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Brain networks for working memory and factors of intelligence assessed in males and females with fMRI and DTI

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ABSTRACT

Neuro-imaging studies of intelligence implicate the importance of a parietal–frontal network. One unresolved issue is whether this network underlies a general factor of intelligence (*g*) or other specific cognitive factors. A second unresolved issue is whether males and females use different parts of this network. Here we obtained intelligence factors (general, speed of reasoning, spatial, memory, and numerical) from a large set of tests completed by 6929 young adults, 40 of whom (21 males, 19 females) also completed DTI and fMRI during a working memory *n*-back task. Within brain areas activated during this task, correlations were computed between percent activation and scores on the intelligence factors. The main findings were: (1) individual differences in activation during the *n*-back task were correlated to the general intelligence factor (*g*), as well as to distilled estimates (removing *g*) of speed of reasoning, numerical ability, and spatial ability, but not to memory, (2) the correlations were mainly bilateral for females and unilateral for males, and (3) differences in the integrity of the axonal connections were also related to the functional findings showing that integrity of interhemispheric connections was positively correlated to some intelligence factors in females but negatively correlated in males. This study illustrates the potential for identifying aspects of the neural basis of intelligence using a combination of structural and functional imaging.

1. Introduction

Neuro-imaging studies of the underlying structural and functional anatomy of intelligence implicate areas throughout the brain, irrespective of the intelligence tests used. Jung and Haier (2007) characterized these findings as mostly, but not exclusively, in frontal and parietal areas. They proposed a model of how these areas may form overlapping networks underlying individual differences in intelligence: the Parieto-Frontal Integration Theory—P-FIT. The P-FIT areas represent stages of information processing from posterior sensory perception to abstraction in parietal areas to anterior hypothesis testing and decision-making. Integration of information among the areas is key. Based on functional imaging studies that found inverse correlations between regional brain activation and performance on intelligence tests (Haier et al., 1988; Neubauer & Fink, 2009) the P-FIT includes the hypothesis that efficient flow of information around these networks is related to intelligence. Similar networks have been identified for performance on fundamental cognitive tasks including aspects of attention and memory (Cabeza & Nyberg, 2000; Naghavi & Nyberg, 2007; Wager, Jonides, & Reading, 2004; Wager & Smith, 2003), although inverse correlations with such tasks are not reported, possibly because fundamental cognitive tasks used

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in imaging studies usually are chosen to minimize individual differences in performance.

Since intelligence tests tap more than one cognitive domain, it remains to be seen if the P-FIT or other models of brain networks represent a general factor of intelligence (*g*), common among all tests, or more specific group factors like memory or spatial ability. So far, only two structural imaging studies have extracted a *g*-factor score from a battery of tests and then correlated these and other more specific group factor scores (with *g* removed) to gray matter (Colom et al., 2009; Haier et al., 2009). Both studies showed similar results for a spatial factor, but not for a *g*-factor, suggesting that there may not be a single neural basis for *g* (Haier et al., 2009). Johnson et al. (2008) also, for example, extracted other cognitive factors with *g* removed in a small sample and showed some gray matter correlates different than those associated with *g*.

Functional imaging studies of networks related to intelligence have not yet used *g*-factor scores as dependent variables, instead relying on single tests like the Raven Progressive Matrices Test (Gray, Chabris, & Braver, 2003; Haier et al., 1988; Lee et al., 2006; Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997). The interpretation of functional imaging data, moreover, is constrained by the task performed during the imaging, unlike structural imaging (Toga & Thompson, 2005), so task selection is a key element of research design. Two functional imaging studies with fMRI (Gray et al., 2003; Waiter et al., 2009) have used the working memory *n*-back task because working memory is highly related to intelligence (Colom, Abad, Quiroga, Shih, & Flores-Mendoza, 2008; Colom et al., 2005; Colom, Rebollo, Palacios, Juan-Espinosa, & Kyllonen, 2004; Engle, 2002; Grabner, Fink, Stipacek, Neuper, & Neubauer, 2004; Kane, Hambrick, & Conway, 2005; Oberauer, Schulze, Wilhelm, & Suss, 2005). These two fMRI studies of intelligence using the *n*-back test report that activation in frontal and parietal areas is correlated to single intelligence test scores. Inverse correlations are not reported. All the subjects were males.

In addition to issues about the use of single test scores rather than factor scores, another unresolved issue concerns sex differences. A number of imaging studies show male/female differences related to intelligence (Haier, Jung, Yeo, Head, & Alkire, 2005; Luders et al., 2008; Schmithorst & Holland, 2007; Sowell et al., 2007) and other cognitive abilities (Haier & Benbow, 1995; Jausovec & Jausovec, 2008). Findings regarding brain efficiency also show strong sex differences (Neubauer, Fink, & Schrausser, 2002) that may be related to any number of brain differences between males and females (e.g. (Luders et al., 2004; Rabinowicz, Dean, Petetot, & de Courten-Myers, 1999). Due to cost, most imaging studies focus on one sex (usually males) or partial out sex when male and female samples are combined to increase statistical power at the cost of obscuring any actual sex differences. In our view, separate analyses for males and females are required to explore any differences that may be unique to the study sample or to a more general finding.

Here we extend the two previous *n*-back studies to determine fMRI correlates of intelligence using factors derived from a battery of tests rather than a single test score; these factors are independent of the *g*-factor. Based on the structural studies of (Colom et al., 2009) and (Haier et al., 2009), we hypothesize that individual factors will have functional correlates different from the g-factor. Further, we present analyses separately for males and females to test whether the P-FIT areas differ in activation during the non-verbal *n*-back memory task and whether inverse correlations consistent with brain efficiency may be stronger in males, as suggested by Neubauer and Fink (2009). The P-FIT also noted the potential importance of individual differences in white matter connectivity, especially the arcuate fasciculus; and there is some suggestion that white matter may be more important for intelligence in women than in men (Haier et al., 2005). Therefore, we added a second imaging method, Diffusion Tensor Imaging (DTI), to characterize white matter tracts among any areas identified with functional imaging as related to *n*-back performance. DTI provides information on the integrity of the axonal connections in the brain (Basser, 1997). By combining DTI with fMRI it is possible to provide a more comprehensive picture of structural and functional integration during cognitive performance (Fjell et al., 2008). For example Schmithorst and Holland (2007) found differences in activated brain areas between boys and girls during a verbal task as well as differences in white matter pathways (Schmithorst, Holland, & Dardzinski, 2008). Older girls showed greater inter-hemispheric connectivity. Yu et al (2008) computed correlations between the integrity of several tracts (corpus callosum, cingulum, uncinate fasciculus, optic radiation, and corticospinal tract) and intelligence. The 79 participants (men and women; mean age 23.8) were divided in two groups: average and high intelligence. White matter integrity was assessed by fractional anisotropy (FA). The results, controlling for age and sex, showed that high intelligence participants display more white matter integrity than average intelligence participants only in the right uncinate fasciculus. The authors concluded that the right uncinate fasciculus is an important neural basis of intelligence differences. There were no separate analyses by sex, but a sample of 15 participants with mental retardation was also studied. These participants were compared with the 79 healthy controls and they showed extensive damage in the integrity of the brain white matter tracts: corpus callosum, uncinate fasciculus, optic radiation, and corticospinal tract.

A recent paper (Chiang et al., 2009) reported the first study combining a genetically informative design and a DTI approach for analyzing the relationships between the white matter integrity and human intelligence. Intelligence was assessed by the Multidimensional Aptitude Battery, which provides measures of general intelligence, verbal (information, vocabulary, and arithmetic), and non-verbal intelligence (spatial and object assembly). The sample included 23 pairs of identical twins and 23 pairs of fraternal twins (males and females but all pairs were same sex; mean age 25 years). White matter integrity, quantified using fractional anisotropy (FA), was used to fit structural equation models (SEM) at each point in the brain. They then generated three-dimensional maps of heritability. White matter integrity was found to be under strong genetic control in bilateral frontal, bilateral parietal, and left occipital lobes. FA measures were correlated with the estimate of general intelligence and with non-verbal intelligence in the cingulum, optic radiations, superior fronto-occipital fasciculus, internal capsule, callosal isthmus, and the corona radiate. Further, common genetic factors mediated the correlation between intelligence and white matter integrity. This latter finding suggested a common physiological mechanism and common genetic determination.

DTI studies of intelligence are relatively new and there are not yet data in adult samples, so our analyses are exploratory. Since integrity of white matter could relate to efficient flow of information, we generally expect positive correlations with intelligence factors.

2. Method

2.1. Participants

The sample was the same as reported in a previous study focused on structural MRI assessments of gray matter only (Haier et al., 2009). During 2002–2003, 6889 individuals sought consultation from the Johnson O'Connor Research Foundation (JOCRF), a non-profit organization dedicated to using psychometric assessments for vocational guidance. Each completed the same battery of eight cognitive tests listed below in one of 11 testing centers in major cities throughout the United States. The mean age was 25.4 years (*SD* = 10.6); there were 3722 males (mean age = 25.0, *SD* = 10.2, and there were 3207 females (mean age = 25.9, *SD* = 11.0). In addition, participants who completed the same test battery in 2006 and 2007 in the New York City center were invited to return for structural and functional MRI, and Diffusion Tensor Imaging (DTI) at Mt. Sinai Medical Center. All who volunteered were screened using our own structured interview to exclude anyone with a major medical or psychiatric illness including a history of head injury and substance abuse. After informed consent was obtained, the final 40 participants in this study completing imaging included 21 males (mean age = 26.62, SD = 4.60) and 19 females (mean age = 26.63, SD = 4.90). JOCRF clients are generally college-bound or college-educated, and they tend to be spread across the ability range of that population. This is a somewhat narrower range than for the general population, and so any correlations found are likely to be somewhat attenuated relative to the larger population. In a recent study (Condon & Schroeder, 2005), it was found that for undergraduate education, 39.0% of JOCRF examinees attend “most” or “very difficult” schools, per Peterson's guide to four-year colleges, 41.5% “moderately difficult” schools, and 16.2% “minimally difficult” or two-year schools, while 3.3% do not attend college.

2.2. Intelligence testing and factors

The eight tests in the JOCRF battery were: Inductive Speed (IS), Analytical Reasoning (AR), Number Series (NS), Number Facility (NF), Wiggly Block (WB), Paper Folding (PF), Verbal-Associative Memory (VAM), and Number Memory (NM). A description of these tests, including the constructs they measure and their reliabilities can be found in Haier et al. (Haier, 2009) along with confirmation that this battery loads on four factors—Speed of Reasoning (IS and AR), Numerical (NS and NF), Spatial (WB and PF), and Memory (VAM and NM) in addition to a *g*-factor. The means and standard deviation for all tests are shown in Table 1. The correlations among the tests and factors are shown in Table 2. In terms of gender differences, the eight JOCRF tests show mean-level differences that are more-or-less in line with those reported in the literature (Halpern, 2000).The largest difference in favor of males in the JOCRF population is for Wiggly Block (.51 standard deviation units), a test of spatial visualization, while the largest difference in favor of females is for Verbal-Associative Memory (.45 *SD* units). In terms of variability, although there have been reports of greater variability among males (Halpern, 2000), for the JOCRF population on these tests, the *SD*s for males and females are very similar, with the exception of Paper Folding, for which the male *SD* is 18.4% larger than the female *SD*. Finally, in terms of correlations among the tests, they are quite similar for the two genders. An SEM analysis showed no significant differences in the factor structures for males and females for these measures (Condon & Schroeder, 2003).

We computed standardized scores (*z*-scores) for the eight tests and computed average *z*-scores for each factor. Test scores were partialled for sex and age in order to eliminate nuisance variance. The general intelligence *g*-score for each subject was the average of their *z*-scores on the eight tests (see (Haier et al., 2009) for additional details) with an alpha reliability of .80. The *g* and residualized (that is, *g*-partialled) *z*-scores for each factor for these 40 subjects were used to determine the correlations to fMRI activations and DTI, as described below. Note that residualized scores for speed of reasoning, numerical, spatial, and memory represent participants' performance not shared with the general factor score (*g*). This distinction is often neglected in neuroimaging studies of intelligence and cognitive abilities (Colom, 2007).

2.3. fMRI task

Based on a single letter *n*-back paradigm, a multi-back paradigm was developed using E-Prime (PST Inc., Pittsburgh, PA). Four levels of memory load were presented using *N*s varying between 0, 1 , 2 and 3. Each *n* was presented 3 times with different randomizations. All letter sequences were

Table 1
Descriptive statistics for samples.

Test	Large sample		Small sample	
	M	*SD*	*M*	*SD*
Speed of reasoning				
Inductive speed	143.14	23.10	140.38	24.51
Analytical reasoning	53.80	14.49	60.33	14.17
Numerical				
Number series	23.58	4.55	24.48	4.98
Number facility	94.36	17.06	100.43	19.97
Spatial				
Wiggly block	261.03	98.55	320.35	88.60
Paper folding	22.38	14.08	28.73	14.68
Memory				
Verbal-assoc. memory	20.41	9.64	24.40	10.14
Number memory	80.55	28.89	91.55	28.17

Note. For the large sample, *N*s ranged from 6778 to 6889; for the small sample, *N* was 40 for all tests. The reported values are for raw scores unpartialled for sex or age. The small sample scored significantly higher than the large sample on all the tests except for Inductive speed and Number series ($p<.05$).

Table 2
Correlations among the tests and factors for the combined sample.

Measure	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Inductive speed	–	0.42	0.19	0.30	0.30	0.23	0.16	0.14	−0.20	−0.21	−0.09	0.73	0.47
2. Analytical reasoning		–	0.40	0.44	0.41	0.43	0.27	0.27	−0.12	−0.28	0.16	0.35	0.67
3. Number series			–	0.50	0.34	0.44	0.35	0.39	−0.18	−0.09	0.49	−0.29	0.69
4. Number facility				–	0.29	0.30	0.28	0.36	−0.40	−0.16	0.54	0.08	0.62
5. Wiggly block					–	0.59	0.17	0.24	0.38	−0.31	−0.20	0.10	0.66
6. Paper Folding						–	0.26	0.31	0.56	−0.26	−0.21	−0.23	0.77
7. Verbal-associative memory							–	0.48	−0.36	0.49	0.05	−0.17	0.53
8. Number memory								–	−0.35	0.55	0.07	−0.27	0.61
9. Spatial factor									–	−0.45	−0.53	−0.22	0.00
10. Memory factor										–	−0.27	−0.25	0.00
11. Numerical factor											–	−0.22	0.00
12. Speed of reas. factor												–	0.00
13. *G* factor													–

Note. *N*s range from 6712 to 6929. All correlations significant at alpha .01 except for the correlations between *g* and the group factors, which were zero.

randomized and counterbalanced. Each trial was preceded by a 2 s instruction screen indicating which *n*-back was to follow. Each trial lasted for 30 s. In between the trials was a 20 s rest period where the subjects were presented with a fixation screen. All participants received instructions on the task before the imaging session. Each BOLD (Blood Oxygenation Level Dependent) scan consisted of twelve trials of different *n*-back stimuli.

2.4. Imaging

All imaging was performed on a 3T Allegra MRI scanner (Siemens, Ehrlangen, Germany). For fMRI, EPI (Echo Planar Imaging) BOLD scans were acquired using a GE-EPI sequence with the parameters: TR = 2 s, TE = 27 ms, FOV = 21 cm, 2.5 mm thick, skip = 0.5 mm, Matrix size = 64 × 64, 34 slices, 246 measurements with a total scan time of about 8 min. DTI used a pulsed-gradient spin-echo sequence with EPI-acquisition (TR = 4100 ms, TE = 80 ms, FOV = 21 cm, matrix = 128 × 128, 34 slices, thickness = 3 mm skip 1 mm, b-factor = 1250 s/mm^2, 12 gradient directions, 5 averages). For incidental pathology screening we also acquireT2-weighted anatomical scans of the whole brain using a turbo spin-echo (TSE) pulse sequence (34 axial slices, repetition time [TR] = 5380 ms, echo time [TE] = 99 ms, flip angle = 170°, field of view [FOV] = 210 mm, matrix = 512 × 336, voxel size = 0.41 × 0.41 × 4 mm). For coregistration and normalization purposes a high resolution T1-weighted structural image with good gray/white matter contrast was acquired using an 3D-MP-RAGE (Magnetization Prepared Rapid Gradient Echo) sequence with the following protocol: matrix size = 256 × 256 × 208, FOV = 21CM, TR = 2500 ms, TE = 4.38 ms, TI = 1100 ms and an 8° flip angle FLASH acquisition giving a total imaging time of about 10 min.

3. Analyses

3.1. fMRI

Prior to analyses, the anatomical scans were read by staff radiologists to screen for any incidental clinical findings; none were found. BOLD data were processed using SPM5 (Wellcome Department of Cognitive Neurology, Institute of Neurology, University College London, London, UK). Functional data was slice-time corrected by interpolation to the middle slice prior to motion correction. Functional images were co-registered to each subject's anatomical scan. Co-registered anatomical images were then segmented to produce the parameters used for normalization into a standard anatomical brain reference template developed by the Montreal Neurological Institute (MNI). Images were spatially smoothed using a 6 mm isotropic Gaussian smoothing kernel. Individual contrast images were produced in the context of the general linear model using a boxcar function [0-back versus 1,2,3-back] convolved with a canonical hemodynamic response function. Next, a one-sample *t*-test was performed using each subject's contrast images to determine areas of increased activity during the active (1,2,3-back) state compared to baseline (0-back) (Fig. 1). Significant clusters were identified ($p<.001$, uncorrected; separate analyses of the 1 vs. 0, 2 vs. 0, and 3 vs. 0 conditions did not yield appreciably different results; there were no sex differences in *n*-back performance) and coordinates for spherical Regions-of-Interest (ROI) with 3 mm radii were obtained from the local maxima of these clusters. Percent activation values for these ROIs were extracted from individual subjects' normalized scans and transferred to Statistica V7 (Statsoft Inc., Tulsa, OK) for further analysis.

3.2. DTI

Raw DTI data were transferred to an off-line workstation for post-processing. The Diffusion data set was eddy-current and motion corrected using an adaptation of the Camino/SPM package (Cook, 2006). In-house software was developed in Matlab v2007a (The Mathworks Inc., Natick, MA) for further processing of the DTI and tractography, a method to extract and visualize fiber tract bundles based on the geometric information contained in adjacent voxels obtained by DTI scans. Fractional Anisotropy (FA) and directionally color-coded FA maps were also computed. Color coded FA maps improve inter-rater reliabilities for ROI-based analysis of FA data by segmenting the different adjacent fiber bundles into different colors based on their orientation. For fiber tracking a commonly used "multiple region brute-force" fiber tracking method was used (Huang, Zhang, van Zijl, & Mori, 2004). First, fibers were traced using a streamline tractography algorithm from every voxel throughout the entire volume that exceeded a minimum fractional anisotropy (Basser, Pajevic, Pierpaoli, Duda, & Aldroubi, 2000; Conturo et al.,

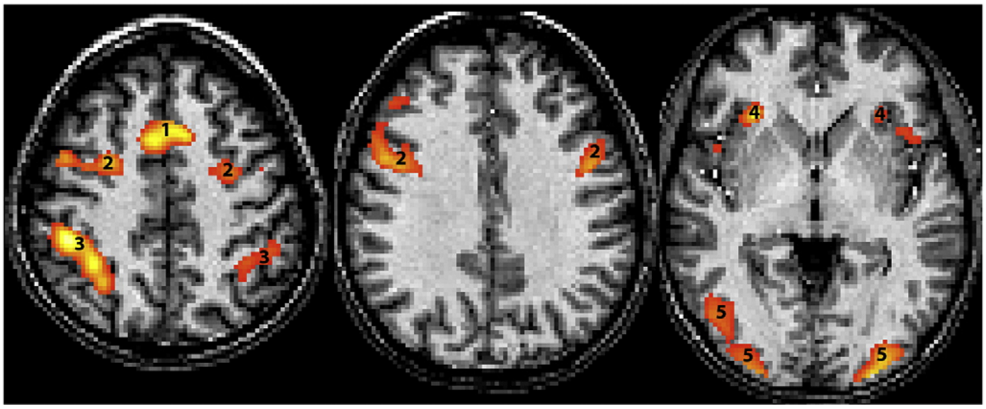

Fig. 1. fMRI-SPM group activation clusters superimposed on anatomical MRI (radiological convention), 1 Anterior Cingulate Cortex (ACC), 2 Prefrontal Cortex (PC) , 3 Parietal Cortex (PC), 4 Internal Capsule (IC), 5 Visual Cortex (VC).

1999; Mori, Crain, Chacko, & van Zijl, 1999). Tracking was terminated when FA fell below a 0.1 or when the algorithm encountered a sharp angle change in the principal diffusion direction between sequential voxels (45°). Second, FA maps were analyzed using a region of interest (ROI) approach. ROIs were defined on color-coded tract directional maps by two independent raters and then averaged. Portions of the following white matter tracts were surveyed using ROIs: Cingulum Bundle, Internal Capsule, Corpus Callosum, Forceps Minor, Forceps Major, Inferior- and Superior Longitudinal Fasciculus and corona radiata (Fig. 2). The ROI voxel locations were used to extract the FA values, which were then transferred to *Statistica* V7.1 (Statsoft Inc., Tulsa, OK) and merged with intelligence factor scores for correlation analysis.

4. Results

4.1. fMRI

As shown in Fig. 1, clusters of activation during the *n*-back task were identified (1,2,3 back vs. 0 back; $p<.001$, uncorrected) in: Anterior Cingulate (ACC), bilateral Prefrontal Cortex (PFC), bilateral Parietal cortex (PC), bilateral Insular Cortex (IC) and bilateral visual cortex (VC). As noted, we used these areas to correlate percent activation with intelligence factor scores; two regions, although activated during the *n*-back task, did not produce any significant correlations: namely, Insular Cortex and Visual Cortex.

Significant correlations between percent activation in the ACC, PFC areas, and PC areas and intelligence factor scores are shown in Table 3. For the whole sample, activation in the cluster in the right parietal cortex (PC) was inversely correlated with general intelligence ($r=-.34$, $p<.03$) and spatial intelligence ($r=-.39$, $p<.01$). Spatial intelligence was also inversely correlated with activation at the right prefrontal cortex ($r=-.35$, $p<.03$). For males, activation in the right prefrontal and right parietal cortices was inversely correlated with spatial intelligence ($r=-.58$ and $-.45$, $p<.01$ and $.04$, respectively). Activation at the right prefrontal cortex was also inversely correlated with general intelligence in males ($r=-.45$, $p<.04$). Finally, for females, general intelligence was inversely correlated with activation in left ($r=-0.52$, $p<0.02$) and right parietal cortex ($r=-.50$, $p<.03$). In the females, numerical intelligence was also inversely related to

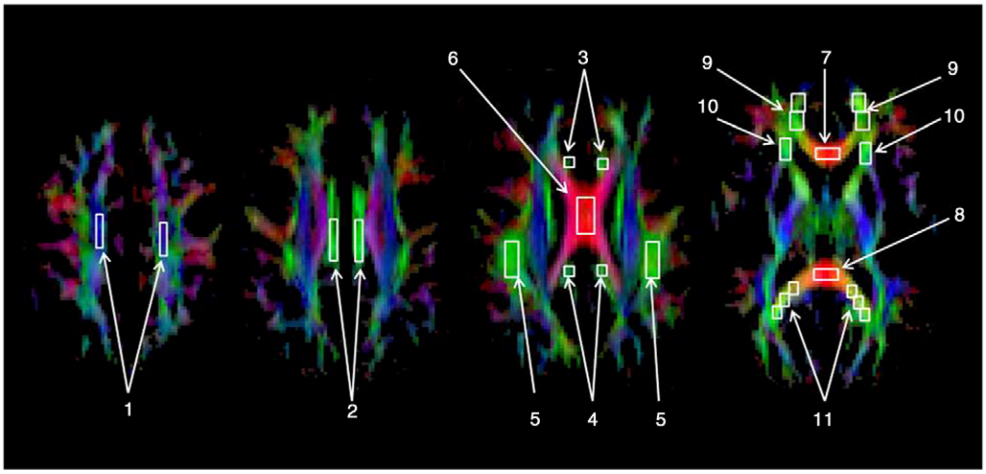

Fig. 2. DTI–ROI positions superimposed on directional color-coded fractional anisotropy maps. 1: Superior Corona Radiata, 2: Body Cingulum Bundle, 3: Anterior Cingulum, 4: Posterior Cingulum, 5: Superior Longitudinal Fasciculus, 6: Body of Corpus Callosum, 7: Genu Corpus Callosum, 8: Splenium Corpus Callosum, 9: Forceps Minor, 10: Anterior Horn Internal Capsule, 11: Forceps Minor.

Table 3
Significant correlations of intelligence factor scores with % fMRI activation.

fMRI		Region†				
Subjects		Ant. Cing.	L-PFC	R-PFC	L-PC	R-PC
All	Spatial	−0.16	−0.20	**−0.35***	−0.25	**−0.39***
	Memory	−0.10	0.96	−0.03	−0.21	0.20
	Numerical	−0.27	−0.00	−0.24	−0.24	−0.25
	Reasoning	0.14	−0.16	−0.08	−0.02	0.05
	g	−0.24	−0.09	−0.28	−0.27	**−0.34***
Males	Spatial	−0.17	−0.42	**−0.58***	−0.42	**−0.45***
	Memory	−0.38	−0.07	−0.20	−0.07	−0.08
	Numerical	−0.07	0.07	−0.19	0.07	−0.04
	Reasoning	0.04	−0.24	−0.16	−0.24	0.03
	g	−0.23	−0.26	**−0.45***	−0.26	−0.26
Females	Spatial	−0.24	0.16	−0.27	−0.36	−0.33
	Memory	0.06	0.34	−0.15	−0.20	−0.41
	Numerical	**−0.50***	−0.01	−0.35	**−0.55***	**−0.50***
	Reasoning	−0.19	−0.14	−0.00	**−0.48***	−0.19
	g	−0.33	0.13	−0.30	**−0.52***	**−0.50***

†Ant. Cing. is Anterior Cingulate Gyrus, L-PFC: Left, Right Prefrontal Cortex; L,R PC: Left, Right Parietal Cortex. All significances are at $p<0.05$.

activation in the anterior cingulate ($r=-.50$, $p<.03$), left ($r=-0.55$, $p<0.02$) and right parietal cortex ($r=-.50$, $p<.03$). Speed of reasoning was inversely correlated with activation in the left parietal cortex ($r=-.48$, $p<.04$). It is noteworthy that all the correlations were negative (higher intelligence scores were associated with less brain activation); no significant correlations were positive. Only the memory factor showed no correlations with activation. None of the correlations survived Bonferroni correction for multiple comparisons, although most imaging studies have samples too small for this correction given the number of possible comparisons.

4.2. DTI

We computed brute-force streamline tractography (Carpenter et al., 2008; Huang et al., 2004) to identify the connection networks between the selected areas shown in Fig. 1. Significant activated clusters in the prefrontal cortex and parietal cortex were used as seed regions for fiber tracking through the genu and splenium of the corpus callosum; these formed the forceps minor and forceps major respectively Segments of the anterior cingulated where the cingulum was clearly visible were used as a seed region for tracking of the cingulum bundle. All fMRI activation clusters were dilated by one voxel in all directions before being used as seed region making them closer to nearby white matter tracts for better tracking. We have integrated the fMRI activated regions together with the interconnecting white matter tracts in Fig. 3. This figure illustrates the relationship of the functional and structural anatomy and the correlations that we have detected.

We then investigated FA correlates of the intelligence factors. FA in ROIs in interhemispheric fibers showed correlations with intelligence factors as detailed in Table 4 and shown in Fig. 3. FA in the genu of the corpus callosum was positively correlated with the memory factor scores for the whole sample ($r=.34$, $p<.03$) as well as for females ($r=.56$, $p<.01$). FA in the genu of the corpus callosum was also inversely related to spatial intelligence in males ($r=-.51$, $p<.02$). FA in the left Forceps Major was inversely correlated with general intelligence in males ($r=-.53$, $p<.01$) and positively in females ($r=.48$, $p<.04$). FA in the right Forceps Major was also inversely related to general intelligence in males ($r=-.45$, $p<.04$). Finally, FA in the Splenium of Corpus Callosum was inversely related to numerical intelligence in males ($r=-.46$, $p<.04$). None of these correlations survived Bonferroni correction.

ROIs in ipsilateral fibers also showed correlations with intelligence factors as detailed in Table 5 and shown in Fig. 3. FA in the left Cingulum Bundle was positively related to speed of reasoning for the whole sample ($r=.36$, $p<.02$) and for males ($r=.58$, $p<.01$). FA in the right Cingulum Bundle was also correlated with speed of reasoning in males ($r=.53$, $p<.01$). FA in the right Superior Corona Radiata was positively correlated with spatial intelligence in the whole sample ($r=.32$, $p<.04$). Finally, FA in the left Superior Longitudinal Fasciculus was inversely related to memory in males ($r=-.47$, $p<.03$). None of these correlations survived Bonferroni correction.

5. Discussion

This study examined intelligence factors with *g* removed to determine if the parieto-frontal integration theory of intelligence (P-FIT) characterizes specific cognitive abilities beyond the pervasive influence of the *g*-factor representing general intelligence. This was examined separately in males and females and uniquely combined fMRI and DTI imaging to study the neuroanatomy of intelligence. Since the sample sizes are relatively small and none of the significant findings survived correction for multiple comparisons, all results should be regarded as illustrative and interpreted with caution. Most neuroimaging studies have small samples and limited statistical power, so reporting uncorrected results allows for potential replication across studies.

5.1. Relationship to P-FIT and other *n*-back studies

Functional correlations between the BOLD signal obtained from the working memory task (*n*-back) and intelligence factors were mostly detected in the right prefrontal and bilateral parietal cortices. All these correlations were negative

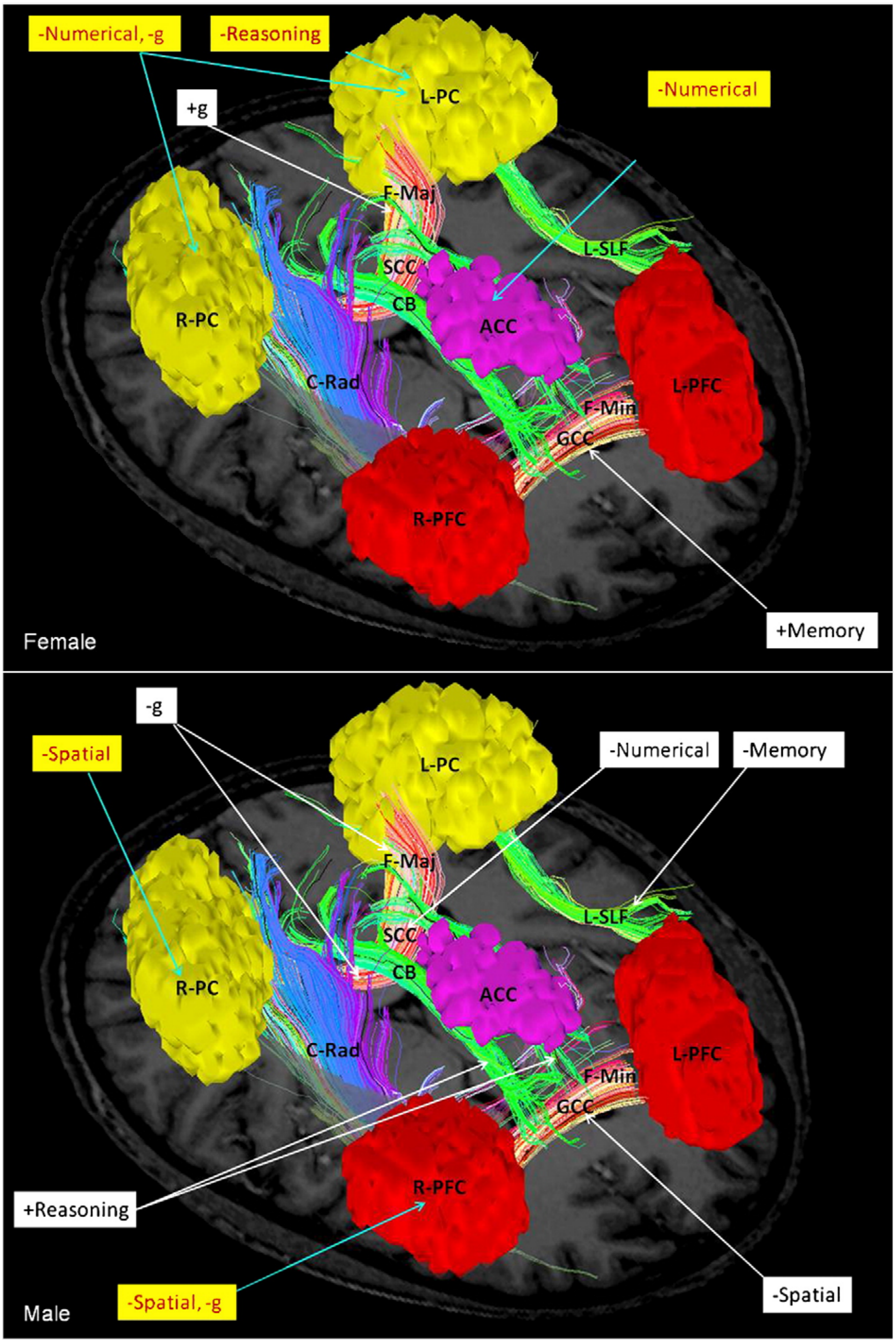

Fig. 3. 3D illustration of the significantly correlated fMRI activation clusters* and their interconnecting fiber tracts° for females (top) and males (bottom). Significant fMRI correlations are labeled with yellow legends, all fMRI correlations are negative with performance scores; Significant white matter tracts correlations are labeled with white legends where + indicate a positive correlation with better connectivity and − indicates a negative correlation with better connectivity for the indicated performance scores. (*R,L-PC: right,left parietal cortex; R,L-PFC: right, left prefrontal cortex; ACC: anterior cingulate cortex; ° F-Maj: forceps major; F-min: forceps minor; GCC: genu of corpus callosum; SCC: splenium of corpus callosum; CB: cingulum bundle, L-SLF: Superior Longitudinal Fasciculus, C-Rad: Corona Radiata; Only regions or tracts for which significances were found are rendered).

indicating that subjects with high intelligence factor scores had less activation during the n-back memory task, in support of the efficiency model of brain function (Haier, 1993; Haier et al., 1988; Neubauer & Fink, 2009). Gray et al (2003) reported that, on more demanding n-back conditions, participants with higher intelligence scores were more accurate and showed greater activity in several frontal and parietal regions. It should be noted that the focus of their analysis was based on an event related design but their report also included the results using a block design which showed a

Table 4
DTI correlations with intelligence factor scores for interhemispheric fibers.

DTI		White matter tracts†					
Subjects		L Fcp Maj	R Fcp Maj	GCC	SCC	L Fcp Min	R Fcp Min
All	Spatial	−0.11	0.01	−0.28	−0.07	0.06	−0.06
	Memory	0.12	0.19	**0.34***	0.14	−10	0.01
	Numerical	0.20	−0.03	−0.21	−0.31	0.07	−0.26
	Reasoning	−0.20	−0.15	0.11	0.22	0.11	−0.21
	g	0.10	0.03	−0.05	−0.15	−0.14	0.14
Males	Spatial	−0.08	−0.05	−**0.51***	−0.00	0.28	0.03
	Memory	−0.10	−0.09	0.20	0.14	−0.10	0.07
	Numerical	0.16	−0.14	−0.13	−**0.46***	r−0.01	0.30
	Reasoning	0.04	0.22	0.33	0.19	−0.12	−0.30
	g	−**0.53***	−**0.45***	−0.17	−0.11	0.11	0.10
Females	Spatial	−0.24	0.00	0.05	−0.15	−0.15	−0.26
	Memory	0.24	0.38	**0.56***	0.15	−0.14	−0.18
	Numerical	0.19	−0.04	−0.26	−0.21	−0.11	0.21
	Reasoning	−0.30	−0.36	0.30	0.27	0.45	0.16
	g	**0.49***	0.14	0.08	−0.17	−0.32	0.13

†L,R Fcp Maj: Left, Right Forceps Major; GCC: Genu of Corpus Callosum; SCC: Splenium of Corpus Callosum; L,R Fcp Min: Left, Right Forceps Minor. All significances are at $p<0.05$.

trend of lower activity with higher scores on a single test of fluid intelligence. Waiter et al. (2009) did not find significant correlations between individual differences in brain activity during an *n*-back task and intelligence scores. Activation levels are known to fluctuate across working memory loads in an inverted-U shape response (Callicott et al., 1999). The position of the inverted-U can shift depending on the working memory capacity of the group or individual (Callicott et al., 2003). Waiter et al. (2009) used a simple version of the *n*-back task with only 0- and 2-back levels . The limited levels and range of task difficulties in their study may have created confounds related to shifts in the inverted-U curve. In addition, their study focused on elderly (mid to late 60-years-old) subjects, a population that shows a decrease in working memory capacity and related neurophysiology (Mattay et al., 2006) as well as a wide variability among individuals in the extent, rate and pattern of age-related changes that are exhibited at both neural and behavioral levels (Hedden & Gabrieli, 2004). For the current study, a greater range of working memory task was used on a younger population, which could help avoid inconsistencies due to shifts of the inverted-U. This method does not completely avoid the potential anomalies as equal sampling of both sides of the inverted-U is not guaranteed but is less risky than sampling only one level of working memory difficulty. The optimal method would include enough levels and range in the task difficulty to determine the point of peak activation for each subject.

Our *n*-back results are in agreement with the single published study aimed at quantifying the neuro-anatomical overlap between the general factor of intelligence (*g*) and working memory capacity (Colom, Jung, & Haier, 2007). That study showed that a common neuro-anatomic framework for these constructs implicates mainly frontal gray matter regions belonging to the right superior frontal gyrus, the left middle frontal gyrus, and the right inferior parietal lobule. These findings (a) were thought to support the role of a discrete parieto-frontal network, as proposed by the P-FIT model, and (b) were consistent with Cowan's (2005) theory which distinguished a capacity limit (related to parietal regions) and the control of attention (related to frontal areas). It was suggested that capacity limits and attention control relate to the

Table 5
DTI FA correlations with intelligence factor scores for ipsilateral fibers.

DTI		White matter tracts†					
Subjects		L Cing.	R Cing.	LS Cor R	RS Cor R	L Sup L F	R Sup L F
All	Spatial	−0.08	−0.21	0.08	**0.32***	−0.13	−0.18
	Memory	−0.25	−0.11	−0.70	0.03	−0.09	0.19
	Numerical	−0.05	−0.07	−0.06	−0.18	0.15	−0.10
	Reasoning	**0.36***	0.34	−0.05	−0.08	0.05	−0.06
	g	−0.23	−0.09	−0.00	−0.08	0.04	−0.01
Males	Spatial	−0.22	−0.38	−0.09	0.40	−0.05	−0.17
	Memory	−0.36	−0.30	−0.07	−0.21	−**0.47***	0.27
	Numerical	−0.11	0.07	−0.24	−0.14	0.10	−0.16
	Reasoning	**0.58***	**0.53***	0.31	−0.00	0.39	0.02
	g	−0.22	−0.03	−0.05	−0.08	−0.13	0.07
Females	Spatial	0.12	0.04	0.37	0.25	−0.28	−0.21
	Memory	−0.17	0.11	−0.09	0.15	0.27	0.06
	Numerical	−0.04	−0.30	0.12	−0.21	0.16	−0.06
	Reasoning	0.13	0.25	−0.42	−0.11	−0.25	0.21
	g	−0.32	−0.26	0.05	−0.08	0.12	−0.07

†L,R Cing: Left, Right Cingulum Bundle; L, R Cor R; Left, Right Superior Corona Radiata; L, R Sup L F: Left, Right Superior Longitudinal Fasciculus. All significances are at $p<0.05$.

commonality between intelligence and working memory. We also note that we found no correlations between our memory factor and any fMRI activations, possibly because the factor was derived as a broader assessment of memory than the more focused processes required for the n-back task, although this is not determined.

5.2. Sex differences

Because of the small sample sizes, the sex differences observed in the present study should be interpreted with particular caution. Therefore, we do not interpret individual correlations, but note that all the fMRI correlations with intelligence factors were negative, consistent with the brain efficiency hypothesis for both males and females. We tested the male/female difference of each fMRI/factor correlation using *z*-transform. Only the difference for Numerical/Left Parietal Cortex was significant ($p<.045$, 2-tailed); there was a trend for Spatial/Left Prefrontal Cortex ($p<.077$).

Similarly, the DTI results show sex differences but the same cautions apply, especially because these analyses were exploratory, so we will discuss specific correlations only to make general illustrative points about each factor. Using *z*-transform comparisons for DTI interhemisphere/factor correlations, the male/female difference was significant for *g*/Left Forceps Major ($p<.001$, 2-tailed), and there were trends ($p<.05$ to .09) for Speed of Reasoning and for *g* in the Right Forceps Major; for the Spatial Factor and the Genu of the Corpus Callosum; and, for Speed of Reasoning and the Left Forceps Minor. For DTI ipsilateral/factor correlations, the male/female difference was significant (2-tailed) for Speed of Reasoning/Left Superior Corona Radiata ($p<.026$) and for Memory/Left Superior Longitudinal Fasciculus ($p<.022$); Speed of Reasoning/Left Superior Longitudinal Fasciculus showed a trend ($p<.052$). These differences, for both fMRI and DTI correlations, support the view that separate analyses by sex are justified, even when there is no task performance difference.

5.2.1. Spatial factor

In our study, spatial factor scores were correlated with fMRI activation in the right prefrontal and posterior parietal cortex in the whole group. However, when analyzed separately for males and females, only the males showed significant correlations. Although there is a general notion that spatial ability is a right hemisphere function, recent studies have found that sex matters. A meta-analysis (Vogel, Bowers, & Vogel, 2003) showed that females are much less lateralized than their male counterparts in terms of brain function and spatial tasks. In that study females showed no hemispheric preference while males showed a right hemisphere advantage. It was hypothesized that women use both verbal abilities, a left hemisphere function, as well as spatial abilities, a right hemisphere function, to accomplish spatial tasks. This might be contributing to the variances in our dataset. The lack of any significant correlations in our dataset for spatial factors in the female group might be additional support for these findings.

Contrary to our expectation of positive correlations, the DTI results show that the FA of the genu of the corpus callosum was negatively correlated with spatial factor scores ($r=-51$, $p<0.02$) in males. This is the section of the corpus callosum that connects parts of the prefrontal cortex. FA is believed to be an indirect measure of myelination and the purpose of myelin is to allow rapid and efficient transmission of signals along the axons (Ritchie, 1984; Yakovlev & Lecours, 1967). The negative correlation means that stronger connections between the two hemispheres decrease performance. Increased anisotropy (better connectivity) in the corpus callosum can be interpreted as an interference factor for brains using only one region or one hemisphere for a certain task. Enhanced interhemispheric connectivity increases unnecessary information flow from the contralateral side of the brain, possibly consistent with efficient information flow. We also note that although both the right prefrontal and right parietal lobes had significant fMRI signal correlation with spatial factor scores in males, the prefrontal cortex showed stronger correlations than the parietal ($r=-0.58$ vs. $r=-0.45$). This is consistent with the DTI finding in the genu, which showed decreased spatial performance scores with increased FA in the genu in the male group.

5.2.2. Numerical factor

Females had significant negative correlations with the numerical factor in terms of activation in the anterior cingulate as well as both sides of the parietal cortex. Other studies (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999) have shown that numerical cognitive abilities recruit both sides of the parietal cortex. To our knowledge, no other studies have shown any gender effect for this function. There were no significant fMRI correlations with the numerical factor for the male group.

5.2.3. Speed of reasoning factor

The integrity of the cingulum bundle, a white matter tract inside the cingulate gyrus, as quantified using FA, was positively correlated with the speed of reasoning factor scores in males. This is not an interhemispheric connection and thus it is expected that better ipsilateral connections are positively correlated with performance. The cingulate gyrus is an area in the brain that is involved with early learning and problem solving, anticipation of tasks, motivation, and modulation of emotional responses (Posner & Raichle, 1998).

5.2.4. Memory factor

We note that for the group as a whole there was a significant correlation ($r=0.34$) between the memory factor and the interhemispheric white matter tracts in the genu of the corpus callosum (GCC), but when separated by gender we find that the effect was mainly due to the female group ($r=0.56$) with the males no longer significant. This significant positive correlation is additional support for the notion that females rely on both hemispheres and benefit from better interhemispheric connections. No significant correlations between functional activation and the memory factor were detected. It is conceivable that the GCC connects larger and more diffuse brain regions used for many memory processes and that our working memory task uses a more narrow set of processes.

5.2.5. g-factor

The *g*-factor was correlated with activation in the right prefrontal area in males, but was correlated to both left and right sides of the parietal cortices in females. While the FA of the forceps major was negatively correlated with *g* in males, the females had parts of the forceps major positively correlated with *g*. Again, this negative correlation may be an indicator of interference from contralateral side of the brain in males who rely mostly on the right side of the brain. The positive FA correlations in the forceps major in females are also compatible with the bilateral fMRI correlations in the parietal regions connected by the forceps major. Also, our finding that part of the FA of the forceps major (an extension of the splenium) is positively correlated with *g* ($r = 0.49$, $p < 0.034$) in females is consistent with some evidence that the splenium may be larger in females (Dubb, Gur, Avants, & Gee, 2003). Overall, our DTI results are also consistent with a report on DTI/IQ correlations in a cohort of subjects aged 5–18 where correlations were mainly negative in older males and positive in older females (Schmithorst et al., 2008). There are also other higher-order latent variable models that show sex differences that could be explored with imaging (Johnson & Bouchard, 2007a,b; Keith, Reynolds, Patel, & Ridley, 2008).

In summary, in this study, we have shown that: (a) individual differences in activation during the *n*-back task are correlated with the general intelligence factor (*g*), as well as to distilled estimates (removing *g*) of speed of reasoning, numerical ability, and spatial ability, but not to memory, (b) the correlations are mainly bilateral for females and unilateral for males, and (c) differences in the integrity of the axonal connections are also related to the functional findings: integrity of interhemispheric connections is positively related to several intelligence factors in females but is negatively correlated in males. It should be noted that none of these correlations survived correction for multiple comparisons, so replication in larger samples is necessary. Nevertheless, these results show encouraging trends to support further studies regarding the relationship between working memory and intelligence factors. They support the growing recognition that brain structure and function underlie individual differences in general intelligence and other specific cognitive abilities. These results also underscore the importance of analyzing neuroimaging data separately for males and females.

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