

General intelligence and memory span: Evidence for a common neuroanatomic framework

Roberto Colom

Facultad de Psicología, Universidad Autónoma de Madrid, Madrid, Spain

Rex E. Jung

Department of Neurology and the MIND Institute, University of New Mexico, Albuquerque, NM, USA

Richard J. Haier

School of Medicine, University of California, Irvine, CA, USA

General intelligence (g) is highly correlated with working-memory capacity (WMC). It has been argued that these central psychological constructs should share common neural systems. The present study examines this hypothesis using structural magnetic resonance imaging to determine any overlap in brain areas where regional grey matter volumes are correlated to measures of general intelligence and to memory span. In normal volunteers ($N = 48$) the results ($p < .05$, corrected for multiple comparisons) indicate that a common anatomic framework for these constructs implicates mainly frontal grey matter regions belonging to Brodmann area (BA) 10 (right superior frontal gyrus and left middle frontal gyrus) and, to a lesser degree, the right inferior parietal lobule (BA 40). These findings support the nuclear role of a discrete parieto-frontal network.

Keywords: General intelligence; Memory span; Magnetic resonance imaging; Voxel-based morphometry; Working-memory capacity.

The general factor of intelligence (g) and working-memory capacity (WMC) are central psychological constructs. The g factor is usually measured by standardized intelligence tests (Lubinski, 2004), whereas WMC is measured by memory span tasks (Miyake & Shah, 1999). WMC and g are highly related, although we still do not know why (Colom, Abad, Rebollo, &

Shih, 2005a; Colom, Rebollo, Palacios, Juan-Espinosa, & Kyllonen, 2004; Colom & Shih, 2004; Engle, 2002; Kane et al., 2004; Kyllonen & Christal, 1990). There also is research focusing on how WMC is related to fluid intelligence (Gf) rather than to g (Engle, Tuholski, Laughlin, & Conway, 1999; Gray, Chabris, & Braver, 2003). Engle and associates have done important research

Correspondence should be addressed to Facultad de Psicología, Universidad Autónoma de Madrid, 28049 Madrid, Spain (E-mail: roberto.colom@uam.es)

We thank Kevin Head for the assistance with data analyses. The University of California, Irvine (UCI) portion of this work was funded in part by a grant from the National Institute of Child Health and Human Development (NICHD) to Dr. Haier (HD037427). The MIND Institute portion of this work was supported in part by a generous donation from Carl and Ann Hawk (Sandia National Laboratories, retired). The Universidad Autónoma de Madrid (UAM) portion of this work was funded in part by a grant from the Ministerio de Educación y Ciencia (MEC) to R. Colom (SEJ-2006-07890).

examining the *Gf*–WMC relationship (Conway, Kane, & Engle, 2003; Engle & Kane, 2004), finding that controlled attention—that is, the ability to maintain a representation active in the face of interference or distraction—underlies the commonality to both constructs. Jensen (1998) and Carroll (2003) both have argued that *Gf* and *g* appear to be either the same factor or so highly related as to be redundant.

Ackerman, Beier, and Boyle (2005) used structural equation modelling (SEM) to examine the relationship between verbal, reasoning, and spatial cognitive abilities to WMC tasks. They conceptualized WMC as a first-order factor, aligned with Carroll's (1993) hierarchical model of cognitive abilities, finding a strong relationship between the higher order *g* and WMC ($r = .89$). Using the same hierarchical approach, Colom et al. (2004) found similar values across four independent studies.

After this strong relationship, there are some reports arguing for discrete neural systems for *g* and WMC (Gray et al., 2003; Kane & Engle, 2002). For instance, in their functional magnetic resonance (fMRI) study, Prabhakaran, Smith, Desmond, Glover, and Gabrieli (1997) claimed that “strong links between WMC and intelligence [measured by the Progressive Matrices Test] occur because the tasks measuring those processes are, in fact, measuring common neural systems. The Matrices Test reflects the status of numerous, perhaps, almost all, WMC systems” (p. 60).

Wager and Smith (2003) reported a meta-analysis of 60 PET and fMRI studies of WMC tasks published between 1993 and 2002. Regarding short-term memory tasks they found that Brodmann area (BA) 37 showed preference for object storage and BA 7 for spatial storage. There was no preferential activation in left BA 44 and 45 (Broca's area) for verbal tasks. With respect to executive processing, BA 7 was the most frequently activated region, and the distribution of peaks was symmetrical across hemispheres. Their general findings suggested that working-memory representations in the frontal cortex are organized by process rather than by material type. Further, they noted that executive

demand produces reliable activations in regions largely in the frontal cortex, but also quite consistently in the superior parietal cortex. Finally, they noted that increasing processing demand produces bilateral activations in verbal storage and greater right lateralization in spatial storage. In short, the main BAs related to WMC were: frontal BAs 6, 8, 9, 10, 32, and 47, as well as parietal BA 7.

With respect to intelligence, Jung and Haier (2007) reviewed 37 neuroimaging studies published between 1988 and 2006. There were a number of brain areas common across studies where imaging results correlated to psychometric measures of intelligence. These included BAs 40, 39, and 7 in the parietal lobes; BAs 9, 46, 45, and 47 in the frontal lobes; BAs 21, 22, and 37 in the temporal lobes, and BAs 18 and 19 in the occipital lobes. Note that frontal BAs 9 and 47, as well as parietal BA 7 overlap with the Wager and Smith's (2003) WMC findings, but this is not the case for temporal and occipital areas.

To date, the presence or absence of overlap between brain sites for general intelligence and WMC has been addressed by the simple inspection of brain areas identified for both constructs. The present study uses a quantitative approach and addresses whether there are brain areas where there is a relationship between grey matter and both general intelligence (*g*) and WMC in the same participants. This approach can identify an anatomic framework common to *g* and WMC, as suggested by Toga and Thompson (2005). These researchers note that structural mapping is the necessary first step to get less exploratory and more fine-grained functional studies, because the latter show great variability of response along with limitations of instrumentation and protocols.

We have published four previous reports regarding the relationship between grey matter density and the intelligence construct using the same dataset. However, they were focused on different research questions: (a) Are there significant associations between grey matter density and IQ scores (Haier, Jung, Yeo, Head, & Alkire, 2004); (b) are these associations different

for males and females (Haier, Jung, Yeo, Head, & Alkire, 2005); (c) IQ scores and the general factor of intelligence (g) represent distinguishable facets of the intelligence construct, so the findings might differ for IQ (resulting from the simple summation of several subtests' scores) and for g (resulting from the correlation among subtests) as explained elsewhere (Colom, Jung, & Haier, 2006a, 2006b). We found that (a) there are significant associations between variations in grey matter density across discrete areas of the frontal, parietal, temporal, and occipital lobes and IQ scores; (b) there are pronounced sex differences; and (c) the associations are informatively distinguishable for IQ and for the g factor (see Colom, 2007).

Here we focus on a quite different research question. The current article explores a specific issue relating working memory to general intelligence (g) providing data not published previously by any other research group. These data address the question of a common neuroanatomic framework for these central psychological constructs.

Method

Participants

A total of 48 normal adult volunteers from two independent samples, ranging in age from 18 to 84 years, took part in the study (Haier et al., 2004, 2005). The considered age range is especially appropriate to increase sample's representativeness, which is a shortcoming of the majority of published studies (Jung & Haier, 2007). The younger sample was tested at the University of New Mexico (Sample 1) and consisted of 14 women and 9 men (mean age = 27 years, $SD = 5.9$, range = 18–37). The older sample was tested at the University of California, Irvine (Sample 2) and consisted of 13 men and 12 women (mean age = 59 years, $SD = 15.9$, range = 37–84). They gave written informed consent, and the study was approved by the institutional Human Subjects Committees.

Measures and procedure

Eight subtests from the Wechsler Adult Intelligence Scale (WAIS) were individually administered: Information, Vocabulary, Similarities, Picture Completion, Block Design, Arithmetic, Digit Span, and Digit Symbol Substitution. Scores were based on age norms (Wechsler, 1981).

Colom et al. (2006a) have reported that of the subtests measuring verbal intelligence (Vocabulary, Information, Arithmetic, Similarities) and spatial-fluid intelligence (Block Design, Picture Completion, Digit Symbol), Vocabulary and Block Design show the largest values on a higher order factor representing g (.72 and .89, respectively) for this sample. Therefore, these two subtests were chosen to tap the general factor of intelligence (g).

The forward (FDS) and backward (BDS) versions of the Digit Span subtest were chosen to tap WMC. It is sometimes argued that BDS employs the same cognitive mechanisms as does FDS (Richardson, 1977), whereas at other times this is not accepted (Hoshi et al., 2000). It is sometimes claimed that BDS taps WMC, while FDS taps short-term memory (Hedden & Gabrieli, 2004). However, this latter view can be empirically questioned both from a behavioural and from a biological perspective. Colom, Flores-Mendoza, Quiroga, and Privado (2005b) summarized behavioural findings analysing the empirical relationship between short-term memory and WMC at the latent variable level, reporting correlations as large as .99 (median = .86).¹ Gerton et al. (2005) examined the neural systems for FDS and BDS in normal participants, finding that both measures rely on an overlapping functional neural system associated with WMC. Here we analyse the combined FDS and BDS scores, as well as each subtest individually.

MRIs for Sample 1 were obtained with a 1.5-T scanner, head coil, and software (Signa 5.4; General Electric Medical Systems, Waukesha,

¹ Very recently, Unsworth and Engle (in press) wrote: "we conclude, as a matter of parsimony, that simple and complex span largely measure the same basic processes, and we reject the notion that short-term memory and working memory are different constructs."

WI). A T1 sagittal localizer sequence (TE = 6.9 ms, TR = 200 ms, FOV = $24 \times 24 \text{ cm}^2$, 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 = 256, matrix = 256×192 , 120 slices, thickness = 1.5 mm) to give full brain coverage. MRIs for Sample 2 were obtained with a 1.5-T clinical Phillips Eclipse scanner (Philips Medical Systems, N.A., Bothell, WA). T1-weighted, volumetric SPGR MRI scans (FOV = 24 cm, flip angle = 40, TR = 24, TE = 5) were used. The eight images consisted of 120 contiguous 1.2-mm thick axial slices, each with an in-plane image matrix of 256×256 image elements.

Subsequently, voxel-based morphometry (VBM) methods (Ashburner & Friston, 2000; Good et al., 2001) were applied to the obtained images. VBM is based on mathematical algorithms that segment grey and white matter from structural MRIs (only grey matter is considered in the present analyses). We used statistical parametric mapping (SPM2) to create a study-specific template and then applied the optimized VBM protocol. A 12-mm smoothing kernel was used, as in our previous reports. For each of the selected subtest analyses, SPM2 computed where grey matter intensities for each voxel correlated to scores. The design matrix included age, sex, and handedness as nuisance variables to remove any effects they might have. Correction for multiple comparisons was based on the SPM family wise error, and the false discovery rate is noted where applicable.

Because the two samples were tested with different scanners, statistical conjunction analyses (global null) were applied (Price and Friston, 1997) as in our previously published reports (Colom et al., 2006a; Haier et al., 2004, 2005). Note that these analyses do not combine data from different scanners into one dataset, avoiding calibration problems. Rather, they are based on analysing each sample separately and then asking what voxels show the same result in both samples. As Nichols, Brett, Andersson, Wager, and Poline (2005) have noted, the interpretation

of the global null conjunction requires caution because it can allow a very significant p level in one sample to offset a not-quite-significant p level at the same voxel in the other sample. This can result in an “and” or in an “either” conclusion for whether a voxel is significant in either or both samples. Friston, Penny, and Glaser (2005), however, counter that the global null is appropriate for cognitive neuroimaging studies because alternatives are too statistically conservative. Here we use the global null approach to combine samples and to combine block design and vocabulary scores (our g score), but we then use a more conservative approach (xj view extension in SPM2; Cui & Li, Human Neuroimaging Lab, Baylor College of Medicine) to quantify the overlap between g and digit span where the p levels are the same for each part of the analysis allowing a true “and” interpretation.

Results

Figure 1 (left panel) depicts the results of the conjunction between vocabulary and block design, as reported previously (Colom et al., 2006a). These results estimate brain areas related to the general factor of intelligence (g) since these two subtests have the highest g loadings. Significant correlations ($p < .0001$) to grey matter were found in frontal BAs 10 and 47 along with smaller clusters in BAs 8, 11, and 46; temporal BAs 20, 21, 37, 41, and 13; parietal BAs 7, 19, and 40; occipital BAs 18 and 19, as well as BA 24 (limbic lobe), and four sublobar structures. Although frontal areas clearly show the most relationship to g , many other areas also are related (Colom et al., 2006a).

Table 1 shows the localization of correlations between regional grey matter variation and individual differences in digit span (see Figure 1, middle panel). Significant correlations ($p < .0001$) are found in frontal BAs 10, 47, 11, 8, and 6; parietal BAs 39, 40, 19, 7, 31, and 3; temporal BAs 37, 36, 41, 40, 42, 22, 37, 13, and 20, as well as occipital BAs 19, 39, and 18. The thalamus and the limbic BA 24 also show significant correlations.

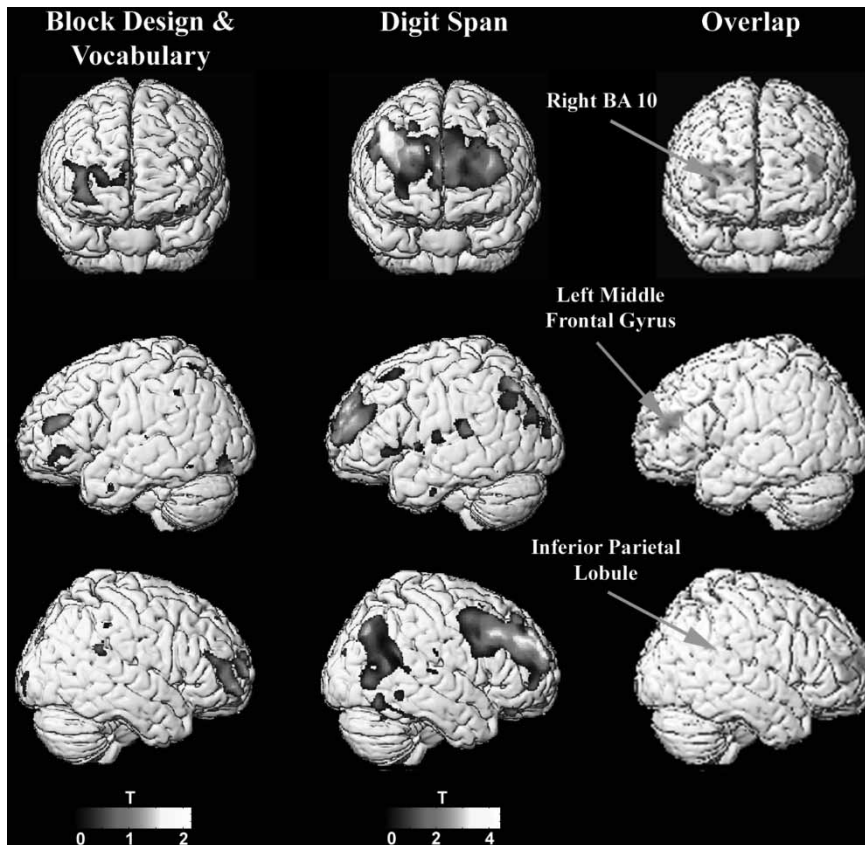


Figure 1. Correlations between grey matter and measures of g (conjunction of block design and vocabulary; left panel), working-memory capacity (WMC; total digit span score; middle panel), and the overlap between the two (right panel) are shown on standard magnetic resonance imaging (MRI) templates (frontal, left, and right, respectively). Correlations with g and WMC are shown at $p < .0001$; overlap correlations are at $p < .000001$ (i.e., the square of .001; the three overlap correlations labelled are significant at $p < .05$ corrected for multiple comparisons). (Figure can be seen in colour online.)

Results for both g (vocabulary & block design) and WMC (digit span total) show significant correlations with grey matter in areas distributed throughout the brain. Furthermore, many regions overlap: frontal BAs 10, 47, 11, and 8; parietal BAs 7, 19, and 40; temporal BAs 13, 37, and 41, as well as occipital BAs 18 and 19, show grey matter correlating with general intelligence (g) and WMC.

Nevertheless, it is important to note that the simple inspection of the qualitative overlap between measures of the constructs of interest is not powerful. Therefore, here we compute the quantitative structural overlap between

these measures. The right panel of Figure 1 depicts the empirical overlap analysis of g (Figure 1, left panel) and WMC (Figure 1, middle panel). Table 2 shows the localizations for the overlap. This overlap is determined using the xj view extension within SPM2, and it shows the actual voxels from g and WMC where there is a significant correlation between scores and grey matter. The p level applied for computing the overlap is the square of .001. There are three areas significant at $p < .05$ corrected for multiple comparisons as labelled in Figure 1 (right panel). These are the right superior frontal gyrus (BA 10), the left middle

Table 1. Localization of correlations between regional grey matter and digit span

| Brain region | Coordinates (x, y, z) | Cluster size |
|-----------------------------|--------------------------|-----------------|
| Left frontal | | |
| BA 47 | -30 26 -2 | 1,572 |
| Sublobar claustrum | -32 17 2 | |
| BA 8 | -36 23 51 | 462 |
| BA 8 | -33 30 46 | |
| Right frontal | | |
| BA 10 | 41 41 23 | 40,831 |
| BA 8 | 46 21 40 | |
| BA 10 | -1 61 15 | |
| BA 11 | 6 14 -27 | 452 |
| BA 11 | 26 33 -18 | 595 |
| BA 6 | 27 16 53 | 12 |
| Total voxels frontal lobes | | 43,924 |
| Percentage of total | | 63.7 |
| Right parietal | | |
| BA 19 | 39 -67 42 | 8,149 |
| BA 39 | 49 -64 35 | |
| BA 39 | 54 -54 15 | |
| BA 3 | 57 -16 23 | 17 |
| Left parietal | | |
| BA 7 | -30 -60 48 | 3,404 |
| BA 40 | -48 -59 36 | |
| BA 40 | -43 -64 43 | |
| BA 31 | -12 -44 33 | 276 |
| Total voxels parietal lobes | | 11,846 |
| Percentage of total | | 17.2 |
| Left temporal | | |
| BA 41 | -49 -30 13 | 1,608 |
| BA 40 | -55 -25 20 | |
| BA 41 | -38 -31 13 | |
| BA 20 | -61 -8 -27 | 164 |
| BA 42 | -61 -9 11 | 299 |
| BA 22 | -58 -14 5 | |
| BA 37 | -39 -51 -13 | 258 |
| BA 22 | -50 2 1 | 181 |
| BA 13 | -41 3 2 | |
| Right temporal | | |
| BA 37 | 34 -45 -15 | 7,283 |
| BA 37 | 40 -61 -9 | |
| BA 36 | 21 -44 -10 | |
| BA 37 | 57 -46 -4 | 180 |
| BA 42 | 66 -20 9 | 55 |
| Total voxels temporal lobes | | 10,028 |
| Percentage of total | | 14.6 |
| Left occipital | | |
| BA 19 | -43 -79 27 | 774 |
| BA 39 | -48 -75 23 | |

(Continued)

Table 1. (Continued)

| Brain region | Coordinates (x, y, z) | Cluster size |
|------------------------------|--------------------------|-----------------|
| BA 39 | -54 -69 27 | |
| BA 18 | -28 -89 14 | 361 |
| BA 19 | -25 -89 22 | |
| Right occipital | | |
| BA 19 | 28 -83 26 | 75 |
| Total voxels occipital lobes | | 1,210 |
| Percentage of total | | 1.7 |
| Right sublobar | | |
| Thalamus, pulvinar | 7 -25 15 | 1,796 |
| Thalamus | 24 -22 15 | |
| Thalamus | -1 -22 17 | |
| Total voxels sublobar | | 1,796 |
| Percentage of total | | 2.6 |
| Right limbic lobe | | |
| BA 24 | 9 24 13 | 123 |
| Total voxels limbic lobe | | 123 |
| Percentage of total | | 0.2 |

Note: Significant correlations ($p < .0001$) are shown. Brain regions (approximate Brodmann areas, BAs) are estimated from the Talairach and Tournoux atlas (Talairach & Tournoux, 1988). Coordinates refer to maximum voxel of identified clusters (x, y, z). Cluster size is number of voxels with a significant correlation to digit span (a blank size indicates a subcluster of the preceding major cluster). Maximum false discovery rate = .002.

frontal gyrus (BA 10), and the right inferior parietal lobule (BA 40).

Since vocabulary, block design, and digit span total are correlated to each other (range between .58 and .61, $p < .01$) we repeated these same analyses after partialling digit span out when computing the conjunction of vocabulary and block design correlations with grey matter. These results, based on this refined estimate of g , with digit span removed, did not change appreciably or significantly from the first analysis.

All analyses were repeated for FDS and BDS separately (they correlated with each other at .56). We expected BDS to show more areas related to g than did FDS, because of its higher complexity (Colom et al., 2006a; Jensen, 1998). This is exactly what we found (see Tables 3 and 4 and Figure 2). Nevertheless, both FDS and BDS showed significant overlap with g across

Table 2. Areas of overlap in grey matter correlations between digit span and the conjunction of block design and vocabulary

| Brain region | Coordinates (x, y, z) | Cluster size |
|------------------------------|--------------------------|-----------------|
| Left frontal | | |
| BA 10 | -40 46 19 | 2,517* |
| BA 47 | -34 28 -3 | 1,036 |
| | -48 35 -3 | |
| | -43 28 -7 | |
| BA 11 | -31 39 -17 | 160 |
| Right frontal | | |
| BA 10 | 3 63 20 | 6,276* |
| | 26 63 14 | |
| | 38 45 19 | |
| BA 8 | 28 44 49 | 130 |
| BA 11 | 4 46 -27 | 256 |
| BA 11 | 26 42 -20 | 83 |
| Total voxels frontal lobes | | 10,458 |
| Percentage of total | | 57 |
| Left parietal | | |
| BA 7 | -30 -60 48 | 3,404 |
| BA 40 | -48 -59 36 | |
| BA 40 | -43 -64 43 | |
| BA 31 | -12 -44 33 | 276 |
| BA 7 | -33 -66 49 | 530 |
| | -26 -65 56 | |
| Right parietal | | |
| BA 40 | -34 -61 57 | |
| BA 40 | 48 -45 24 | 214* |
| BA 7 | 40 -62 50 | 435 |
| | 38 -53 58 | |
| | 47 -57 47 | |
| | (BA 40) | |
| BA 39 | 47 -76 36 | 19 |
| Total voxels parietal lobes | | 4,878 |
| Percentage of total | | 26 |
| Left temporal | | |
| BA 20 | -67 -10 -29 | 211 |
| | -63 -8 -37 | |
| BA 41 | -39 -39 13 | 349 |
| Right temporal | | |
| Hippocampus | 29 -24 -8 | 18 |
| Total voxels temporal lobes | | 578 |
| Percentage of total | | 3 |
| Right occipital | | |
| BA 19 | 48 -77 5 | 197 |
| BA 19 | 25 -90 27 | 47 |
| BA 18 | 25 -96 8 | 28 |
| Total voxels occipital lobes | | 272 |
| Percentage of total | | 1.5 |

(Continued)

Table 2. (Continued)

| Brain region | Coordinates (x, y, z) | Cluster size |
|--------------------------------|--------------------------|-----------------|
| Left sublobar insula | | |
| BA 13 | -37 0 6 | 1,990 |
| | -34 9 8 | |
| | -37 -4 -1 | |
| Right sublobar extranuclear | | |
| BA 24 | 11 27 11 | 91 |
| Right sublobar thalamus | | |
| Medial dorsal nucleus | 2 -12 8 | 160 |
| Left inferior semilunar lobule | -27 -73 -40 | 26 |
| Total voxels sublobar | | 2,267 |
| Percentage of total | | 12.5 |

Note: The *p* level applied for computing the overlap is the square of .001 (i.e., *p* < .000001). Brain regions (approximate BAs) are estimated from the Talairach and Tournoux atlas (Talairach & Tournoux, 1988). Coordinates refer to maximum voxel of identified clusters (x, y, z). Cluster size is number of voxels with a significant correlation (a blank size indicates a subcluster of the preceding major cluster).

**p* < .05 family wise error corrected for multiple comparisons; maximum false discovery rate = .02.

frontal, parietal, temporal, and occipital lobes; BA 10 displayed the most overlap.

Finally, we deconstructed the main conjunction analyses into their component parts to estimate the correlations between grey matter and test scores in the main overlap brain areas in each sample separately. The results (Table 5) confirm that each sample considered separately shows similar results to those attained with the global null conjunction of both samples.

Discussion

The present findings suggest discrete overlapping brain sites underlying two of the most powerful constructs in differential and cognitive psychology—namely, general intelligence (*g*) and working-memory capacity (WMC). The largest overlap in the number of voxels was in BA 10.

The results are consistent with the view of Carpenter, Just, and Reichle (2000) who argued against the frontal lobe only thesis regarding the neural substrate of WMC: “The emerging view suggests that cognitive processes emerge from

Table 3. FDS overlap with g

| Brain region | Coordinates (x, y, z) | Cluster size |
|------------------------------|--------------------------|-----------------|
| Left frontal | | |
| BA 10 | -41 49 12 | 357 |
| BA 10 | -40 54 0 | |
| BA 11 | -34 45 -14 | 415 |
| BA 11 | -24 44 -17 | |
| BA 11 | -17 43 -21 | |
| BA 44 | -56 8 16 | 26 |
| BA 6 | 0 46 35 | 87 |
| Right frontal | | |
| BA 10 | 3 64 16 | 1,602 |
| BA 10 (left) | -5 63 16 | |
| BA 10 (left) | | |
| BA 10 | 29 62 13 | 2,830 |
| BA 10 | 42 52 7 | |
| BA 46 | 44 43 15 | |
| BA 11 | 6 48 -24 | 1,499 |
| BA 11 | 25 42 -21 | |
| BA 11 | 16 42 -24 | |
| BA 10 | 1 63 -4 | 343 |
| BA 10 | 3 64 5 | |
| BA 11 | 33 55 -11 | 26 |
| BA 11 | 1 58 -16 | 31 |
| Total voxels frontal lobes | | 7,216 |
| Percentage of total | | 93.6 |
| Left parietal | | |
| BA 7 | -27 -64 51 | 21 |
| Right parietal | | |
| BA 39 | 47 -72 37 | 254 |
| BA 19 | 41 -71 43 | |
| BA 40 | 49 -50 46 | 19 |
| Total voxels parietal lobes | | 294 |
| Percentage of total | | 3.8 |
| Left temporal | | |
| BA 39 | -58 -65 23 | 31 |
| Right temporal | | |
| BA 13 | 46 -44 23 | 20 |
| Total voxels temporal lobes | | 51 |
| Percentage of total | | 0.66 |
| Left occipital | | |
| BA 19 | -39 -83 25 | 124 |
| BA 19 | -36 -81 34 | |
| Total voxels occipital lobes | | 124 |
| Percentage of total | | 1.6 |
| Right sublobar | | |
| Thalamus | 5 -20 14 | 17 |
| Total voxels sublobar | | 17 |
| Percentage of total | | 0.22 |

Table 4. BDS overlap with g

| Brain region | Coordinates (x, y, z) | Cluster size |
|-----------------------------|--------------------------|-----------------|
| Left frontal | | |
| BA 47 | -49 40 -4 | 10,475 |
| BA 10 | -41 50 10 | |
| BA 10 | -40 42 15 | |
| BA 6 | -62 -16 38 | 209 |
| BA 6 | -43 7 54 | 59 |
| BA 8 | -38 22 53 | 14 |
| BA 6 | -1 47 34 | 155 |
| Right frontal | | |
| BA 10 | 2 62 17 | 5,792 |
| BA 11 | 6 46 -24 | |
| BA 11 | 25 41 22 | |
| BA 13 | 46 -41 22 | 576 |
| BA 10 | 40 50 7 | 6,413 |
| BA 10 | 42 43 13 | |
| BA 10 | 33 59 -6 | |
| BA 8 | 51 11 40 | 310 |
| BA 4 | 43 -16 40 | 79 |
| BA 9 | 45 40 35 | 22 |
| BA 47 | 30 32 -3 | 245 |
| BA 47 | 39 22 -8 | |
| BA 9 | 39 20 28 | 45 |
| Total voxels frontal lobes | | 24,394 |
| Percentage of total | | 77.3 |
| Left parietal | | |
| BA 7 | -26 -64 53 | 386 |
| BA 7 | -35 -56 56 | 104 |
| BA 40 | -41 -48 58 | |
| BA 7 | -20 -78 43 | 38 |
| Right parietal | | |
| BA 40 | 50 -52 48 | 298 |
| BA 40 | 50 -44 49 | |
| BA 7 | 46 -59 50 | |
| BA 3 | 56 -13 42 | 164 |
| BA 19 | 39 -71 42 | 84 |
| Total voxels parietal lobes | | 1,074 |
| Percentage of total | | 3.4 |
| Left temporal | | |
| BA 41 | -41 -36 11 | 290 |
| BA 39 | -58 -65 22 | 130 |
| BA 19 | -55 -71 16 | |
| Right temporal | | |
| BA 21 | 54 10 -23 | 230 |
| Subgyral | 34 -59 6 | 11 |
| BA 19 | 47 -69 -12 | 37 |
| BA 37 | 53 -64 -14 | |
| Total voxels temporal lobes | | 698 |
| Percentage of total | | 2.2 |

Note: FDS = forward version of the Digit Span subtest. g = general factor of intelligence. Maximum false discovery rate = .235.

(Continued opposite)

Table 4. (Continued)

| <i>Brain region</i> | <i>Coordinates (x, y, z)</i> | <i>Cluster size</i> |
|------------------------------|----------------------------------|-------------------------|
| Left occipital | | |
| BA 19 | -42 -71 -1 | 42 |
| Total voxels occipital lobes | | 42 |
| Percentage of total | | 0.13 |
| Left sublobar | | |
| Thalamus | -1 -10 4 | 5,097 |
| Caudate body (right) | 11 6 13 | |
| Caudate body (left) | -13 -10 18 | |
| Hypothalamus | -2 -6 -11 | 59 |
| Right sublobar | | |
| Caudate tail | 38 -25 -3 | 120 |
| Total voxels sublobar | | 5,276 |
| Percentage of total | | 16.7 |
| Left limbic lobe | | |
| BA 24 | -16 -12 41 | 52 |
| Right limbic lobe | | |
| BA 34 | 14 -7 -14 | 19 |
| Total voxels limbic lobe | | 71 |
| Percentage of total | | 0.23 |

Note: BDS = backward version of the Digit Span subtest.
g = general factor of intelligence. Maximum false discovery rate = .224.

networks that span multiple cortical sites with closely collaborative and overlapping functions" (p. 196).

Haier et al. (2004) also supported the distributed nature of brain areas related to intelligence as reflected in Full Scale IQ (FSIQ). The distributed nature of grey matter correlations was also found using the general factor of intelligence (*g*) instead of FSIQ (Colom et al., 2006a, 2006b).

Nevertheless, the distributed nature of *g* and WMC does not preclude more focused brain structures for the overlap between these psychological constructs. Individual differences in *g*, as well as in WMC, involve a wide array of discrete brain regions, but their common neural substrate could rely in a small number of brain areas. The results point to the right and left frontal lobe (BA 10), and they are partially consistent with Kane and Engle (2002) who, after their exhaustive review, suggest that BAs 46, 9, and 10 could be the biological basis of the link between WMC and intelligence.

As indicated in the extensive empirical review of 275 positron emission tomography (PET) and fMRI studies reported by Cabeza and Nyberg (2000), BA 10 activations are present for problem-solving tasks (Raven Matrices, Tower of London, Wisconsin Card Sorting Task, etc.) as well as for high-level WMC operations. Their review also indicates that middorsal regions from BAs 9 and 46 appear to be implicated when monitoring and manipulating information in working memory.

However, BAs 9 and 46 are also activated when subjects perform sustained attention tasks that do not implicate the simultaneous consideration of various pieces of information (e.g., WMC). Therefore, perhaps only regions belonging to BA 10 are necessary and sufficient to account for the behavioural overlap between *g* and WMC. Note that VBM studies of intelligence identify BAs 10 and 9 as central brain regions, whereas BA 46 was more weakly identified (Jung & Haier, 2007). BA 10 receives inputs from the anterior cingulate cortex and other prefrontal areas, as well as from the temporal lobe. Therefore, it seems reasonable to presume that BA 10 is devoted to processing high-level abstract information and to coordinating several cognitive functions (Ramnani & Owen, 2004). These functions may be linked to the communality of *g* and WMC.

Nevertheless, we also found significant overlap (corrected for multiple comparisons) in a small part of the right inferior parietal lobe (BA 40). Cowan (2005) reviewed the neural basis of WMC, suggesting that "the frontal lobe contain pointers to the appropriate information in the parietal lobes and other posterior parts of the brain . . . the inferior parietal areas appear to receive input from multiple sensory systems and therefore maybe a site of the representation of integrated or abstract information" (p. 188). Jung and Haier (2007) also concluded that a parietal-frontal network was key for performance on intelligence tests.

The theory proposed by Cowan (2005) fits the findings reported here. This theory distinguishes a capacity limit (related to parietal regions) and the control of attention (related to frontal areas). We

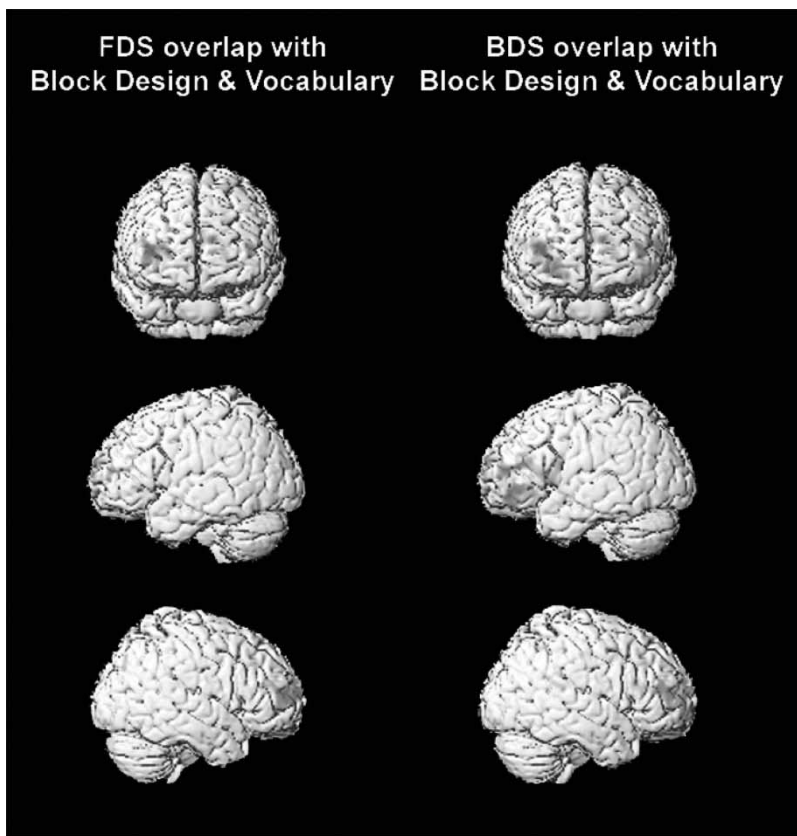


Figure 2. The overlap of correlations between grey matter and *g* (conjunction of block design and vocabulary) and grey matter and forward (FDS) and backward (BDS) digit span scores are shown ($p < .01$). (Figure can be seen in colour online.)

suggest that both capacity limits and attentional control relate to *g* and WMC. Actually, Vogel, McCollough, and Machizawa (2004) found that individual differences in capacity limits and attentional control are strongly related, and Gray et al.

(2003) reported frontal and parietal activations, evoked by a working-memory task (3 back) correlating with fluid intelligence (*Gf*).

In conclusion, the present study suggests that the common anatomic framework for *g* and

Table 5. Conjunction analysis results deconstructed for each grey matter/test score correlation in three brain areas for each sample

| | University of New Mexico | | | University of California at Irvine | | |
|---------------------|------------------------------|---------------------------|--------------------------------|------------------------------------|---------------------------|--------------------------------|
| | Right superior frontal gyrus | Left middle frontal gyrus | Right inferior parietal lobule | Right superior frontal gyrus | Left middle frontal gyrus | Right inferior parietal lobule |
| Forward digit span | .50 | .47 | .47 | .37 | .37 | .35 |
| Backward digit span | .69 | .52 | .62 | .30 | .37 | .41 |
| Digit span total | .46 | .56 | .55 | .68 | .59 | .55 |
| Block design | .56 | .66 | .60 | .63 | .50 | .54 |
| Vocabulary | .55 | .67 | .53 | .51 | .49 | .48 |

WMC implicates grey matter belonging to BA 10 (right superior gyrus and left middle frontal gyrus) but also BA 40 (right inferior parietal lobule). Grey matter in these discrete brain regions may be the structural basis for the commonality between these central psychological constructs.

Manuscript received 12 April 2007

Revised manuscript received 30 October 2007

Revised manuscript accepted 1 November 2007

REFERENCES

- Ackerman, P. L., Beier, M. E., & Boyle, M. O. (2005). Working memory and intelligence: The same or different constructs? *Psychological Bulletin*, *131*, 30–60.
- Ashburner, J., & Friston, K. J. (2000). Voxel-based morphometry—the methods. *NeuroImage*, *11*, 805–821.
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*, 1–47.
- Carpenter, P. A., Just, M. A., & Reichle, E. D. (2000). Working memory and executive function: Evidence from neuroimaging. *Current Opinion in Neurobiology*, *10*, 195–199.
- Carroll, J. B. (1993). *Human cognitive abilities*. Cambridge, UK: Cambridge University Press.
- Carroll, J. B. (2003). The higher-stratum structure of cognitive abilities: Current evidence supports *g* and about ten broad factors. In H. Nyborg (Ed.), *The scientific study of general intelligence: Tribute to Arthur R. Jensen* (pp. 5–20). New York: Elsevier Science/Pergamon Press.
- Colom, R. (2007). Intelligence? What intelligence? *Behavioural and Brain Sciences*, *30*, 155–156.
- Colom, R., Abad, F., Rebollo, I., & Shih, P. C. (2005a). Memory span and general intelligence: A latent-variable approach. *Intelligence*, *33*, 623–642.
- Colom, R., Flores-Mendoza, C., Quiroga, M. A., & Privado, J. (2005b). Working memory and general intelligence: The role of short-term storage. *Personality & Individual Differences*, *39*, 1005–1014.
- Colom, R., Jung, R. E., & Haier, R. J. (2006a). Distributed brain sites for the *g*-factor of intelligence. *NeuroImage*, *31*, 1359–1365.
- Colom, R., Jung, R. E., & Haier, R. J. (2006b). Finding the *g*-factor in brain structure using the method of correlated vectors. *Intelligence*, *34*, 561–570.
- Colom, R., Rebollo, I., Palacios, A., Juan-Espinoso, M., & Kyllonen, P. C. (2004). Working memory is (almost) perfectly predicted by *g*. *Intelligence*, *32*, 277–296.
- Colom, R., & Shih, P. C. (2004). Is working memory fractionated onto different components of intelligence? *Intelligence*, *32*, 431–444.
- Conway, A. R. A., Kane, M. J., & Engle, R. W. (2003). Working memory capacity and its relation to general intelligence. *Trends in Cognitive Sciences*, *7*, 547–552.
- Cowan, N. (2005). *Working memory capacity*. New York: Psychology Press.
- Engle, R. W. (2002). Working memory capacity as executive attention. *Current Directions in Psychological Science*, *11*, 19–23.
- Engle, R. W., & Kane, M. J. (2004). Executive attention, working memory capacity, and a two-factor theory of cognitive control. In B. Ross (Ed.), *Psychology of learning and motivation: Advances in research and theory* (Vol. 44, pp. 145–199). New York: Elsevier.
- Engle, R. W., Tuholski, S. W., Laughlin, J. E., & Conway, A. R. A. (1999). Working memory, short-term memory, and general fluid intelligence: A latent-variable approach. *Journal of Experimental Psychology: General*, *128*, 309–331.
- Friston, K. J., Penny, W. D., & Glaser, D. E. (2005). Conjunction revisited. *NeuroImage*, *25*, 661–667.
- Gerton, B. K., Brown, T. T., Meyer-Lindenberg, A., Kohn, P., Holt, J. L., Olsen, R. K., et al. (2005). Shared and distinct neurophysiological components of the digits forward and backward tasks as revealed by functional imaging. *Neuropsychologia*, *42*, 1781–1787.
- Good, C. D., Johnsrude, I. S., Ashburner, J., Henson, R. N., Friston, K. J., & Frackowiak, R. S. (2001). A voxel-based morphometric study of ageing in 465 normal adult human brains. *NeuroImage*, *14*, 21–36.
- Gray, J. R., Chabris, C. F., & Braver, T. S. (2003). Neural mechanisms of general fluid intelligence. *Nature Neuroscience*, *6*, 316–322.
- Haier, R. J., Jung, R. E., Yeo, R. A., Head, K., & Alkire, M. T. (2004). Structural brain variation and general intelligence. *NeuroImage*, *23*, 425–433.
- Haier, R. J., Jung, R. E., Yeo, R. A., Head, K., & Alkire, M. T. (2005). The neuroanatomy of general intelligence: Sex matters. *NeuroImage*, *25*, 320–327.
- Hedden, T., & Gabrieli, J. D. (2004). Insights into the ageing mind: A view from cognitive neuroscience. *Nature Neuroscience Reviews*, *5*, 87–96.

- Hoshi, Y., Oda, I., Wada, Y., Ito, Y., Yamashita, Y., Oda, M., et al. (2000). Visuospatial imagery is a fruitful strategy for the digit span backward task: A study with near-infrared optical tomography. *Cognitive Brain Research*, *9*, 339–342.
- Jensen, A. R. (1998). *The g factor. The science of mental ability*. Westport, CT: Praeger.
- Jung, R. E., & Haier, R. J. (2007). The parieto-frontal integration theory (P-FIT) of intelligence: Converging neuroimaging evidence. *Behavioral and Brain Sciences*, *30*, 135–187.
- Kane, M. J., & Engle, R. W. (2002). The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychonomic Bulletin & Review*, *9*, 637–671.
- Kane, M. J., Hambrick, D. Z., Tuholski, S. W., Wilhelm, O., Payne, T. W., & Engle, R. W. (2004). The generality of working memory capacity: A latent-variable approach to verbal and visuospatial memory span and reasoning. *Journal of Experimental Psychology: General*, *133*, 189–217.
- Kyllonen, P. C., & Christal, R. E. (1990). Reasoning ability is (little more than) working-memory capacity. *Intelligence*, *14*, 389–433.
- Lubinski, D. (2004). Introduction to the special section on cognitive abilities: 100 years after Spearman's (1904) "General intelligence," objectively determined and measured. *Journal of Personality and Social Psychology*, *86*, 96–111.
- Miyake, A., & Shah, P. (1999). *Models of working memory*. Cambridge, UK: Cambridge University Press.
- Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J. B. (2005). Valid conjunction inference with the minimum statistic. *NeuroImage*, *25*, 653–660.
- Prabhakaran, V., Smith, J. A., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1997). Neural substrates of fluid reasoning: An fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. *Cognitive Psychology*, *33*, 43–63.
- Price, C. J., & Friston, K. J. (1997). Cognitive conjunction: A new approach to brain activation experiments. *NeuroImage*, *5*, 261–270.
- Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nature Neuroscience*, *5*, 184–194.
- Richardson, J. T. E. (1977). Functional relationship between forward and backward digit repetition and a non-verbal analogue. *Cortex*, *13*, 317–320.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: A 3-dimensional proportional system, an approach to cerebral imaging*. New York: Thieme Medical Publishers.
- Toga, A. W., & Thompson, P. M. (2005). Genetics of brain structure and intelligence. *Annual Review of Neuroscience*, *28*, 1–23.
- Unsworth, N., & Engle, R. W. (in press). On the division of short-term memory and working memory: An examination of simple and complex span and their relation to higher order abilities. *Psychological Bulletin*.
- Vogel, E., McCollough, A., & Machizawa, M. (2004, November). *Visual short-term memory capacity and the efficiency of attentional control*. Paper presented at the annual meeting of the Psychonomic Society, Minneapolis, MN.
- Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: A meta-analysis. *Cognitive, Affective, and Behavioral Neuroscience*, *3*, 255–274.
- Wechsler, D. (1981). *WAIS-R manual*. San Antonio, TX: The Psychological Corporation

Copyright of *Cognitive Neuropsychology* is the property of Psychology Press (UK) and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.