Mother's but Not Father's Education Predicts General Fluid Intelligence in Emerging Adulthood: Behavioral and Neuroanatomical Evidence

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Abstract: Lower parental education impairs cognitive abilities of their offspring such as general fluid intelligence dependent on the prefrontal cortex (PFC), but the independent contribution of mother's and father's education is unknown. We used an individual difference approach to test whether mother's and father's education independently affected general fluid intelligence in emerging adulthood at both the behavioral and neural level. Behaviorally, mother's but not father's education accounted for unique variance in general fluid intelligence in emerging adulthood (assessed by the Raven's advanced progressive matrices). Neurally, the whole-brain correlation analysis revealed that the regional gray matter volume (rGMV) in the medial PFC was related to both mother's education and general fluid intelligence but not father's education. Furthermore, after controlling for mother's education, the association between general fluid intelligence and the rGMV in medial PFC was no longer significant, indicating that mother's education plays an important role in influencing the structure of the medial PFC associated with general fluid intelligence. Taken together, our study provides the first behavioral and neural evidence that mother's education is a more important determinant of general cognitive ability in emerging adulthood than father's education. *Hum Brain Mapp* 36:4582–4591, 2015. © 2015 Wiley Periodicals, Inc.

Key words: mother's education; father's education; intelligence; prefrontal cortex; voxel-based morphometry

INTRODUCTION

Parental education, a nonmaterial indicator of early socioeconomic status can impact a broad range of cognitive, social, and physiological functions of offspring [Lorant

et al., 2003; Pinquart and Sörensen, 2000; Roberts et al., 1999]. Exposure to low parental education, for example, appears to have deleterious effects on their offspring, such as damaged cognitive functioning [Roberts et al., 1999], poorer physical health [Cochrane et al., 1982], lower self-

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esteem [Pinquart and Sörensen, 2000], lower life satisfaction [Pinquart and Sörensen, 2000], higher depression [Lorant et al., 2003], and adverse neurobiological changes, such as alterations in the prefrontal cortex (PFC) and hippocampus and higher cortisol levels [e.g., Gianaros et al., 2007, 2011; Jednoróg et al., 2012; Noble et al., 2012, 2015; Piras et al., 2011; Sheridan et al., 2012, 2013; Wolf et al., 2008]. Whereas the effects of parental education have received empirical attention, little is known about the independent contribution of mother's and father's education.

An aspect of human cognitive ability known as "general fluid intelligence" appears to be particularly vulnerable to the negative effects of low parental education. General fluid intelligence is a major dimension of individual differences and refers to reasoning and novel problem-solving ability [Cattell, 1971]. Previous studies have demonstrated that lower parental education is associated with lower intellectual levels of their offspring at different age stages [Gianaros et al., 2007; Kagan and Moss, 1959; Neiss and Rowe, 2000; Roberts et al., 1999; Zhou et al., 2007]. Furthermore, mother's and father's education are found to explain unique variance (nearly 10%) in general fluid intelligence of their children [Mercy and Steelman, 1982; Zhou et al., 2007], suggesting the independent contribution of mother's and father's education to children's intellectual development. Notably, mother's education tends to have a greater impact on the intellectual development of their children at 6 to 11 years of age than father's education [Mercy and Steelman, 1982]. As the primary childcare provider, mothers teach their children appropriate behavior, academic, language, and social skills. Because mothers spend much more time rearing and disciplining their children than fathers do [Baxter, 2002; Casper and Bianchi, 2002], children might be more influenced by their mothers. This previous research has been conducted in children; it is not clear whether this pattern would be seen in early adult life.

At the neural level, a large body of research in individuals who have suffered brain damage has consistently linked general fluid intelligence with the function of the PFC [e.g., Duncan et al., 1995; Krawczyk et al., 2010; Roca et al., 2009; Waltz et al., 1999; Woolgar et al., 2010]. Furthermore, in healthy individuals, general fluid intelligence is consistently linked with the brain structure of the PFC, especially its medial portion [Frangou et al., 2004; Goh et al., 2011; Gong et al., 2005; Haier et al., 2004; Ullén et al., 2008; Wilke et al., 2003]. In addition, parental education has also been linked with developmental alterations in the PFC including medial and lateral PFC [Gianaros et al., 2007, 2011; Kishiyama et al., 2009; Lawson et al., 2013; Noble et al., 2015; Sheridan et al., 2012]. These findings suggest that the PFC, especially the medial PFC may be an important site linking parental education to general fluid intelligence. However, little is known whether the independent contribution of mother's and father's education to the development of the medial PFC associated with general fluid intelligence.

To answer these questions, we used well-validated assessments of parental education and general fluid intelligence,

and voxel-based morphometry (VBM) methodology, which can be used to explore the structural neural correlates of individual differences in behavior [e.g., DeYoung et al., 2010; Li et al., 2014; Takeuchi et al., 2014; for a review, see Kanai and Rees, 2011]. First, we conducted a multiple regression analysis to examine whether mother's and father's education independently affected general fluid intelligence in emerging adulthood. Given that mother's education tends to have a greater impact on the intellectual development in children than father's education [Mercy and Steelman, 1982], we hypothesized that mother's education would be able to more strongly predict general fluid intelligence in young adults than father's education. Second, we related, for the first time, regional gray matter volume (rGMV) to mother's and father's education to identify the unique structural correlates of mother's and father's education. Based on the previous neuroscience findings on parental education [Gianaros et al., 2007, 2011; Kishiyama et al., 2009; Lawson et al., 2013; Noble et al., 2015; Sheridan et al., 2012], we expected that mother's education would be able to more strongly predict the PFC morphometry than father's education. Third, we conducted another correlation analysis between rGMV and general fluid intelligence to identify the structural correlates of individual differences in general fluid intelligence. Notably, some previous studies have reported a positive correlation between the medial PFC volume and general fluid intelligence [e.g., Gong et al., 2005; Haier et al., 2004; Ullén et al., 2008; Wilke et al., 2003], while others have reported a negative correlation [Krawczyk et al., 2010; Goh et al., 2011; Smolker et al., 2014]. Interestingly, the studies reporting the negative correlation mainly focused on young adults (mean age: 17–22 years). Thus, we expected that there would be a negative correlation between general fluid intelligence and the medial PFC volume in young adults. Finally, we examined the relationship between the cluster of the medial PFC associated with general fluid intelligence and the cluster associated with parental education. We expected that the cluster of the medial PFC associated with general fluid intelligence would substantially overlap with the cluster associated with parental education, especially mother's education.

METHODS

Participants

Two hundred and ninety-nine college students [159 females; mean age = 21.57 years, standard deviation (SD) = 1.01] from Beijing Normal University were recruited as paid participants. This study is as part of an ongoing research project to explore the associations among gene, environment, brain, and behavior [e.g., Kong et al., 2015a,c; Wang et al., 2012, in press]. Data that are irrelevant to the scope of this study were not reported here. Participants were screened to confirm healthy development by a self-report questionnaire before the scanning, and thus, those who had past or current neurological or

psychiatric disorders were excluded. The majority of the participants were right-handed ($n = 280$) based on a single-item handedness questionnaire ["Are you (a) right-handed, (b) left-handed, (c) mixed-handed?"]. Both behavioral and MRI protocols were approved by the Institutional Review Board of Beijing Normal University. Written informed consent was obtained from all participants prior to study onset.

Measures

Parental education

Parental education was assessed by an item that asked about level of education for mother and father, respectively. The possible educational categories were 1 = never went to school; 2 = primary school; 3 = middle school; 4 = high school or business, trade, or vocational school after middle school; 5 = business, trade, or vocational school after high school or junior college graduate; 6 = college graduate; and 7 = postcollege (masters, doctoral, or other professional). According to previous studies [e.g., Hanson et al., 2011; Nobel et al., 2012], the number of years of education of parents was roughly calculated, and the range of education spanned from 0 (never went to school) to 18 years (postcollege). Two participants were removed from further analysis because they did not report education levels of their parents or report only education levels of their father or mother. In this study, mother education was related to father education ($r = 0.65$, $p < 0.001$). According to the literature, multicollinearity occurred when features are highly correlated, that is, with a correlation of 0.90 and above [Hair et al., 2010; Hayduk, 1987], so multicollinearity did not appear to be problem in this study.

General fluid intelligence

Participants' general fluid intelligence was measured using the Raven's Advanced Progressive Matrices (APM) test. The APM test contains 36 multiple-choice items of abstract reasoning, in which participants are asked identify the missing figure required to complete a larger pattern. The number of correctly answered items was used as a measure of each individual's general cognitive ability. Five participants were removed from further analysis because they did not conduct the test and one participant was removed because his scores fell beyond 4 SDs below the mean.

Family social status

To rule out the effect of family social status at various points in development (e.g., childhood, adolescence, and adulthood) on brain structures and general intelligence, we also assessed participants' general family subjective social status (SSS) using a graphical representation of a

ladder with 10 rungs (1 being the lowest rank; 10 being the highest rank) [Adler et al., 2000]. The instructions are as follows: "Think of this ladder as representing where people stand in our society. At the top of the ladder are the people who are the best off—those who have the most money, most education, and best jobs. At the bottom are the people who are the worst off—who have the least money, least education, and the worst jobs or no jobs. The higher up your parents are on this ladder, the closer they are to the people at the very top and the lower your parents are, the closer they are to the people at the very bottom. Please mark a cross on the rung on the ladder where your parents would place them when you are in childhood, adolescence, and adulthood." In this study, the correlations among family SSS childhood, adolescence, and adulthood ranged 0.67–0.87, so multicollinearity did not appear to be problem in this study.

MRI Acquisition

Participants were scanned using a Siemens 3T scanner (MAGENTOM Trio, a Tim system) with a 12-channel phased-array head coil at BNU Imaging Center for Brain Research, Beijing, China. MRI structural images were acquired using a 3D magnetization prepared rapid gradient echo (MP-RAGE) T1-weighted sequence (TR/TE/TI = 2,530/3.39/1,100 ms, flip angle = 7° , FOV = 256×256 mm). One hundred and twenty-eight contiguous sagittal slices were acquired with 1×1 mm in-plane resolution and 1.33 mm slab thickness for whole brain coverage.

Image Processing for Voxel-Based Morphometry

MRI images were processed using the SPM8 (Statistical Parametric Mapping, Wellcome Department of Imaging Neuroscience, London, UK). Each image was first displayed in SPM8 to screen for artifacts or gross anatomical abnormalities. Six participants whose images had excessive scanner artifacts or showed gross anatomical abnormalities were excluded. For better registration, the origin of the brain was manually set to the anterior commissure for each participant. Segmentation of T1-weighted anatomical images into gray matter (GM) was done using the unified segmentation in SPM8. Subsequently, we performed Diffeomorphic Anatomical Registration through Exponentiated Lie (DARTEL) algebra for registration, normalization, and modulation [Ashburner, 2007]. GM images were rigidly aligned and resampled to $2 \times 2 \times 2$ mm³ and normalized to a study-specific template in MNI152 space. To ensure that local GM volumes were conserved, the image intensity of each voxel was modulated by multiplying the Jacobian determinants derived from the normalization to preserve the volume of tissue from each structure after warping. Then, registered images were then smoothed with an 8-mm full-width at half-maximum Gaussian

TABLE I. Demographic and psychometric measures

Variables	Range	Mean	SD	Skewness	Kurtosis
Age	18–25	21.55	1.01	−0.07	0.67
Total GMV	0.39–0.60	0.49	0.04	0.22	−0.13
Total WMV	0.42–0.70	0.54	0.05	0.57	0.17
Childhood family SSS	1–9	3.88	1.86	0.40	−0.62
Adolescence family SSS	1–9	4.27	1.74	0.25	−0.48
Adulthood family SSS	1–9	4.71	1.74	0.03	−0.60
Father's education	1–18	10.47	3.46	−0.16	−0.62
Mother's education	1–18	9.40	3.71	−0.11	−0.45
Fluid intelligence	14–35	26.09	4.06	−0.16	−0.22

Note: Total GMV, Total gray matter volume; Total WMV, Total white matter volume; SSS, Subjective social status. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

kernel. To exclude noisy voxels, the modulated images were masked using absolute masking with a threshold of 0.2.

Statistical Analysis of VBM

Statistical analyses of the GMV data were performed using SPM8. To explore the brain structures associated with individual differences in father's and mother's education, we carried out two whole-brain correlation analyses. To detect whether the brain structures were specific to father's or mother's education, the corresponding type of education, as well as age, sex and total GMV, were removed as confounding factors when calculating partial correlations between rGMV and father's or mother's education.

In addition, to explore the brain structures associated with individual differences in general fluid intelligence, we carried out a whole-brain correlation analysis. Age, sex, and total GMV were removed as confounding factors. We conducted all statistical analyses using a mask volume that comprised the entire brain with the exception of the cerebellum. For all analyses, the cluster-level statistical threshold was set at $P < 0.05$, and corrected at the nonstationary cluster correction [Hayasaka et al., 2004] according to the random field theory with an underlying voxel level of $P < 0.001$.

Prediction Analysis

To confirm the robustness of the relation between rGMV and behavioral performance, a machine-learning approach with balanced fourfold cross-validation combined with linear regression was conducted [Cohen et al., 2010; Qin et al., 2014; Supekar et al., 2013]. Parent education as an independent variable and the rGMV of the regions as a dependent variable were treated as input to a linear regression algorithm. The $r_{(\text{predicted}, \text{observed})}$ was used to measure how well the independent variable predicts the dependent variable. The correlation was estimated using a

balanced fourfold cross-validation procedure in following steps. First, data were divided into four folds such that the distributions of these variables were balanced across folds. Second, a linear regression model was built using three folds, leaving out one fold, and this model was then used to predict the data in the left-out fold (i.e., predicted values). This procedure was repeated four times to compute a final $r_{(\text{predicted}, \text{observed})}$ representing the correlation between the values predicted by the regression model and the observed values. Nonparametric testing approach was used to assess the statistical significance of the model. The empirical null distribution of $r_{(\text{predicted}, \text{observed})}$ was estimated by generating 1,000 surrogate datasets under the null hypothesis that there was no association between rGMV and behavioral performance. We generated each surrogate dataset D_i of size equal to the observed dataset by permuting the labels on the observed data points. The $r_{(\text{predicted}, \text{observed})i}$ (i.e., $r_{(\text{predicted}, \text{observed})}$ of D_i) was computed using the observed labels of D_i and predicted labels using the fourfold-balanced cross-validation procedure described above. This procedure produced a null distribution of $r_{(\text{predicted}, \text{observed})}$ for the regression model. The statistical significance (P value) of the model was then determined by counting the number of $r_{(\text{predicted}, \text{observed})i}$ greater than $r_{(\text{predicted}, \text{observed})}$ and then dividing that count by the number of D_i datasets (i.e., 1,000).

RESULTS

Table I shows means, SDs, skewness, and kurtosis for all measures. The kurtosis and skewness of all the scores ranged from -1 to $+1$, which indicated the normality of the data [Marcoulides and Hershberger, 1997]. Total GMV and WMV (white matter volume) were not correlated with father's education, mother's education or general fluid intelligence ($r = 0.01$ – 0.11 , $ps > 0.05$). As expected, we also observed a moderate relation of family SSS in childhood, adolescence and adulthood with father's education ($r_{\text{childhood}} = 0.33$, $P < 0.001$; $r_{\text{adolescence}} = 0.42$, $P < 0.001$; $r_{\text{adulthood}} = 0.40$, $P < 0.001$) as well as mother's education

Figure 1.

Brain regions that are correlated with mother's education. **A:** The rGMV in the medial PFC was negatively correlated with mother's education. The coordinate is shown in the MNI stereotactic space. **B:** Scatter plots depicting correlations between

rGMV in the medial PFC and individual variability in general fluid intelligence after adjusting age, sex, and total GMV ($r = -0.43$, $P < 0.001$). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

($r_{\text{childhood}} = 0.39$, $P < 0.001$; $r_{\text{adolescence}} = 0.45$, $P < 0.001$; $r_{\text{adulthood}} = 0.45$, $P < 0.001$), suggesting that parental education and family social status were two correlated but distinct constructs. Note that all the correlations were adjusted for the effect of sex and age.

To test the independent contribution of mother's and father's education to general fluid intelligence in emerging adulthood, we conducted a multiple regression analysis. The results revealed that mother's but not father's education accounted for 12.7% of the variance in general fluid intelligence ($R^2 = 0.127$; $F_{[1, 288]} = 20.52$; $P < 0.001$). Specifically, there was a moderate relation between mother's education and general fluid intelligence ($\beta = 0.33$, $P < 0.001$), whereas the relation between father's education and general fluid intelligence was not significant ($\beta = 0.04$, $P = 0.541$), suggesting that only mother's education made a significant contribution to general fluid intelligence. Furthermore, this effect remained significant after controlling for age, sex, and total GMV ($\beta = 0.32$, $P < 0.001$). To examine whether this effect is specific to mother's education, we also excluded the general factor of family SSS. Behaviorally, we observed a significant relationship of general fluid intelligence with family SSS ($r_{\text{childhood}} = 0.23$, $P < 0.001$; $r_{\text{adolescence}} = 0.26$, $P < 0.001$; $r_{\text{adulthood}} = 0.22$, $P < 0.001$). After controlling for family SSS in childhood, adolescence and adulthood, the effect of mother's education on general fluid intelligence remained significant ($\beta = 0.30$, $P < 0.001$), suggesting the specificity to mother's education. Next, we explored the links between brain

structure, parental education, and general fluid intelligence.

We first explored the structural correlates of father's and mother's education by correlating the scores of father's and mother's education with the GMV of each voxel across the whole brain. After controlling for age, sex, global GMV and father's education, mother's education had a significant negative correlation with the rGMV in the medial PFC, mainly including ventromedial, dorsomedial, and anterior cingulate cortices (MNI coordinate: -4 , 38 , -22 ; $r = -0.43$, $t = -5.07$; Cluster size = 3,925 voxels; $P < 0.001$; See Fig. 1). No other significant relations were observed. However, after controlling for age, sex, global GMV, and mother's education, father's education had no significant correlation with the rGMV in any cluster. To examine the robustness of the relation between rGMV and mother's education, we extracted the rGMV of the aforementioned cluster from the participants and applied a balanced fourfold cross-validation approach combined with linear regression (i.e., prediction analysis). After adjusting for father's education and family SSS in childhood, adolescence and adulthood, mother's education reliably predicted individual differences in the rGMV in the medial PFC ($r_{(\text{predicted}, \text{observed})} = 0.28$; $P < 0.001$).

Then, we explored the structural correlates of general fluid intelligence by correlating the scores of general fluid intelligence with the GMV of each voxel across the whole brain. After controlling for age, sex, and total GMV, general fluid intelligence had a significant negative correlation

Figure 2.

Brain regions that are correlated with general fluid intelligence. **A:** The rGMV in the medial PFC was negatively correlated with general fluid intelligence. The coordinate is shown in the MNI stereotactic space. **B:** Scatter plots depicting correlations

between rGMV in the medial PFC and individual variability in general fluid intelligence after adjusting age, sex and total GMV ($r = -0.27$, $P < 0.001$). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

with the rGMV in the medial PFC, mainly including ventromedial, dorsomedial, and anterior cingulate cortices (MNI coordinate: 0, 52, 2; $r = -0.27$, $t = -4.78$; Cluster size = 1,094 voxels; $P < 0.001$; See Fig. 2). No other significant relations were observed. To examine the robustness of the relation between the rGMV and general fluid intelligence, we conducted a prediction analysis. We found that structural differences in the medial PFC reliably predicted general fluid intelligence in adulthood ($r_{(\text{predicted}, \text{observed})} = 0.24$, $P < 0.001$). These results indicated that correlations between rGMV and general fluid intelligence largely resembled the pattern of correlations between rGMV and mother's education. In addition, the number of the overlapping voxels was calculated to quantify the extent to which the cluster of the medial PFC related to general fluid intelligence overlapped with the cluster related to mother's education. We found that the number of the overlapping voxels was 796, which made up 73% of all the voxels associated with general fluid intelligence (i.e., 796/1,094; See Fig. 3). Therefore, it is likely that mother's education and general fluid intelligence may share common neural substrates in the medial PFC.

Finally, we additionally conducted a whole-brain correlation analysis to examine how the structural neural correlates of general fluid intelligence were influenced by mother's education. Mother's education, as well as age, sex, and total GMV were removed as confounding factors. After controlling for mother's education, the correlation between general fluid intelligence and the rGMV in the medial PFC was no longer significant (MNI coordinate: 2,

52, 4; $t = -3.52$; Cluster size = 31 voxels; $P = 0.889$). No other significant correlations were observed. Furthermore, a small-volume correction (SVC) was performed in the medial PFC region (11,011 voxels) selected from the Wake Forest University Pick Atlas [Maldjian et al., 2003]. The SVC analysis revealed that the correlation between general fluid intelligence and the rGMV in the medial PFC was still non-significant (MNI coordinate: 2, 52, 4; $t = -3.52$; Cluster size = 31 voxels; $P = 0.419$). Taken together, these results indicated that mother's education plays an important role in influencing the structure of the medial PFC associated with general fluid intelligence.

DISCUSSION

In this study, we used an individual difference approach to investigate the independent contribution of mother's and father's education to general cognitive ability in emerging adulthood at both the behavioral and neural level. Behaviorally, we found that mother's but not father's education accounted for the unique variance in general fluid intelligence in emerging adulthood. Neurally, we found that the rGMV in the medial PFC was related to both mother's education and general fluid intelligence but not father's education. Furthermore, after controlling for mother's education, the association between general fluid intelligence and the medial PFC volume was no longer significant, indicating mother's education plays an important role in influencing the rGMV in the medial PFC associated

Figure 3.

The overlapping region related to both mother's education and general fluid intelligence. The blue represents the region associated with mother's education. The red represents the region associated with general fluid intelligence. The green represents the overlapping region associated with both mother's education and general fluid intelligence. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

with general fluid intelligence. Taken together, our study provides the first behavioral and neural evidence that mother's education is more important in influencing general cognitive ability in emerging adulthood than father's education.

The finding that mother's education made a significant, independent contribution to general fluid intelligence of their offspring rather than father's education is partly consistent with research showing that mother's education tends to have a greater impact on the intellectual development of their children at 6–11 years of age than father's education [Mercy and Steelman, 1982]. This may be because as the primary childcare provider, mothers teach their children appropriate behavior and academic skills and spend much more time rearing and disciplining their children than fathers [Baxter, 2002; Casper and Bianchi 2002]. However, as mentioned previously, mother's and father's education were found to independently predict general fluid intelligence of children [Mercy and Steelman, 1982; Zhou et al., 2007]. This implies that the relative contribution of mother's and father's education differs across development. Specifically, there is a temporary effect of fathers' education during childhood/adolescence, but this effect vanishes by young adulthood and mothers' effects are observable in young adulthood. In addition, we argue that the relation between parental education and intellectual levels of offspring might be also of an environmental

nature despite of high heritability of brain structure and intelligence [Pol et al., 2006; Toga and Thompson, 2005], because the impact of mother's and father's education should be equally strong if parental education is merely a proxy for genetic stock.

Neurally, we found that the cluster of medial PFC related to general fluid intelligence substantially overlapped with the cluster related to mother's education. Furthermore, after controlling for mother's education, the medial PFC volume was no longer related to general fluid intelligence. Based on these findings, the structure of the medial PFC may mediate the link between mother's education and general fluid intelligence. On the one hand, the association of the medial PFC volume with general fluid intelligence is broadly consistent with several structural imaging studies of intelligence in healthy populations, which found a correlation between general fluid intelligence and GM signal in the medial PFC [Frangou et al., 2004; Goh et al., 2011; Gong et al., 2005; Haier et al., 2004; Ullén et al., 2008; Wilke et al., 2003]. Previous studies have demonstrated the medial PFC participates in several higher order functions including selective attention, response selection, reasoning, decision making and goal-directed behaviors [Dalley et al., 2004; Hitchcott et al., 2007; Kroger et al., 2002; Rushworth et al., 2004]. All these kind of functions seem to play an important role in approaching and solving the tasks in the standard tests of human intelligence. On the other hand, the finding that mother's education predicts the medial PFC volume provides a neurobiological basis for the deleterious effects of low mother's education. Previous neuroimaging studies suggest that as an indicator of socioeconomic disadvantage, lower parental education is associated with developmental alterations in medial prefrontal regions including ACC and dorsomedial PFC [Gianaros et al., 2011; Lawson et al., 2013; Noble et al., 2015]. Our findings further demonstrate that the medial PFC is specific to mother's education during the emerging adulthood period. In short, our findings demonstrate a neurobiological mechanism (i.e., the medial PFC) linking mother's education with general fluid intelligence of their offspring in early adult life.

In addition, in accordance with our expectation, we observed a negative correlation between general fluid intelligence and medial PFC volume. This finding is consistent with some previous studies that mainly focused on young adults (mean age: 17–22 years) [Krawczyk et al., 2010; Goh et al., 2011; Smolker et al., 2014]. This negative correlation has been often observed in recent studies of young adults in which less GM volume in the PFC is associated with better behavioral performance including creativity [Jung et al., 2010], interference processing [Takeuchi et al., 2012], achievement motivation [Takeuchi et al., 2014], reality monitoring [Buda et al., 2011], emotional intelligence [Takeuchi et al., 2011] and mental well-being [Kong et al., 2014, 2015b]. We speculated that the direction of the correlation (i.e., positive versus negative) might

depend on the age of the sample studied. Indeed, after the early phase of development, GM tends to decrease, probably caused by synaptic pruning and myelination [Huttenlocher et al., 1982; Huttenlocher and Dabholkar, 1997; Paus, 2005; Sowell et al., 2001]. Furthermore, developmental studies of intelligence suggest that children with the highest level of intelligence show the most vigorous cortical thinning (which is observed as a decrease in rGMV) in the medial PFC during adolescence [Shaw et al., 2006]. Further, more intelligent children have a slightly thinner cortex than children with lower IQs, and this relationship becomes more pronounced as a function of age due to faster developmental cortical thinning in more intelligent children [Schnack et al., 2015]. In more intelligent adults, this relation reverses so that by the age of 42 a thicker cortex is associated with higher intelligence [Schnack et al., 2015]. Thus, a possible interpretation of our data is that more intelligent young adults may have experienced a more efficient synaptic pruning or cortical myelination, leading to a less GM morphometry in the medial PFC.

This study had limitations, and the prospect of addressing them yields exciting directions for future research. First, to our knowledge, the independent contribution of mother's and father's education to fluid intelligence has not been tested in early adolescents, so future research could explore whether this sensitive period for the impact of father's education on intellectual development can be extended to early adolescence. Second, the findings of the present study relied on exclusively the measure of GMV of brain structure. Future research could explore the association between the brain and parental education through other types of measures on the brain structure (e.g., cortical thickness and surface area) and measures on functional brain activity (e.g., task-related functional activity and resting-state brain activity). Third, the temporal sequence of our measures in the study prohibits us from making strong claims about the effects of the early environment, so caution should be taken when interpreting the outcomes. In addition, although our data demonstrated the neurobiological pathways linking mother's education with adult intelligence, no measure on parents' child-rearing attitudes and caregiving behaviors (e.g., parents' time with children) is available in this study. Therefore, another critical task for future studies is to identify potential factors, especially parents' beliefs and caregiving behaviors through which mother's education influences offspring's general intelligence.

REFERENCES

- Adler NE, Epel ES, Castellazzo G, Ickovics JR (2000): Relationship of subjective and objective social status with psychological and physiological functioning: Preliminary data in healthy, White women. *Health Psychol* 19:586–592.
- Ashburner J (2007): A fast diffeomorphic image registration algorithm. *Neuroimage* 38:95–113.
- Baxter J (2002): Patterns of change and stability in the gender division of household labour in Australia, 1986–1997. *J Sociol* 38: 399–424.
- Buda M, Fornito A, Bergström ZM, Simons JS (2011): A specific brain structural basis for individual differences in reality monitoring. *J Neurosci* 31:14308–14313.
- Casper LM, Bianchi SM (2001): Continuity and change in the American family. Thousand Oaks, CA: Sage.
- Cattell RB (1971): Abilities: Their structure, growth, and action. Boston, MA: Houghton Mifflin.
- Cochrane SH, Leslie J, O'Hara DJ (1982): Parental education and child health: Intracountry evidence. *Health Policy Educ* 2: 213–250.
- Cohen JR, Asarnow RF, Sabb FW, Bilder RM, Bookheimer SY, Knowlton BJ, Poldrack RA (2010): Decoding developmental differences and individual variability in response inhibition through predictive analyses across individuals. *Front Hum Neurosci* 4:47.
- Dalley JW, Cardinal RN, Robbins TW (2004): Prefrontal executive and cognitive functions in rodents: Neural and neurochemical substrates. *Neurosci Biobehav Rev* 28:771–784.
- DeYoung CG, Hirsh JB, Shane MS, Papademetris X, Rajeevan N, Gray JR (2010): Testing predictions from personality neuroscience: Brain structure and the big five. *Psychol Sci* 21:820–828.
- Duncan J, Burgess P, Emslie H (1995): Fluid intelligence after frontal lobe lesions. *Neuropsychologia* 33:261–268.
- Frangou S, Chitins X, Williams SC (2004): Mapping IQ and gray matter density in healthy young people. *Neuroimage* 23:800–805.
- Gianaros PJ, Horenstein JA, Cohen S, Matthews KA, Brown SM, Flory JD, Critchley HD, Manuck SB, Hariri AR (2007): Perigenual anterior cingulate morphology covaries with perceived social standing. *Soc Cogn Affect Neurosci* 2:161–173.
- Gianaros PJ, Manuck SB, Sheu LK, Kuan DC, Votruba-Drzal E, Craig AE, Hariri AR (2011): Parental education predicts corticostriatal functionality in adulthood. *Cereb Cortex* 21:896–910.
- Goh S, Bansal R, Xu D, Hao X, Liu J, Peterson BS (2011): Neuroanatomical correlates of intellectual ability across the life span. *Dev Cogn Neurosci* 1:305–312.
- Gong Q-Y, Sluming V, Mayes A, Keller S, Barrick T, Cezayirli E, Roberts N (2005): Voxel-based morphometry and stereology provide convergent evidence of the importance of medial prefrontal cortex for fluid intelligence in healthy adults. *Neuroimage* 25:1175–1186.
- Haier RJ, Jung RE, Yeo RA, Head K, Alkire MT (2004): Structural brain variation and general intelligence. *Neuroimage* 23:425–433.
- Hair JF, Black WC, Babin BJ, Anderson RE, Tatham RL (2010): Multivariate data analysis. New Jersey: Pearson Education Inc.
- Hanson JL, Chandra A, Wolfe BL, Pollak SD (2011): Association between income and the hippocampus. *PLoS one* 6:e18712.
- Hayasaka S, Phan KL, Liberzon I, Worsley KJ, Nichols TE (2004): Nonstationary cluster-size inference with random field and permutation methods. *Neuroimage* 22:676–687.
- Hayduk LA (1987): Structural equation modeling with LISREL: Essentials and advances. Baltimore: Johns Hopkins University Press.
- Hitchcott PK, Quinn JJ, Taylor JR (2007): Bidirectional modulation of goal-directed actions by prefrontal cortical dopamine. *Cereb Cortex* 17:2820–2827.
- Huttenlocher PR, Dabholkar AS (1997): Regional differences in synaptogenesis in human cerebral cortex. *J Comp Neurol* 387: 167–178.

- Huttenlocher PR, de Courten C, Garey LJ, Van der Loos H (1982): Synaptogenesis in human visual cortex—evidence for synapse elimination during normal development. *Neurosci Lett* 33: 247–252.
- Jednoróg K, Altarelli I, Monzalvo K, Fluss J, Dubois J, Billard C, Dehaene-Lambertz G, Ramus F (2012): The influence of socioeconomic status on children's brain structure. *PLoS One* 7: e42486.
- Jung RE, Segall JM, Jeremy Bockholt H, Flores RA, Smith SM, Chavez RS, Haier RJ (2010): Neuroanatomy of creativity. *Hum Brain Mapp* 31:398–409.
- Kagan J, Moss HA (1959): Parental correlates of child's IQ and height: a cross-validation of the Berkeley growth study results. *Child Dev* 30:325–332.
- Kanai R, Rees G (2011): The structural basis of inter-individual differences in human behaviour and cognition. *Nat Rev Neurosci* 12:231–242.
- Kishiyama MM, Boyce WT, Jimenez AM, Perry LM, Knight RT (2009): Socioeconomic disparities affect prefrontal function in children. *J Cogn Neurosci* 21:1106–1115.
- Kong F, Ding K, Yang Z, Dang X, Hu S, Song Y, Liu J (2014): Examining gray matter structures associated with individual differences in global life satisfaction in a large sample of young adults. *Soc Cogn Affect Neurosci* 144.
- Kong F, Hu S, Wang X, Song Y, Liu J (2015a): Neural correlates of the happy life: The amplitude of spontaneous low frequency fluctuations predicts subjective well-being. *Neuroimage* 107: 136–145.
- Kong F, Hu S, Xue S, Song Y, Liu J (2015b): Extraversion mediates the relationship between structural variations in the dorsolateral prefrontal cortex and social well-being. *Neuroimage* 105: 269–275.
- Kong F, Liu L, Wang X, Hu S, Song Y, Liu J (2015c): Different neural pathways linking personality traits and eudaimonic well-being: A resting-state functional magnetic resonance imaging study. *Cogn Affect Behav Neurosci* 15:299–309.
- Krawczyk DC, Hanten G, Wilde EA, Li X, Schnelle KP, Merkley TL, Vasquez AC, Cook LG, McClelland M, Chapman SB, Levin HS (2010): Deficits in analogical reasoning in adolescents with traumatic brain injury. *Front Hum Neurosci* 4:1–13.
- Kroger JK, Sabb FW, Fales CL, Bookheimer SY, Cohen MS, Holyoak KJ (2002): Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: A parametric study of relational complexity. *Cereb Cortex* 12:477–485.
- Lawson GM, Duda JT, Avants BB, Wu J, Farah MJ (2013): Associations between children's socioeconomic status and prefrontal cortical thickness. *Dev Sci* 16:641–652.
- Li H, Li W, Wei D, Chen Q, Jackson T, Zhang Q, Qiu J (2014): Examining brain structures associated with perceived stress in a large sample of young adults via voxel-based morphometry. *Neuroimage* 92:1–7.
- Lorant V, Delière D, Eaton W, Robert A, Philippot P, Ansseau M (2003): Socioeconomic inequalities in depression: A meta-analysis. *Am J Epidemiol* 157:98–112.
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003): An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage* 19:1233–1239.
- Marcoulides GA, Hershberger SL (1997): Multivariate statistical methods: A first course. Mahwah, NJ: Lawrence Erlbaum Associates.
- Mercy JA, Steelman LC (1982): Familial influence on the intellectual attainment of children. *Am Sociol Rev* 47:532–542.
- Neiss M, Rowe DC (2000): Parental education and child's verbal IQ in adoptive and biological families in the National Longitudinal Study of Adolescent Health. *Behav Genet* 30:487–495.
- Noble KG, Grieve SM, Korgaonkar MS, Engelhardt LE, Griffith EY, Williams LM, Brickman AM (2012): Hippocampal volume varies with educational attainment across the life-span. *Front Hum Neurosci* 6:307.
- Noble KG, Houston SM, Brito NH, Bartsch H, Kan E, Kuperman JM, Akshoomoff N, Amaral DG, Bloss CS, Libiger O (2015): Family income, parental education and brain structure in children and adolescents. *Nature Neurosci* 18:773–778.
- Paus T (2005): Mapping brain maturation and cognitive development during adolescence. *Trends Cogn Sci* 9:60–68.
- Pinquant M, Sörensen S (2000): Influences of socioeconomic status, social network, and competence on subjective well-being in later life: A meta-analysis. *Psychol Aging* 15:187–224.
- Piras F, Cherubini A, Caltagirone C, Spalletta G (2011): Education mediates microstructural changes in bilateral hippocampus. *Hum Brain Mapp* 32:282–289.
- Pol HEH, Schnack HG, Posthuma D, Mandl RC, Baaré WF, van Oel C, van Haren NE, Collins DL, Evans AC, Amunts K (2006): Genetic contributions to human brain morphology and intelligence. *J Neurosci* 26:10235–10242.
- Qin S, Young CB, Duan X, Chen T, Supekar K, Menon V (2014): Amygdala subregional structure and intrinsic functional connectivity predicts individual differences in anxiety during early childhood. *Biol Psychiatry* 75:892–900.
- Roberts E, Bornstein MH, Slater AM, Barrett J (1999): Early cognitive development and parental education. *Infant Child Dev* 8:49–62.
- Roca M, Parr A, Thompson R, Woolgar A, Torralva T, Antoun N, Manes F, Duncan J (2009): Executive function and fluid intelligence after frontal lobe lesions. *Brain* 132:269.
- Rushworth M, Walton M, Kennerley S, Bannerman D (2004): Action sets and decisions in the medial frontal cortex. *Trends Cogn Sci* 8:410–417.
- Schnack HG, van Haren NEM, Brouwer RM, Evans A, Durston S, Boomsma DI, Kahn RS, Hulshoff Pol HE (2015): Changes in thickness and surface area of the human cortex and their relationship with intelligence. *Cereb Cortex* 25:1608–1617.
- Shaw P, Greenstein D, Lerch J, Clasen L, Lenroot R, Gogtay N, Evans A, Rapoport J, Giedd J (2006): Intellectual ability and cortical development in children and adolescents. *Nature* 440: 676–679.
- Sheridan MA, Sarsour K, Jutte D, D'Esposito M, Boyce WT (2012): The impact of social disparity on prefrontal function in childhood. *PLoS one* 7:e35744.
- Sheridan MA, How J, Araujo M, Schamberg MA, Nelson CA (2013): What are the links between maternal social status, hippocampal function, and HPA axis function in children? *Dev Sci* 16:665–675.
- Smolker H, Depue B, Reineberg A, Orr J, Banich M (2014): Individual differences in regional prefrontal gray matter morphometry and fractional anisotropy are associated with different constructs of executive function. *Brain Struct Funct* 1–16.
- Sowell ER, Thompson PM, Tessner KD, Toga AW (2001): Mapping continued brain growth and gray matter density reduction in dorsal frontal cortex: Inverse relationships during postadolescent brain maturation. *J Neurosci* 21:8819–8829.

- Supekar K, Swigart AG, Tenison C, Jolles DD, Rosenberg-Lee M, Fuchs L, Menon V (2013): Neural predictors of individual differences in response to math tutoring in primary-grade school children. *Proc Natl Acad Sci U S A*, 110:8230–8235.
- Takeuchi H, Taki Y, Sassa Y, Hashizume H, Sekiguchi A, Fukushima A, Kawashima R (2011): Regional gray matter density associated with emotional intelligence: Evidence from voxel-based morphometry. *Hum Brain Mapp* 32:1497–1510.
- Takeuchi H, Taki Y, Sassa Y, Hashizume H, Sekiguchi A, Nagase T, Nouchi R, Fukushima A, Kawashima R (2012): Regional gray and white matter volume associated with Stroop interference: Evidence from voxel-based morphometry. *Neuroimage* 59:2899–2907.
- Takeuchi H, Taki Y, Nouchi R, Sekiguchi A, Kotozaki Y, Miyauchi CM, Yokoyama R, Iizuka K, Hashizume H, Nakagawa S (2014): Regional gray matter density is associated with achievement motivation: evidence from voxel-based morphometry. *Brain Struct Funct* 219:71–83.
- Toga AW, Thompson PM (2005): Genetics of brain structure and intelligence. *Annu Rev Neurosci* 28:1–23.
- Ullén F, Forsman L, Blom Ö, Karabanov A, Madison G (2008): Intelligence and variability in a simple timing task share neural substrates in the prefrontal white matter. *J Neurosci* 28:4238–4243.
- Waltz JA, Knowlton BJ, Holyoak KJ, Boone KB, Mishkin FS, de Menezes Santos M, Thomas CR, Miller BL (1999): A system for relational reasoning in human prefrontal cortex. *Psychol Sci* 10:119–125.
- Wang R, Li J, Fang H, Tian M, Liu J (2012): Individual differences in holistic processing predict face recognition ability. *Psychol Sci* 23:169–177.
- Wang Y, Kong F, Huang L, Liu J: Neural correlates of biased responses: The negative method effect in the rosenberg self-esteem scale is associated with right amygdala volume. *J Pers* (in press).
- Wilke M, Sohn J-H, Byars AW, Holland SK (2003): Bright spots: Correlations of gray matter volume with IQ in a normal pediatric population. *Neuroimage* 20:202–215.
- Wolf JM, Nicholls E, Chen E (2008): Chronic stress, salivary cortisol, and α -amylase in children with asthma and healthy children. *Biol Psychol* 78:20–28.
- Woolgar A, Parr A, Cusack R, Thompson R, Nimmo-Smith I, Torralva T, Roca M, Antoun N, Manes F, Duncan J (2010): Fluid intelligence loss linked to restricted regions of damage within frontal and parietal cortex. *Proc Natl Acad Sci U S A* 107:14899–14902.
- Zhou SJ, Baghurst P, Gibson RA, Makrides M (2007): Home environment, not duration of breast-feeding, predicts intelligence quotient of children at four years. *Nutrition* 23:236–241.