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Cognitive abilities independent of IQ correlate with regional brain structure

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Abstract

There is increasing evidence relating psychometric measures of general intelligence and reasoning to regional brain structure and function assessed with a variety of neuroimaging techniques. Cognitive dimensions independent of general intelligence can also be identified psychometrically and studied for any neuroanatomical correlates. Here we investigated two such dimensions, rotation–verbal and focus–diffusion. We used structural MRI and voxel-based morphometry (VBM) in two independent samples to identify gray and white matter correlates of both dimensions. Based on statistical conjunction of both samples, ($N=45$; $p<.001$), there were correlations with gray matter in Brodmann areas (BA) 20 and 9 involving the rotation–verbal dimension and in BA 18 involving the focus–diffusion dimension. There were white matter correlations involving the rotation–verbal dimension near BA 18, 40, 39, 10, 8, and 4 and involving the focus–diffusion dimension near BA 5 and the right sub-lobar amygdala. These correlations may have implications for understanding individual differences in the manifestation of intelligence.
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There is increasing evidence relating psychometric measures of intelligence and reasoning to regional brain structure and function assessed with a variety of neuroimaging techniques (Jung et al., 1999; Haier, Jung, Yeo, Head, & Alkire, 2004; Haier, White, & Alkire, 2003; Haier et al., 1988; Jung & Haier, in press; Schmithorst & Holland, 2006; Shaw et al., 2006). These findings act to allay concerns about whether psychometric approaches to intelligence have sufficient construct validity (Ceci, 1996; Gardner, 1983; Horn, 1989; Sternberg, 1985). The neuroimaging studies support both the concept of a general factor of intellectual ability (g; Colom, Jung, & Haier, 2006b; Gottfredson, 1997; Jensen, 1998), as well as the importance of specific abilities. In our view, the data converge generally on the factor model proposed by Carroll (1993), which includes a general intelligence factor that contributes to performance on all tasks, as well as factors contributing to performance on more specific, narrowly construed abilities. Johnson and Bouchard (2005, in press) have articulated how the situation summarized by this general model may arise. They hypothesized that general intelligence is of

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general-purpose use, yet it is manifested through the accession of components of ability that vary from individual to individual. They argued that this means that different individuals manifesting similar performance on specific tasks may attain that similar level of performance through different brain pathways, making use of different brain structures. If general intelligence is sufficiently powerful, it may effectively mask many of the associations among more specific abilities that reflect brain structure.

This argument could be correct if, at the biological level, general intelligence were primarily reflected in a trait such as neuronal plasticity (Garlick, 2002) or processing efficiency (Neubauer, Grabner, Freudenthaler, Beckman, & Guthke, 2004; Haier, 1993; Haier et al., 1988; Vernon, 1993; see also Kovas & Plomin, 2006), while specific abilities were reflected in localized structural brain formations such as neuronal density and brain matter volume and integrity. At the level of problem solving, this could be the case if general intelligence were used to apply existing knowledge, skills, and specific perceptual abilities to develop a strategy to address any problem, while specific abilities were reflected in the functional and perceptual capacities of the localized brain formations. For example, a person with high general intelligence may be able to use that general intelligence to address image rotation problems even when s/he has little specific image rotation ability. Such a person may achieve similar levels of success on such problems as a person of lower general intelligence but good image rotation ability. The analogy is that the specific abilities are the tools available to the general intelligence of the user. Users differ in their skill and ability in tool use, as well as in the tools available to them. If this analogy is appropriate, there are substantive individual differences in abilities that are independent of general intelligence yet these abilities are reflected in both sizes of brain regions and performance on tasks that have been associated with general intelligence. To understand general intelligence, it will be necessary to characterize these individual differences in specific abilities both psychometrically and in the brain, and to link the psychometric and neuroanatomical perspectives.

To describe variations in ability beyond general intelligence in greater psychometric detail, Johnson and Bouchard (2005) developed the Verbal-Perceptual-Image Rotation (VPR) model from a battery of 42 mental ability tests administered to a sample of 436 adults from a broad range of backgrounds. The VPR model is a more specific, accurate, and detailed version of the general factor model proposed by Carroll (1993).

As shown in Fig. 1, it consists of a fourth-stratum *g* factor that contributes strongly to broad third-stratum verbal, perceptual, and image rotation abilities, which in turn contribute to 8 second-stratum factors representing more specialized abilities that contribute to specific test performance. The model operationalizes the situation we are describing, in which a *g* factor permeates performance on mental ability tests, yet special abilities are also important. Johnson and Bouchard (2006) used this model to examine patterns of ability independent of general intelligence. They regressed the effects of general intelligence from the VPR model in the same sample, and then used confirmatory factor analysis to develop a model of the residual ability structure (Fig. 2). The model they developed grouped residual ability test scores according to general content at the second stratum. At the third stratum, however, three independent dimensions of cognitive orientation could be observed. One represented a rotation–verbal dimension, a second represented an analogous dimension we labeled focus–diffusion of attention, and a third represented content memory. The first two of these dimensions shared a particularly interesting feature. Each spanned negatively correlated residual abilities. That is, individuals had normally distributed patterns of ability that lay all along both dimensions. Those lying towards one pole of each dimension, however, tended to have relatively strong abilities in one area and relatively weak abilities in the area associated with the other pole and vice versa. This was true regardless of level of general intelligence.

One dimension spanned a space ranging from image rotation to verbal abilities. The other dimension spanned a space ranging from problem solving orientations involving attentional focus on details one at a time to the
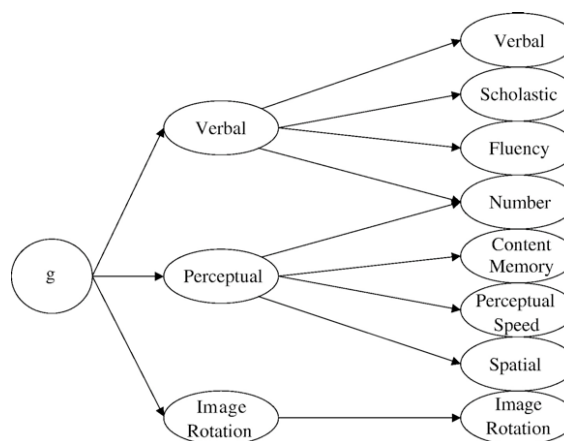

Fig. 1. The four-stratum Verbal-Perceptual-Image Rotation (VPR) model of mental ability.
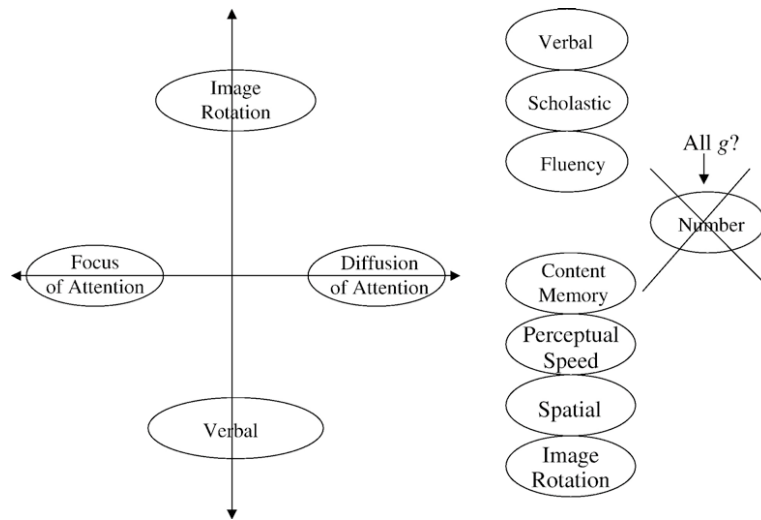
Fig. 2. A model of residual mental abilities based on the Verbal-Perceptual-Image Rotation (VPR) model of mental abilities.

application of diffuse attention to a variety of cues simultaneously. This latter dimension may possibly be related to the cognitive processes that the neuropsychologist Luria (1966, 1973, 1980) proposed underlie mental task performance. He suggested that the brain stem and reticular activating system provide the brain with the appropriate level of arousal for focused attention and resistance to distraction, the occipital–parietal and frontal–temporal areas of the brain receive, analyze, and store incoming sensory information, and the frontal lobes of the brain program and regulate behavior, and that there were individual differences in the ways these systems work in concert that contribute to individual differences in task performance.

The rotation–verbal and focus–diffusion dimensions were derived from the structure of abilities residual of general intelligence. Thus they were independent of it as well as orthogonal to each other. Because of the apparent trade-off in relative levels of specific abilities these dimensions involved, Johnson and Bouchard suggested that these two dimensions of cognitive orientation are particularly likely to outline individual differences in strategy and performance on mental ability tests that reflect individual differences in brain structure and function that should be observable in neuroanatomical brain studies. We therefore made these two dimensions the focus of this study.

Gray matter (GM) and white matter (WM) volumes are two structural components of the brain that have been linked to intelligent performance (Gignac, Vernon, & Wickett, 2003; Haier et al., 2004; Haier, Jung, Yeo, Head, & Alkire, 2005). GM is composed of neuron cell bodies; WM is composed of neuron axons

that connect areas of gray matter. Thus WM appears to be directly involved in communication among brain areas. Both GM and WM appear to be under strong genetic influence (Baare, van Oel, Hulshoff Pol, Schnack, & Durston, 2001; Thompson et al., 2001), and to share their genetic influences with general intelligence (Posthuma et al., 2002). They show characteristic development patterns over time (Sowell et al., 2003; Good et al., 2001), and these development patterns show individual differences related to intelligence (Schmithorst & Holland, 2006; Shaw et al., 2006). At the same time, these structural components are not subject to the task-related variations observed in functional brain imaging studies. They therefore make good candidates for investigating individual differences in the manifestation of intelligent performance in the brain.

Here we investigated whether two psychometrically derived dimensions of cognitive orientation that are independent of general intelligence were associated with individual differences in regional volumes of GM and WM. The rotation–verbal dimension is related to specific task content. We therefore expected to find correlations with dimensional position in relatively localized regions of the brain involved in performing tasks of those kinds. In contrast, the focus–diffusion dimension is related to problem-solving attention and information processing approaches across areas of content. Thus we expected to find correlations distributed more widely across areas of the brain involved with sensory processing and attention, and perhaps involving WM more than GM because of WM's apparent role in communication among brain areas.

1. Materials and methods

1.1. Subjects

Two independent samples of normal volunteers were studied. The first sample of 23 volunteers (14 women and 9 men; mean age=27, SD=5.9, range=18–37) was recruited from the University of New Mexico (UNM). The second sample of 25 volunteers (14 men and 11 women, mean age=59, SD=16; range 37–84) were recruited from the University of California, Irvine (UCI) as middle aged and older normal controls for an imaging study of dementia in Down syndrome and Alzheimer's disease (Haier et al., 2003). These are the same subjects used in our previous report (Haier et al., 2004), except that one additional subject was added to the UCI sample. As described below, 3 subjects were excluded because they were outliers on the dimension scores so the final sample was 45. All of the subjects were in good physical and mental health and none had a history of head injury.

1.2. Intelligence testing

To assess general intelligence, subjects were tested with the WAIS. The WAIS battery (Wechsler, 1981) consists of 11 diverse subtests that tap a variety of verbal and non-verbal mental abilities that contribute to general intelligence. The WAIS full-scale IQ score (FSIQ) is based on performance on all 11 subtests (according to age-based norms). Factor analytic studies (Jensen, 1998) show that each subtest loads on the g factor and the FSIQ score loads the highest (about .90, or 81% of the variance in g). For this reason FSIQ is considered one of the best indexes of individual differences in general intelligence, as first described by Spearman (1904), although we recognize that FSIQ is not a perfect measure of g (Colom et al., 2006b). Mean FSIQ for all 23 males was 118.8 (SD=15.1; range 95–155) and 113.5 (SD=13.4; range 90–134) for all 25 females. This was not significantly different between groups (t=1.29, p=0.20; 2-tailed). In sample 1 (UNM), mean FSIQ for the males was 122.8 (SD=16; range 109–155) and 111.1 (SD=12.4; range 90–133) for females. In sample 2 (UCI), mean FSIQ for the males was 116.3 (SD=14.5; range 95–142) and 116.5 (SD=14.6; range 90–134) for females.

1.3. Measurement of dimensions of cognitive orientation

The dimensions of cognitive orientation were developed from a battery of 42 mental ability tests (Johnson & Bouchard, 2006). As administration of 42 mental ability tests is impractical in neuroimaging contexts, Johnson and Bouchard (2006) recommended the use of formulas based on WAIS subtest scores that correlate with the observed dimensions on the order of .7. We made use of these recommended formulas in this study. They were developed in the original sample used to describe the residual ability dimensions, and it is not known how robust they are to random perturbations in test scores, nor whether the strong correlation with the dimensions in the original sample would be obtained in other samples. This emphasizes the exploratory nature of this study.

Using the recommended formulas, the rotation–verbal dimension was scored as: $100 * (\text{Block Design} - \text{Vocabulary}) / \text{Full Scale IQ}$. This resulted in scores ranging from -6 to 4 ($\mu=-1.5$, $\sigma=2.2$). Negative scores indicate orientation towards verbal ability at the expense of image rotation ability. Positive scores indicate orientation towards image rotation ability at the expense of verbal ability. The participant with the highest FSIQ (155) had a rotation–verbal score of -1.3. One of the participants with the lowest FSIQ (90) had a similar rotation–verbal score of -1.1. This indicates the independence of the dimension from general intelligence in a practical way. Statistically, the correlation between the rotation–verbal dimension scores and FSIQ scores was .06. (p=.69). The focus–diffusion dimension was scored as: $100 * (\text{Block Design} + \text{Information} - \text{Coding} - \text{Digit Span}) / \text{Full Scale IQ}$. This resulted in scores ranging from -12 to 9 ($\mu=1.6$, $\sigma=4.3$). Negative scores indicate an orientation towards application of diffuse attention to a variety of cues simultaneously. Positive scores indicate orientation toward attentional focus on details one at a time. The participant with the highest FSIQ (155) had a focus–diffusion score of 0, the lowest focus–diffusion score among males. Another participant with an FSIQ of 95 had a focus–diffusion score of 1. The correlation between the focus–diffusion scores and FSIQ scores in this sample, however, was .4. This was largely due to 3 highly leveraged points: the 3 lowest focus–diffusion scores (3 or more standard deviations below the mean) belonged to the 3 participants with the lowest FSIQ's (1.5 standard deviations below the mean). Dropping these 3 participants, the correlation was .11 (p=.46). Situations such as this in which particular outlying points induce sample-specific correlations are common in samples of relatively small size. In order to remove the possibility of identifying brain regions related to FSIQ rather than the focus–diffusion dimension, we deleted these points from the analysis, thus artificially restricting the range of focus–diffusion scores somewhat. Fig. 3 provides a scatterplot of the data on the
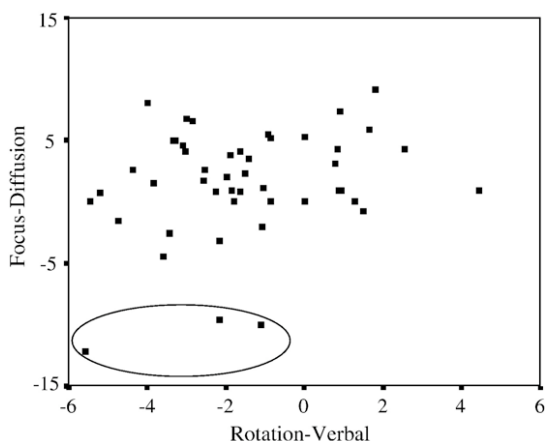
Fig. 3. Scatterplot of rotation–verbal and focus–diffusion scores (N=45), 3 deleted outlying points are indicated in the oval.

two dimensions from the sample used in the analyses (N=45), with the 3 deleted points indicated.

1.4. Structural MRI imaging parameters

Sample 1 MRIs were obtained with a 1.5 T scanner, head coil, and software (Signa 5.4; General Electric Medical Systems, Waukesha, WI). A T1 sagital localizer sequence (TE=6.9 ms, TR=200 ms, FOV=24×24 cm^2, five slices, thickness=5 mm, spacing=2.5 mm, matrix=256×128) was acquired, followed by a T1 weighted axial series (fast RF spoiled gradient-recalled, TE=6.9 ms, TR=17.7 ms, flip angle=25°, matrix=256×192, 120 slices, thickness=1.5 mm) to give full brain coverage. Sample 2 MRIs were obtained with a 1.5 T clinical Phillips Eclipse scanner (Philips Medical Systems, N.A., Bothell, WA). We used T1-weighted, volumetric SPGR MRI scans (FOV=24 cm, flip angle=40, TR=24, TE=5). The images consisted of 120 contiguous 1.2-mm thick axial slices, each with an in-plane image matrix of 256×256 image elements, to achieve full brain coverage. All images in both samples were visually inspected to ensure image quality.

1.5. Voxel-based morphometry (VBM)

We applied VBM to identify brain areas where GM and WM volumes were correlated to each dimension score. We used Statistical Parametric Mapping software (SPM2; The Wellcome Department of Imaging Neuroscience, University College London) to create one study-specific template for the combined sample of UNM and UCI. The optimized VBM protocol was applied to the entire sample using the methods of

Ashburner and Friston (2001) and Good et al. (2001). To preserve the amount of tissue in any given anatomical region after spatial normalization, the optimal GM and WM partitions were multiplied by the Jacobian determinants of their respective spatial transformation matrix. This modulation step was performed so that the final VBM statistics would reflect local deviations in the absolute amount (volume) of tissue in different regions of the brain (Ashburner & Friston, 2000). The modulated GM and WM partitions were then smoothed with a 12-mm FWHM isotropic Gaussian kernel to account for slight misalignments of homologous anatomical structures and to ensure statistical validity under parametric assumptions.

1.6. Statistical conjunction approach

We specifically tested whether regional GM or WM volumes were correlated with each set of dimension scores, treating any effects of age, sex and handedness as nuisance variables in the SPM2 design matrix exactly as in our previous report (Haier et al., 2004). We did not treat FSIQ as a nuisance variable because it was both theoretically and empirically independent of the two dimension scores (after removal of the leveraged points), and because to do so would have excluded the possibility of detecting any brain region related to both FSIQ and to one or both of our dimensions. We used the conjunction approach (Price & Friston, 1997) to show where GM and WM correlations with both dimensions overlapped for the UNM and the UCI samples (i.e. voxels with correlations in common for both samples). We repeated these analyses separately for each dimension. The conjunction approach minimizes potential problems associated with combining data from different scanners, and has the additional advantage of maximizing statistical power because all subjects are used in the analysis. Locations of significant clusters (maximum voxel values) are converted from Montreal Neurological Institute (MNI) to Talairach atlas (Talairach & Tournoux, 1988) coordinates and reported as closest Brodmann area (BA) where possible. Only clusters of at least 10 voxels are reported.

2. Results

Because the sample is relatively small and the study somewhat exploratory, we regarded correlations significant at $p < .001$(uncorrected for multiple comparisons), but we also report all correlations with statistical significance $p \leq .003$ (see Tables 1 and 2; and Fig. 1), to aid in future hypothesis generation and replication

Table 1
Gray matter (GM) correlates of the rotation/verbal and the focus/diffusion dimensions

Cluster size	T	Z	p	X	Y	Z	Brain area
GM correlations with rotation							
146	1.91	3.09	0.001	−66	−27	−26	Left inferior temporal gyrus BA 20
14	1.62	2.72	0.003	−9	−50	74	Left parietal lobe postcentral gyrus BA 7
GM correlations with verbal							
832	2.18	3.42	0.000	−29	20	27	Left middle frontal gyrus BA 9
562	1.80	2.96	0.002	−51	13	41	Left middle frontal gyrus BA 8
210	1.69	2.81	0.002	37	−51	19	Right superior temporal gyrus BA 22
GM correlations with focus							
4510	2.07	3.29	0.001	−26	−4	57	Left frontal lobe sub-gyral BA 6
2712	2.03	3.23	0.001	−53	16	−19	Left superior temporal gyrus BA 38
612	1.90	3.07	0.001	28	25	−13	Right inferior frontal gyrus BA 47
770	1.86	3.02	0.001	41	−4	62	Right frontal lobe precentral gyrus BA 6
172	1.70	2.82	0.002	21	−25	51	Right parietal lobe postcentral gyrus BA 3
505	1.67	2.79	0.003	29	−59	32	Right parietal lobe angular gyrus BA 39
296	1.67	2.79	0.003	−18	14	66	Left superior frontal gyrus BA 6
233	1.66	2.77	0.003	−42	−16	−25	Left temporal lobe fusiform gyrus BA 20
344	1.64	2.75	0.003	−21	−58	39	Left parietal lobe precuneus BA 7
GM correlations with diffusion							
2723	3.14	4.55	0.000	−32	−83	−7	Left middle occipital gyrus BA 18
185	1.96	3.15	0.001	31	−73	0	Right occipital lobe lingual gyrus BA 19

Note: X, Y, and Z coordinates refer to Talairach Atlas.

Table 2
White matter (WM) correlates of the rotation/verbal and the focus/diffusion dimensions

Cluster size	T	Z	p	X	Y	Z	Brain area
WM correlations with rotation							
371	2.06	3.27	0.001	40	−63	−29	Right cerebellum posterior lobe tuber
721	1.91	3.08	0.001	−39	−64	−32	Left cerebellum posterior lobe cerebellar tonsil
91	1.82	2.98	0.001	−51	−31	−1	Left middle temporal gyrus BA 21
WM correlations with verbal							
3292	3.00	4.39	0.000	−2	−75	4	Left occipital lobe lingual gyrus BA 18
2728	2.56	3.87	0.000	−42	−53	39	Left inferior parietal lobule BA 40
1981	2.39	3.68	0.000	43	−61	36	Right parietal lobe angular gyrus BA 39
577	2.32	3.59	0.000	35	49	24	Right superior frontal gyrus BA 10
993	2.32	3.59	0.000	−46	14	38	Left middle frontal gyrus BA 8
4090	2.16	3.40	0.000	53	−7	46	Right frontal lobe precentral gyrus BA 4
417	1.92	3.10	0.001	50	−14	18	Right parietal lobe postcentral gyrus BA 43
361	1.85	3.01	0.001	−60	−46	21	Left temporal lobe supramarginal gyrus BA 40
1182	1.82	2.98	0.001	−52	−12	43	Left parietal lobe postcentral gyrus BA 3
1552	1.79	2.94	0.002	−24	12	43	Left middle frontal gyrus BA 8
677	1.78	2.93	0.002	−38	37	23	Left middle frontal gyrus BA 10
266	1.77	2.92	0.002	−55	−20	19	Left parietal lobe postcentral gyrus BA 40
476	1.71	2.83	0.002	56	−43	21	Right superior temporal gyrus BA 13
164	1.70	2.82	0.002	63	−35	38	Right inferior parietal lobule BA 40
136	1.68	2.81	0.003	5	−3	43	Right limbic lobe cingulate gyrus BA 24
161	1.67	2.78	0.003	−60	−36	30	Left inferior parietal lobule BA 40
203	1.66	2.78	0.003	−22	39	41	Left superior frontal gyrus BA 8
531	1.65	2.76	0.003	−41	−72	12	Left middle temporal gyrus BA 39
WM correlations with focus							
833	1.94	3.13	0.001	57	−42	2	Right middle temporal gyrus

efforts. In discussion, however, we will address only those correlations where $p < .001$.

Fig. 1 (left column) shows the correlations between GM volumes and the rotation–verbal dimension (see Table 1, top). There were both positive and negative correlations. Positive correlations indicated associations between greater GM volumes and greater orientation toward rotation-related abilities. Negative correlations indicated associations between greater GM volumes and verbally-related abilities. Though we conceived of these

Table 2 (*continued*)

Cluster size	T	Z	p	X	Y	Z	Brain area
WM correlations with focus							
364	1.60	2.70	0.003	11	11	64	Right superior frontal gyrus BA 6
WM correlations with diffusion							
2651	2.43	3.72	0.000	23	−12	−10	Right sub-lobar amygdala
527	2.19	3.43	0.000	13	−43	60	Right frontal lobe paracentral lobule BA 5
605	2.07	3.29	0.001	29	−62	38	Right parietal lobe precuneus BA 19
575	1.69	2.82	0.002	−25	−36	50	Left parietal lobe sub-gyral BA 40

Note: *X*, *Y*, and *Z* coordinates refer to Talairach Atlas.

associations as lying along a single dimension, the trade-off between rotation and verbal abilities involved in the dimension produced separate positive and negative associations with GM because we had no way of measuring the trade-off between brain regions directly. Positive correlations (shown in red) were observed bilaterally in the left inferior temporal lobe (BA 20; $p=0.001$), and in the left parietal lobe postcentral gyrus ($p=.003$). Negative correlations (shown in blue) were observed mostly in the left middle frontal lobe (BA9 and BA 8; $p<.001$ and $p=.002$ respectively), and in the right superior temporal gyrus (BA22; $p=.002$). Analogously, Fig. 1 also shows correlations between GM volumes and the focus–diffusion dimension in several locations (see Table 1, bottom). Positive correlations, indicating associations between greater GM volumes and greater use of focus of attention in processing (red), were observed in many locations throughout the brain (BA6, 38, 47, 3, 39, 20, and 7). Negative correlations, indicating association between greater GM volumes and greater use of diffusion of attention in processing (blue), were observed in the left middle occipital gyrus (BA18; $p=.001$) and the right occipital lobe lingual gyrus (BA19, $p=.001$).
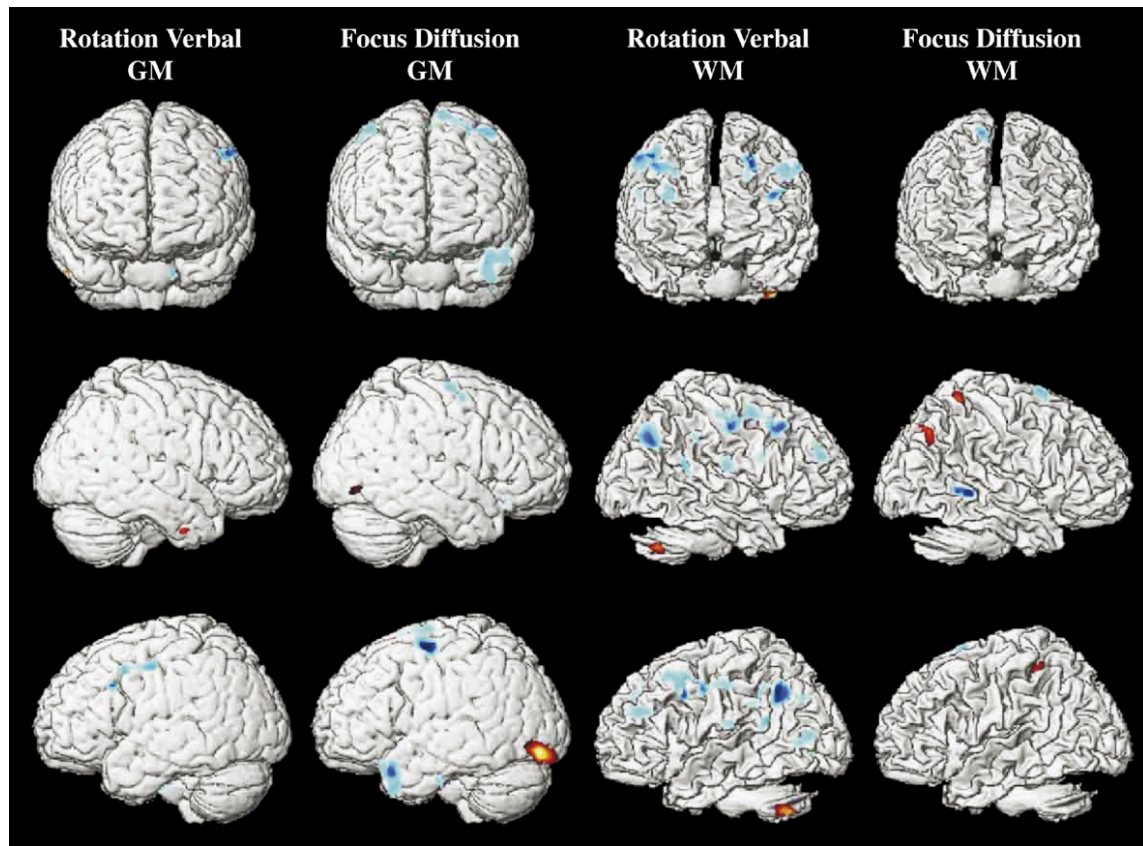

Fig. 4. Correlations between two dimensions (rotation/verbal and focus/diffusion) and gray matter (GM) and white matter (WM). Maximum voxel values within clusters are shown at $p<.003$ uncorrected; clusters include voxels where $p<.01$; red areas show positive correlations (rotation and focus respectively); blue areas show negative correlations (verbal and diffusion respectively); see Tables 1 and 2 for detailed anatomical localization and *p* levels.

Fig. 4 (right columns) and Table 2 show the same analyses for WM volumes. Positive correlations, indicating association between greater WM volume and greater orientation toward rotation-related abilities, were observed in (nearest gray matter) the right cerebellum posterior lobe tuber ($p=.001$), the left cerebellum posterior lobe cerebellar tonsil ($p=.001$), and the left middle temporal gyrus (BA21, $p=.001$). For verbal-related abilities, there were many correlations, in the parietal, occipital, frontal and temporal lobes (BA18, 40, 39, 10, 8, 4, 43, 40, 3, 13, and 24). Similarly, there were correlations between WM volumes and the focus–diffusion dimension (Fig. 4, right column). Positive correlations, indicating associations between greater WM volumes and greater use of focus of attention in processing, were observed in the right middle temporal gyrus ($p=.001$) and the right superior frontal gyrus (BA6; $p=.003$). There were negative correlations, indicating association between greater WM volume and greater use of diffusion of attention in processing, in the right sub-lobar amygdala ($p<.001$), right frontal lobe paracentral lobule (BA5; $p<.001$), the right parietal lobe precuneus (BA19; $p=.001$), and the left parietal lobe sub-gyral (BA40, $p=.002$).

3. Discussion

In this study, we explored possible associations between individual differences in psychometrically derived dimensions of intellectual performance that are independent of general intelligence and volumes of GM and WM in the brain. We found several correlations, both positive and negative, indicating that the psychometrically derived dimensions are related to structural patterns in the brain. As expected, the correlations we found involving the rotation–verbal dimension were relatively localized to areas of the brain that have been implicated in tasks involving the relevant content areas in prior studies. The correlations we observed involving the focus–diffusion dimension that were significant at $p=.001$ or less were primarily with WM volumes and were distributed more widely across areas of the brain involved in sensory processing and attention. Our results should be interpreted cautiously, however, given the complex nature of the associations considered. Our sample is relatively small for either VBM or individual difference analyses, so we regard it as an exploratory effort pending replication in larger samples distributed more representatively of the broader population. In particular, in the broader population the two dimensions of cognitive ability considered should be independent of general intelligence. In this sample,

however, it was necessary to remove 3 highly leveraged points with both low FSIQ and focus–diffusion scores in order to maintain this independence, thus restricting the ranges of both FSIQ and the focus–diffusion in the remaining sample.

There was little overlap between the brain regions associated with FSIQ in this sample reported previously (Haier et al., 2004) and the brain regions associated with the two dimensions considered in this study. This was to be expected, as the dimensions were psychometrically defined to be independent of general intelligence. They were based on WAIS subtest scores, but rather than reflecting magnitude of performance, they reflected different performance orientations. FSIQ was also based on the WAIS subtests and thus reflects specific abilities and skills as well as general intelligence. In a sample that has a reasonable distribution of both general intelligence and relative specific ability and skill levels, however, the associations between brain regions and FSIQ should primarily reflect general intelligence because individuals varied in the degree to which any single subtest contributed to FSIQ. Thus, the nature of the differences in the associations observed here and those observed with FSIQ is of interest in building an understanding of individual differences in the manifestation of intelligence.

There were also some differences between the present structural correlations and the brain regions showing activation in previous positron emission tomography (PET) and functional MRI (fMRI) studies of actual performance of verbal, image rotation, and attention tasks (Cabeza & Nyberg, 2000; Just, Carpenter, Maguire, Diwadkar, & McMains, 2001). There are at least two major reasons for this. First, PET and fMRI studies rely on changes in blood flow patterns in the brain to infer neural activity. Assuming the validity of the association between blood flow and neural activation, the studies compare blood flow in target and reference tasks. The regional differences in blood flow between the comparison and reference tasks are thought to reflect regions of the brain involved in the cognitive processes required by the target task but not the reference task. This will only be the case, however, if the cognitive demands of the target and reference tasks are actually additive in the manner assumed. There is empirical evidence that this is not always the case (Jennings, McIntosh, Kapur, Tulving, & Houle, 1997). It is for this reason that we have focused our investigations in this sample on structural rather than functional imaging (Colom, Jung, & Haier, 2006a; Colom et al., 2006b; Haier et al., 2004, 2005). Moreover, the kind of specificity in task demands

required by this assumption has tended to result in the use of very straightforward tasks that show few individual differences in performance accuracy. This means that the tasks, and thus the brain regions involved in their performance, may not reflect the full range of neural activity associated with the ability in question.

Second, because general intelligence is likely involved in the performance of all cognitive tasks, it is likely that all previous studies have used measures of task performance that confound general intelligence with the specific ability in question. Thus, a possible explanation for the changes in blood flow observed between target and reference tasks is that an increase in task difficulty that primarily requires the greater involvement of general intelligence is responsible rather than the specific demands of the task. This could be the case even when general intelligence is statistically controlled. Because we made use of dimensions of specific ability independent of general intelligence, we removed this potential confound.

As reported previously, in this sample, there were many regions showing significant correlations between FSIQ and GM. In contrast, for the two dimensions reported here there were relatively few brain regions showing GM correlations. The reverse was true with respect to the WM correlations. There was only one significant correlation between FSIQ and WM volume in this sample (Haier et al., 2004), in BA39, a parietal visual area. In contrast, there were several regions showing potentially significant correlations involving WM volumes and the two dimensions, particularly the verbal orientation. This suggests that the problem-solving power represented by general intelligence may be more closely related to GM, while individual differences in the manifestation of this power may be related to both gray and white matter communication patterns among brain regions. Of course, it is also possible that there are sex differences in the ways in which GM and WM in various regions are involved in the manifestations of different aspects of intelligence. Consistent with this, this sample showed sex differences in the GM and WM regions involved with FSIQ (Haier et al., 2005), and there are sex differences on the two dimensions of ability as well (Johnson & Bouchard, 2006).

The associations we observed in this study can be used to inform future research in at least three important ways. First, they add to the growing evidence that individual differences in psychometric measures of cognitive ability reflect basic individual differences in brain structure. Though the question of how these differences in brain structure arise is far from resolved, it is increasingly difficult to argue that individual differences in performance on tests of cognitive ability are purely situational, or solely due to attitudinal factors or exposure to particular kinds of experiences. The associations with brain structure act to increase the face validity of cognitive ability tests in practical applications such as job candidate selection. They also provide direct evidence that both psychometric theory and measurements can be used productively to inform neuroanatomical studies of brain structure and function.

Second, the associations we observed suggest that the same overall level of general intelligence is manifested in different ways in different individuals, at both biological and psychometric levels. For example, within the 48 individuals in the current sample, there were some same-sex pairs with highly similar FSIQ scores. In one pair with FSIQ's of 112, rotation–verbal scores were (4, −4) and the focus–diffusion scores were (1, −4). In another pair with FSIQ's of 135 and 133, rotation–verbal scores were (−5, 5) and focus–diffusion scores were (1, 7). The correlations we observed would suggest that there should be substantial differences within pairs in GM in the hippocampus and in Broca's area and in WM throughout the base of the brain, as well as differences in overall volumes of GM and WM indicative of the IQ difference across pairs.

The existence of these dimensions in addition to general intelligence has several practical implications. It suggests that tests of specific abilities such as those that might be used for assessing job aptitude need to be interpreted in the context of a broader range of abilities including general intelligence. For example, the individual above with a rotation–verbal score of 4 (and an FSIQ of 112) had a score of 16 on the Block Design subtest of the WAIS. Another individual with an FSIQ of 133 also had a score of 16 on Block Design, with a rotation–verbal score of 2. Though Block Design may assess abilities important to occupations such as airplane pilot or engineer and the two individuals were equivalent by this measure, the difference in general intelligence likely carries predictive weight for these jobs as well. We might expect the individual with the higher FSIQ to demonstrate higher performance across a range of tasks. On the other hand, the Vocabulary score of 16 that contributed to an IQ of 127 in another individual with a rotation–verbal score of −5 may indicate that any engineering aptitude is likely primarily the result of the usefulness of general intelligence in addressing any kind of problem, given that the Block Design score was 10.

The existence of these dimensions can also help to explain why two individuals suffering brain lesions in the same location due to stroke, injury, or aging-related

deterioration may have different patterns of net cognitive impairment, since these impairment patterns likely depend on the differences in their pre-morbid patterns of brain function and ability. Finally, despite the increases in the face validity of cognitive ability tests provided by the links with brain structure, the evidence these same links provide for the presence of individual differences in the manifestation of general intelligence indicates that these same tests may not measure the same abilities in the same ways in different individuals. This is because individual differences in the availability of specific brain structural resources related to specific abilities may make necessary the use of problem solving strategies that differ sufficiently that it no longer makes sense to think of the strategies as reflecting the same ability. This should be explored in greater detail in future research.

The third way in which these results can be used to inform future research involves the application of scores on these particular psychometrically derived dimensions in future studies of both brain structure and function. Both structural and functional brain studies have shown different patterns of associations with brain regions across samples and demographic variables such as age and sex (Haier & Benbow, 1995; Haier et al., 2004, 2005; Jung et al., 2005; Schmithorst & Holland, 2006). It is possible that these inconsistencies may be explained at least partly by sampling differences in the patterns of scores on the psychometric dimensions considered here. For example, Bell, Wilson, Wilman, Dave, Silverstone (2006) observed substantial sex differences in brain activation patterns during specific cognitive tasks. As our psychometric dimensions show sex differences as well (Johnson & Bouchard, 2006), it is possible that the differences in brain activation patterns that have been observed to be associated with sex differences particularly in verbal and rotation-related abilities (e.g. Neubauer, Grabner, Fink, & Neuper, 2005) could be related to differences in patterns of scores on the psychometric dimensions considered here. Our ability to interpret the results of such studies may be greatly improved through the inclusion of both measures of general intelligence and these two dimensions that are independent of general intelligence.

In conclusion, our data indicate that two dimensions of ability independent of general intelligence have neuroanatomical correlates in the brain. Though these findings require replication in larger samples more completely representative of the population, they provide an important step in showing how individual differences in brain structure may be related to individual differences in intellectual performance. Moreover, these findings demonstrate that purely psychometrically derived information about intelligent performance may reflect neuroanatomical properties of the brain, and they suggest that such information can be valuable in identifying and disentangling potentially confounding explanations for some of the associations that have been observed in prior studies.

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