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Gray matter and intelligence factors: Is there a neuro-*g*?

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ABSTRACT

Heterogeneous results among neuro-imaging studies using psychometric intelligence measures may result from the variety of tests used. The *g*-factor may provide a common metric across studies. Here we derived a *g*-factor from a battery of eight cognitive tests completed by 6929 young adults, 40 of whom also completed structural MRI scans. Regional gray matter (GM) was determined using voxel-based-morphometry (VBM) and correlated to *g*-scores. Results showed correlations distributed throughout the brain, but there was limited overlap with brain areas identified in a similar study that used a different battery of tests to derive *g*-scores. Comparable spatial scores (with *g* variance removed) also were derived from both batteries, and there was considerable overlap in brain areas where GM was correlated to the respective spatial scores. The results indicate that *g*-scores derived from different test batteries do not necessarily have equivalent neuro-anatomical substrates, suggesting that identifying a "neuro-*g*" will be difficult. The neuro-anatomical substrate of a spatial factor, however, appears more consistent and implicates a distributed network of brain areas that may be involved with spatial ability. Future imaging studies directed at identifying the neural basis of intelligence may benefit from using a psychometric test battery chosen with specific criteria.

Several structural MRI studies show correlations between various psychometric measures of intelligence and the amount of gray matter (GM) tissue in areas distributed throughout the brain. As reviewed recently, there is some convergence among these studies (Jung & Haier, 2007); variation, however, may result from the different measures of intelligence. Since intelligence measures are correlated with each other, the general underlying factor or *g*-factor (i.e. a measure of the common variance among all varieties of mental tests) first noted by Spearman (Spearman, 1904) may provide a common metric for comparison among studies seeking to identify neural correlates of intelligence. Regional GM correlates of the *g*-factor, however, remain elusive, with most neuro-imaging studies using indirect measures of *g* like the WAIS (Colom, Jung, & Haier, 2006a; Haier, Jung, Yeo, Head, & Alkire, 2004) or the method of correlated vectors (Colom, Jung, & Haier, 2006b). The situation with functional imaging studies is no better. One key limiting factor in most studies is the use of single intelligence measures that confound *g*, group or ability factors, and specific skills (Colom, 2007). The most direct way to determine GM correlates of *g* is to start by deriving a *g* score for individuals based on factor analysis of a battery of cognitive tests sampling well-defined core facets of intelligence identified from the extensive psychometric research literature. One recent study (Colom et al., 2009) has done this for a sample of 100 subjects tested in Madrid, who completed 9 tests selected for their relationship to known psychometric intelligence factors (*g*, fluid, crystallized, and spatial). A *g* score was derived for each subject and correlated to regional GM determined by voxel-based-morphometry (VBM). Results for general intelligence were consistent with several aspects of the Parieto-Frontal Integration Theory (PFIT)

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of intelligence, a model based on a detailed review of 37 studies of functional and structural imaging and intelligence (Jung & Haier, 2007).

There is general agreement that the psychometric characteristics of *g*-factors derived from different batteries of cognitive tests are more-or-less equivalent, providing the tests sample a broad range of cognitive abilities and that the sample size is large in number and in range of ability (Jensen, 1998; Johnson, te Nijenhuis, & Bouchard, 2008). A reasonable expectation is that equivalent psychometric *g*-factors should show similar brain correlates. However, if two test batteries, for example, are weighted differently with tests of memory, spatial reasoning, verbal ability and the like, different brain correlates of the respective *g*-factors may emerge, complicating the search for brain correlates of *g*. Group or ability factors, like spatial reasoning, derived from different batteries should be more likely to show similar brain correlates since only spatial tests should contribute to a spatial factor once any *g* variance is removed.

Here we derived a *g* score from a battery of cognitive tests completed by 6929 young adults and calculated its GM correlates for 40 subjects who also volunteered for a structural MRI scan. We used the same methods to derive *g* as used by Colom et al. (2009) in the Madrid sample. However, the Madrid study was based on nine tests selected for representing a previously demonstrated empirical psychometric structure with theoretical meaning. The tests used here were designed to assess distinct abilities in the manner of Thurstone (1938). We hypothesized that, if *g*-factors are essentially equivalent irrespective of the tests used to derive them, provided these tests tap diverse core intelligence facets, the GM correlates of *g* scores based on these tests would be similar to those based on the nine tests in the Madrid sample. If the *g*-factors from the respective batteries reflect the kinds of tests in the battery, different correlates may result. Further, brain correlates of the same group factors derived from different batteries should be more consistent (once any *g* variance is removed) and show more anatomical overlap.

1. Methods

1.1. Subjects

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 for all subjects 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, subjects who completed the same test battery in 2006 and 2007 in the New York City center were invited to return for MRI scanning at Mt. Sinai Medical Center. All who volunteered were screened for medical and psychiatric illnesses including a history of head injury and substance abuse. After being screened and giving informed consent, the final 40 subjects completing MRI included 21 males and 19 females, aged 18–35 years (mean age = 26.6, *SD* = 4.9).

1.2. Intelligence testing

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). In Table 1 we provide a description of these tests, including the constructs they measure and their reliabilities. Previous research (Condon & Schroeder, 2003) showed that these tests load 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 (see confirmation of this structure for this sample in Fig. 1). These tests have been used in research on various aspects of cognition and intelligence (Acton & Schroeder, 2001; Salthouse, Schroeder, & Ferrer, 2004; Schroeder & Salthouse, 2004). For the present study, test scores were partialled for sex and age in order to eliminate nuisance variance.

1.3. Factor analysis and g

We started with all 6929 subjects (6889 plus the 40 with MRI scans) and followed the same procedures as used by Colom et al. (2009) in the Madrid sample to identify scores for groups of tests measuring distinguishable intelligence constructs. We performed a confirmatory factor analysis (CFA) on the eight test scores using the model indicated in Fig. 1, where

Table 1
Johnson O'Connor Research Foundation (JOCRF) test battery

Test name	Reliability	Ability measured	Description of task
Inductive Speed	0.84	Quickness in seeing relationships among separate facts, ideas, or observations.	Given six pictures, quickly identifying the three pictures that go together (highly speeded).
Analytical Reasoning	0.81	Ability to arrange ideas into a logical sequence.	Given a set of words, placing them into a predetermined logical structure so that they make sense (e.g., ANIMAL: DOG, CAT).
Number Series	0.87	Ability to reason (solve problems) with numbers.	Given a series of numbers, identifying the number that would come next in the sequence.
Number Facility	0.86	Ability to perform arithmetic operations quickly.	Given six numbers, placing them into two simple equations so that the equations are true.
Wiggly Block	0.73	Ability to visualize three-dimensional forms.	Re-assembling three-dimensional blocks that have been cut into wavy ("wiggly") pieces.
Paper Folding	0.82	Ability to visualize three-dimensional forms.	Mentally visualizing a piece of paper as it is folded, punched with a paper punch, and unfolded.
Verbal-Associative Memory	0.92	Associative memory for verbal material.	Memorizing paired associates between nonsense words and English words.
Number Memory	0.82	Memory for numbers.	Memorizing six-digit numbers.

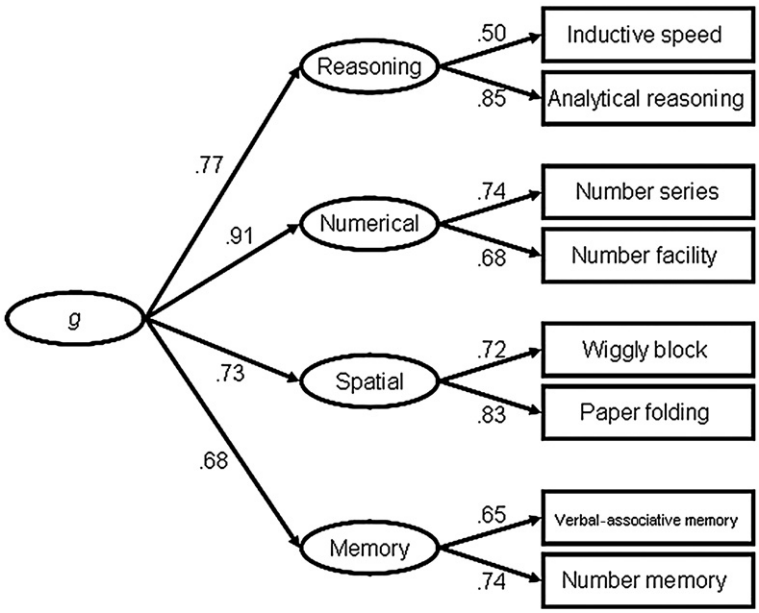

Fig. 1. Factor structure of 8 tests in JOCRF battery (N=6929).

the resulting loadings are shown. Model fit was reasonable: RMSEA=.08, $\chi^2_{(16)}$=760.6, CFI=.95. Therefore, subsequent computations were based on this measurement model. It should be noted that the factor structure in this model is different from the one obtained in the Madrid sample (see Colom et al., 2009). Key differences are that the Madrid battery included more tests of reasoning and three measures per factor; the JOCRF battery did not include measures of verbal ability. In addition to the CFA, we performed an exploratory hierarchical factor analysis (Schmid–Leiman transformation), and it yielded a factor structure similar to that used in the confirmatory factor analysis. Both the battery here and the Colom et al. battery yielded *g*-factors (accounting for 22% of the variance in the Madrid battery and 29% in the JOCRF battery), and spatial factors (9.2% and 5% of the variance, respectively).

Next, we computed standardized scores (*z*-scores) for the eight tests shown in the measurement model (Fig. 1) and then we computed average *z*-scores for Speed of Reasoning (Inductive Speed and Analytical Reasoning), Numerical (Number Series and Number Facility), Spatial (Wiggly Block and Paper Folding), and Memory (Verbal-Associative Memory and Number Memory). The general intelligence *g*-score for each subject was the average of their *z*-scores on the eight tests. We then computed regression analyses using the general score (*g*) to predict Reasoning, Numerical, Spatial, and Memory, respectively. This produced residual scores for these latter factors. Table 2 shows the correlations between these factors and the eight tests. As expected (and desired), the general score (*g*) correlated with all the tests in the battery, whereas residual scores for Reasoning, Numerical, Spatial, and Memory factors show the highest correlations with their respective measures only. Further, the *g* score is unrelated to the residual scores for the group factors. Other than *g*, the only factor comparable to those considered in the Madrid sample is the Spatial factor, since the Madrid battery was constructed to yield fluid, crystallized, and spatial factors.

All the preceding analyses were based on the entire sample. We also examined the correlations between tests and factors for just the 40 Ss who completed MRI scans, and they are similar to those shown for the entire sample (see Table 2). The *g* and residualized (that is, *g*-partialled) spatial *z*-scores for these 40 subjects were used to determine the correlations to GM, as described below.

1.4. Structural MRI acquisition

A 3T Siemens Allegra MRI scanner (Siemens Medical Systems, Ehrlangen, Germany) was used at Mt. Sinai Medical Center, NYC. For each subject, a sagittal T_1-weighted spin echo

Table 2
Correlations between factors (with *g* removed) and tests (full sample/MRI sample)

	General	Reasoning	Numerical	Spatial	Memory
Inductive Speed	.53**/ .38*	.66**/ .75**	−.22**/ −.23	−.16**/ −.29	−.27**/ −.31*
Analytical Reasoning	.71**/ .81**	.48**/ .23	−.13**/ .13	−.09**/ −.14	−.25**/ −.25
Number Series	.70**/ .83**	−.24**/ −.33*	.51**/ .56**	−.14**/ −.16	−.08**/ −.06
Number Facility	.67**/ .72**	−.08**/ −.20	.55**/ .72**	−.27**/ −.49**	−.14**/ −.10
Wiggly Block	.65**/ .71**	−.08**/ −.20	−.25**/ −.05	.61**/ .39*	−.29**/ −.09
Paper Folding	.69**/ .69**	−.18**/ .24	−.20**/ −.10	.57**/ .46**	−.20**/ −.07
Verbal Associative Memory	.58**/ .71**	−.25**/ −.36*	−.15**/ −.02	−.29**/ −.12	.64**/ .52**
Number Memory	.62**/ .58**	−.31**/ −.39*	−.10**/ .05	−.23**/ −.29	.60**/ .62**

*p<.05, **p<.01.

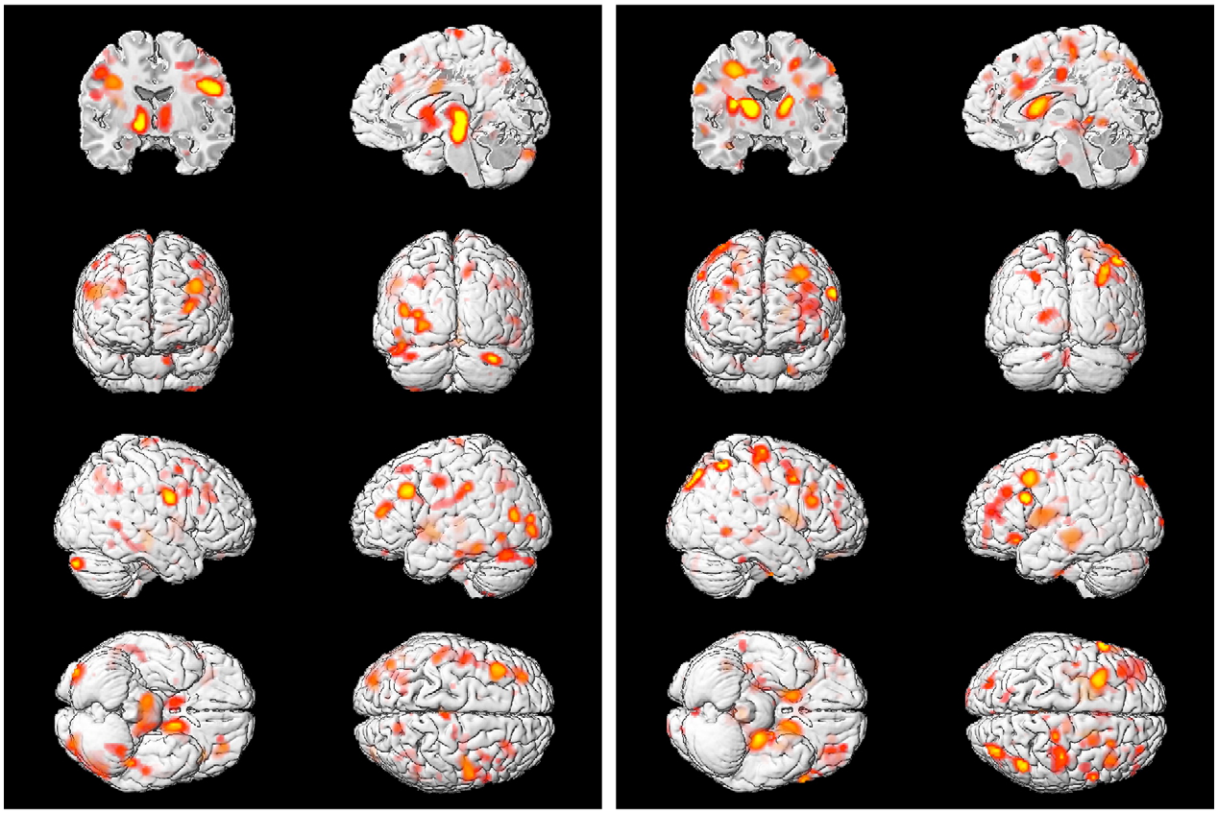

Fig. 2. GM correlates (positive) of *g*-scores (left panel) and spatial scores (right panel) in the JOCRF sample, $N=40$ ($p<.01$ yellow, $p<.025$ orange, $p<.05$ red).

image was performed first as localizer, with the repetition time (TR)=500 ms and the echo time (TE)=10 ms, FOV=18cm×14 cm, matrix size=512×384, 4.3 mm thick. Based on this localizer, structural scans were acquired using a 3D MP-RAGE pulse sequence with the following parameters: TR=2500 ms, TE=4.4 ms, FOV=21 cm, matrix size=256×256, and 208 slices with thickness=0.82 mm.

1.5. Voxel-based-morphometry (VBM) and statistical analyses

We applied VBM to identify brain areas where gray matter (GM) volumes are correlated to factor scores. We used Statistical Parametric Mapping software (SPM5; The Wellcome Department of Imaging Neuroscience, University College London) to apply the optimized VBM protocol to the

Table 3
GM correlates of *g*-scores derived from JOCRF sample ($N=40$, $p<.01$)

Size	*p*(unc)	*x,y,z*				
165	0.000	−36 22 34	Left	Frontal	Middle frontal gyrus	Brodmann area 9
272	0.001	12 −22 −10	Right	Midbrain		Substania Nigra
	0.002	6 −26 0	Right	Sub-lobar	Thalamus	
	0.008	−8 −26 4	Left	Sub-lobar	Thalamus	Pulvinar
121	0.002	52 −2 28	Right	Frontal	Inferior frontal gyrus	Brodmann area 9
91	0.002	−14 −4 −4	Left	Sub-lobar	Lentiform nucleus	Globus Pallidus
31	0.003	−24 −86 0	Left	Occipital	Middle occipital gyrus	Brodmann area 18
22	0.004	−44 −38 −16	Left	Temporal	Fusiform gyrus	Brodmann area 20
31	0.004	−42 −72 12	Left	Temporal	Middle temporal gyrus	Brodmann area 39
27	0.004	−30 46 14	Left	Frontal	Middle frontal gyrus	Brodmann area 10
10	0.006	−48 −32 36	Left	Parietal	Postcentral gyrus	Brodmann area 2
9	0.007	−30 −86 10	Left	Occipital	Middle occipital gyrus	Brodmann area 19
13	0.007	36 −84 −30	Right	Posterior	Declive	
10	0.007	−10 −28 −16	Left	Anterior	Culmen	
3	0.009	−48 −60 −8	Left	Temporal	Inferior temporal gyrus	Brodmann area 19

All correlations are positive; size is number of voxels in significant cluster; *p* is uncorrected; *x,y,z* coordinates are maximum voxel (MNI); left/right is hemisphere; Brodmann areas are best estimates from Talairach and Tournoux Atlas (1988).

Table 4
Overlap[a] of GM/*g*-score correlates in JOCRF ($p<.05$) and Madrid ($p<.005$) samples

Right	Midbrain		Substania Nigra
Left	Midbrain		Red Nucleus
Left	Temporal lobe	Fusiform Gyrus	Brodmann area 19
Right	Frontal lobe	Inferior Frontal Gyrus	Brodmann area 9
Left	Pons		
Left	Temporal lobe	Fusiform Gyrus	Brodmann area 20

[a] This is a qualitative analysis; Brodmann areas are best estimates from Talairach and Tournoux Atlas (1988).

sample using the methods of (Ashburner & Friston, 2000; Good, Johnsrude, Ashburner, Henson, Friston, & Frackowiak, 2001). To preserve the amount of tissue in any given anatomical region after spatial normalization, the optimal GM partitions were multiplied by the Jacobian determinants of their respective spatial transformation matrix. This modulation step is to allow the final VBM statistics to reflect local deviations in the absolute amount (volume) of tissue in different regions of the brain (Ashburner & Friston 2000). The modulated GM partitions were 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. Each individual scan was then fitted to a standardized SPM template specifically created for 3T MRI scans (tissue probability map provided by the International Consortium for Brain Mapping (T1 452 Atlas, John C. Mazziotta & Arthur W. Toga, http://www.loni.ucla.edu/Atlases/Atlas_Detail.jsp?atlas_id=6).

2. Results

GM correlates of the JOCRF *g* score are shown in Fig. 2 (left panel) and detailed in Table 3 ($p<.01$, uncorrected). GM is positively correlated to *g* in 13 clusters distributed throughout the brain, including Brodmann areas (BA) 9, 10, 39, 18, 19, 20, 2 and parts of the midbrain, thalamus, and globus pallidus. Of these 13 clusters, only 2 are less than 10 voxels in size. There were negative correlations in 6 areas (not shown: BAs 13, 18, two parts of 19, 21, 38); 3 were smaller than 10 voxels.

We identified the voxels where there were *g*/GM positive correlations in both the JOCRF and the Madrid samples by using the xj view tool in SPM5, which overlays one set of results on the other. With only 40 subjects, we used the JOCRF findings significant at $p<.05$ (uncorrected) to maximize possible overlap, and with 100 subjects, the Madrid findings

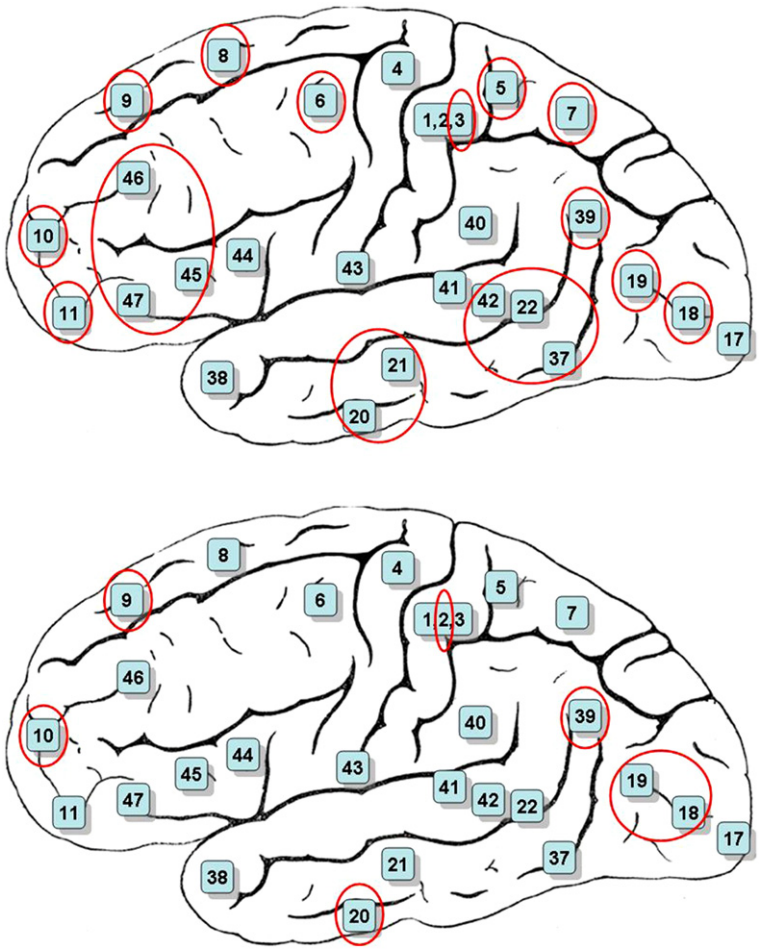

Fig. 3. Comparison of where there are *g*-score/GM correlations (circled Brodmann areas) in the Madrid (top panel) and JOCRF samples (bottom panel), as detailed in Table 4.

Table 5
GM correlates of spatial score from JOCRF sample (N=40, p<.01)

Size	p(unc)	x,y,z				
186	0000	−30 12 44	Left	Frontal lobe	Middle Frontal Gyrus	Brodmann area 8
178	0.001	−26 −24 −4	Left	Sub-lobar		Lateral geniculum body
261	0.002	−14 2 12	Left	Sub-lobar	Lentiform Nucleus	Putamen
	0.006	−28 −4 14	Left	Sub-lobar	Lentiform Nucleus	Putamen
33	0.002	−60 18 28	Left	Frontal lobe	Inferior Frontal Gyrus	Brodmann area 9
30	0.002	48 −56 58	Right	Parietal lobe	Inferior Parietal Lobule	Brodmann area 40
108	0.003	18 4 14	Right	Sub-lobar	Caudate	Caudate body
29	0.004	36 −78 48	Right	Parietal lobe	Superior Parietal Lobule	Brodmann area 7
25	0.006	42 24 24	Right	Frontal lobe	Middle Frontal Gyrus	Brodmann area 46
18	0.006	0 −38 0	Left	Anterior lobe	Culmen	
4	0.007	60 8 44	Right	Frontal lobe	Middle Frontal Gyrus	Brodmann area 6
9	0.007	22 −26 60	Right	Frontal lobe	Precentral Gyrus	Brodmann area 4
9	0.007	28 22 36	Right	Frontal lobe	Middle Frontal Gyrus	Brodmann area 9
3	0.008	−56 26 −10	Left	Frontal lobe	Inferior Frontal Gyrus	Brodmann area 47
4	0.008	−34 40 −24	Left	Frontal lobe	Middle Frontal Gyrus	Brodmann area 11
4	0.009	−18 −14 −40	Left	Limbic lobe	Uncus	Brodmann area 28
1	0.009	−26 −86 44	Left	Parietal lobe	Precuneus	Brodmann area 19
2	0.009	26 8 50	Right	Frontal lobe	Superior Frontal Gyrus	Brodmann area 6
4	0.009	40 −52 −2	Right	Limbic lobe	Parahippocampal Gyrus	Brodmann area 19
3	0.009	38 −20 70	Right	Frontal lobe	Precentral Gyrus	Brodmann area 6

All correlations are positive; size is number of voxels in significant cluster; p is uncorrected; x,y,z coordinates are maximum voxel (MNI); left/right is hemisphere; Brodmann areas are best estimates from Talairach and Tournoux Atlas (1988).

were considered significant at p<.005 (uncorrected). Using these criteria, only 6 areas (3 in the cortex) showed any overlap (BAs 9, 19, 20 and parts of the midbrain and pons), as detailed in Table 4 and shown in Fig. 3. A few additional areas of overlap are suggested in Fig. 3 (BAs 10, 39, 18) because it is a qualitative comparison based on full BAs rather than on specific voxel overlap determined with the xj view tool. Nonetheless, the limited overlap is contrary to the prediction based on the presumed equivalence of g-factors.

In addition to g, the other factor in common between the two samples is the spatial factor. This factor was derived in the same way for both samples, and for each sample common variance with the sample-specific g-score was removed so the spatial factors are not confounded with g for either sample. Positive GM correlates of the JOCRF Spatial score are shown in Fig. 2 (right panel) and detailed in Table 5 (p<.01, uncorrected). There are 20 clusters; 10 are smaller than 10 voxels. Most of the 20 clusters are in the frontal and parietal lobes; other areas include the caudate, putamen, and parahippocampus. Only two areas (both less than 10 voxels; not shown) showed a negative correlation (BA 20 and the pulvinar). Table 6, based on the xj view tool in SPM5, for identifying common significant voxels in two or more analyses, shows 23 areas of overlap distributed throughout the brain (mostly in frontal and parietal lobes; note that more than one area of overlap can appear within a larger cluster) for positive GM correlates of the spatial score for both samples. As predicted, there is considerably more overlap for the spatial scores than for g.

Table 6
Overlap[a] of GM/spatial correlates in JOCRF (p<.05) and Madrid (p<.005) samples

Left	Frontal	Inferior Frontal Gyrus	Brodmann area 9
Left	Frontal	Middle Frontal Gyrus	Brodmann area 11
Right	Parietal	Superior Parietal Lobule	Brodmann area 7
Right	Parietal	Precuneus	Brodmann area 19
Right	Parietal	Precuneus	Brodmann area 19
Left	Parietal	Superior Parietal Lobule	Brodmann area 7
Right	Frontal	Superior Frontal Gyrus	Brodmann area 6
Left	Limbic	Parahippocampal Gyrus	Brodmann area 35
Right	Frontal	Precentral Gyrus	Brodmann area 6
Left	Frontal	Precentral Gyrus	Brodmann area 6
Right	Parietal	Postcentral Gyrus	Brodmann area 1
Left	Frontal	Middle Frontal Gyrus	Brodmann area 6
Right	Parietal	Inferior Parietal Lobule	Brodmann area 40
Left	Frontal	Inferior Frontal Gyrus	Brodmann area 47
Left	Temporal	Superior Temporal Gyrus	Brodmann area 42
Right	Limbic	Parahippocampal Gyrus	Brodmann area 36
Left	Occipital	Inferior Occipital Gyrus	Brodmann area 18
Right	Frontal	Superior Frontal Gyrus	Brodmann area 8
Right	Frontal	Paracentral Lobule	Brodmann area 6
Left	Frontal	Middle Frontal Gyrus	Brodmann area 10
Left	Frontal	Middle Frontal Gyrus	Brodmann area 10
Right	Temporal	Inferior Temporal Gyrus	Brodmann area 20
Left	Frontal	Inferior Frontal Gyrus	Brodmann area 46

[a] This is a qualitative analysis; Brodmann areas are best estimates from Talairach and Tournoux Atlas (1988).

3. Discussion

Does psychometric g have a consistent neuro-anatomical substrate that defines a neuro-g construct? The primary results here indicate that the gray matter (GM) correlates of g depend in part on the tests used to derive g. This suggests that psychometric g may not be a unitary construct as it relates to brain structure. Comparability among studies will depend on having a standard procedure for deriving g, especially with respect to the test battery used and the method of defining scores for factors. Since random differences between small samples also contribute to inconsistencies among studies, large samples are necessary in addition to optimal test batteries. We propose these specific recommendations for discussion, to maximize comparability among studies:

1. Use several diverse measures tapping abstract, verbal, numerical, and spatial content domains.
2. Use three or more measures to define each group factor. These group factors should fit the main factors comprised in models such as those proposed by Carroll (Carroll, 1993),

Johnson and Bouchard (2005), or McGrew (McGrew, 2005; 2009).

3. Measures for each group factor should not be based solely on speeded or non-speeded tests. Both types should be used. This recommendation is based on the fact that Carroll's stratum I abilities comprise both level (non-speeded) and speed factors (see McGrew, 2009).
4. Use three or more group factors to define the higher-order factor representing *g*. Measurement models should reveal that non-verbal, abstract or fluid reasoning is the group factor best predicted by *g*. As discussed by Carroll (1993, 2003) fluid reasoning (e.g. drawing inferences, concept formation, classification, generating and testing hypotheses, identifying relations, comprehending implications, problem solving, extrapolating, and transforming information) is the second stratum ability more closely related to *g*.
5. Find a way to separate sources of variance contributing to participants' performance on the measures. The influence of *g* is pervasive, but it changes for different group (lower-order) factors and specific measures. Participants' scores result from *g*, cognitive abilities (group factors), and cognitive skills (test specificities). Brain correlates for a given cognitive ability, like verbal ability or spatial ability, are influenced by all these sources of variance.

It may be that the apparent inconsistencies for *g*/GM correlates between the JOCRF and Madrid samples result partly from the fact that only the Madrid study followed the recommendations just described. The JOCRF intelligence factors were defined by two measures each, and most of these measures were administered under speeded conditions. Cultural and other unknown sample differences may also be important factors, although we note that the results for the spatial factor were consistent.

Without a standard test battery selected for a known and theoretically meaningful psychometric structure, comparisons of the neuro-correlates of intelligence tests are bound to be inconsistent and difficult to interpret. In our view, future studies using any one test as a shortcut to assess *g* or any other particular intelligence factor are unlikely to add unambiguous findings in the search for the neural basis of intelligence. The Raven's Progressive Matrices test, for example, typically loads high on *g*, but it is not a pure measure of *g*; similarly, the WAIS IQ score is not a good estimate of a single intelligence factor.

Colom et al. (2006a) showed that individual intelligence measures and their components display different neuro-anatomical correlates depending on their *g* loadings. Using the Wechsler battery, these authors noted that the Block Design subtest showed a very high *g* loading (.90), Picture Completion showed an intermediate *g* loading (.59), and Digit Symbol showed a low *g* loading (.20). Their VBM findings revealed that increasing *g*-involvement was associated with increased recruitment of gray matter clusters distributed throughout the brain. This study highlights the fact that combining all these intelligence tests into the same general score or using only a single non-theoretically-defined test may produce confusing findings across studies.

It is also possible that the same intelligence test might show different *g* involvement for different samples. For instance, Colom et al.(2002) have shown that the subtests in the WAIS-III display sharply distinguishable *g* loadings for participants with different academic levels. Block Design could show the highest *g* loadings for participants who have completed primary or secondary school, but their different values indicate that the expected underlying brain correlates may be quite different. Actually, the computed *g* loadings for Block Design in Colom et al.'s (2002) report were .73 and .59 for participants with primary and secondary school, respectively.

To further complicate things, equivalent test performance may be the result of different processes (and different abilities) for different individuals. As noted by Johnson et al. (2008) "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" (p. 27).

Along these lines, there is evidence that to some extent different persons use different strategies to accomplish the tasks posed by various cognitive tests. For example, on tests of spatial ability, some examinees appear to use verbal or logical analyses to reduce the number of possibilities or to generate the desired answer (Lohman, 2000). For such examinees, performance on spatial tests might show greater correlations with brain volumes in verbal areas, such as Broca's area, than in spatially-related areas, such as the parietal cortex. If this is true, then samples with a predominance of examinees using verbal strategies will show different brain areas than samples with a predominance of visually-oriented examinees (Johnson et al., 2008). Many *f*MRI studies show strategy differences reflected in regional brain activations; see for example D'Esposito , Aguirre, Zarahn, Ballard, Shin, and Lease (1998); Iaria, Petrides, Dagher, Pike and Bohbot (2003); Rypma, Berger, Genova, Rebbechi and D'Esposito (2005). With respect to our study, we know of no reason at this time to expect that our samples used different strategies. Nonetheless, we acknowledge that this possibility could account for some of the differences in the results here and in other studies.

While recognizing the heterogeneity among imaging/intelligence studies, Jung and Haier (2007) emphasized the consistencies despite the variety of tests and methods used in 37 studies to find neuro-correlates of intelligence. They focused on a network of parietal and frontal brain areas, i.e., the PFIT model. The *g*/GM correlates in the JOCRF sample show some support for the PFIT model, but not as much as the findings from the Madrid sample. The PFIT model recognizes that intelligence differences among individuals may result from different subsets of brain areas, perhaps leading to or resulting from different cognitive strategies. The GM/spatial correlations for both samples, however, were similar and are consistent with the general PFIT model. Note that spatial and *g* scores are orthogonal, but they share some brain areas, a result also found for the Madrid sample. As suggested by Colom et al. (2009), this finding may be related to the approach endorsed by mathematical models such as developed by van der Maas et al. (2006) and Dickens (2007) based on positive beneficial relationships between cognitive processes (e.g. mutualism).

In addition to the psychometrics of *g* and whether it is a unitary construct or not, many issues require further investigation, including the role of age and sex differences in brain structure and development (Haier et al., 2004; Haier, Jung, Yeo, Head & Alkire, 2005; Jung et al., 2005; Schmithorst & Holland 2007; Schmithorst, Holland & Dardzinski, 2008; Shaw et al., 2006), the role of white matter (Jung et al., 1999; Schmithorst, Wilke, Dardzinski & Holland, 2005) and the role of genetics in GM distribution (Posthuma, Baare, Hulshoff Pol, Kahn, Boomsa, & De Geus, 2002, 2003; Thompson, Cannon & Toga, 2002). All these issues also apply to functional imaging and the dynamics of brain function during tests of intelligence (Haier et al., 1988; Haier, White, & Alkire, 2003; Jung et al., 1999; Lee et al., 2006; Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997; Thoma et al., 2006). We believe that imaging studies of intelligence addressing all these issues have reached a new phase (Haier & Jung, 2007) that requires equal sophistication in both imaging and ability testing methodologies to explore the concept of a neuro-*g* and how it may relate to psychometric *g* and other intelligence factors.

The search for a biological basis for *g* is in early stages, and the key variables are not yet clear. Our focus here on GM may be premature. Moreover, there may not be a single biological basis to be found. For example, both gray matter volumes and intelligence show high heritability indices (Posthuma et al., 2003; Thompson, Cannon, Narr, van Erp, Poutanen, Huttunen, et al., 2001). Heritability is a population statistic, and molecular genetic studies have yet to identify specific genes associated with individual differences in intelligence (Posthuma & de Geus, 2006). At the end, a similar picture could emerge for the presumed brain correlates for *g*. This situation would be expected if *g* is indeed manifested in different ways in different individuals, as noted above. Further studies are needed to address this view. In the meantime, identifying brain correlates of intelligence and *g* with neuro-imaging continues to provide empirical observations for refining theoretical constructs for new hypothesis testing.

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