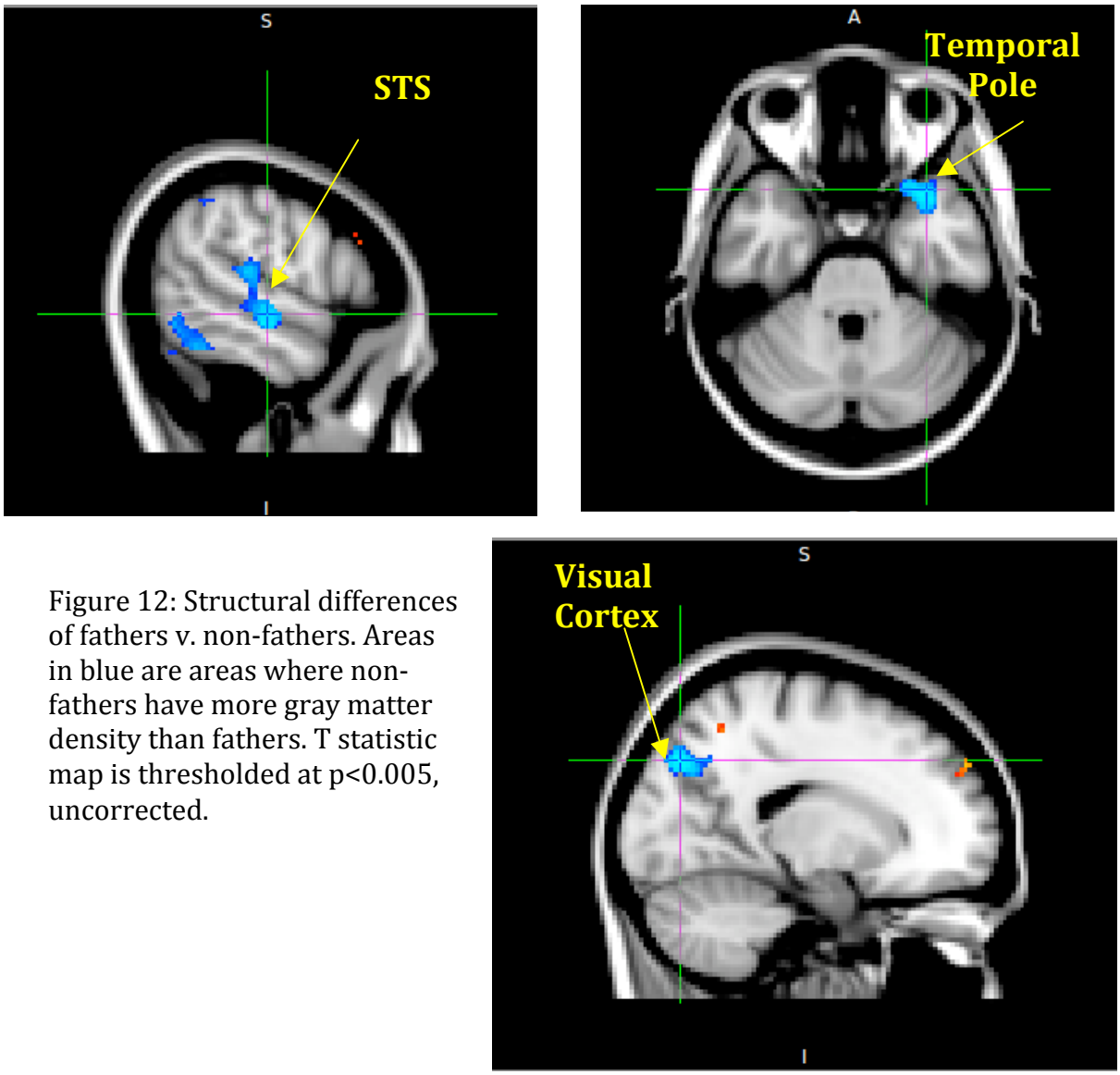


Figure 12: Structural differences of fathers v. non-fathers. Areas in blue are areas where non-fathers have more gray matter density than fathers. T statistic map is thresholded at $p<0.005$, uncorrected.

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