Neuroanatomic overlap between intelligence and cognitive factors: Morphometry methods provide support for the key role of the frontal lobes

Roberto Colom \textsuperscript{a,b,⁎}, Miguel Burgaleta \textsuperscript{a,e}, Francisco J. Román \textsuperscript{a}, Sherif Karama \textsuperscript{f}, Juan Álvarez-Linera \textsuperscript{b}, Francisco J. Abad \textsuperscript{a}, Kenia Martínez \textsuperscript{a}, Mª Ángeles Quiroga \textsuperscript{c}, Richard J. Haier \textsuperscript{d}

\textsuperscript{a} Universidad Autónoma de Madrid, Spain
\textsuperscript{b} Fundación CIEN-Fundación Reina Sofía, Spain
\textsuperscript{c} Universidad Complutense de Madrid, Spain
\textsuperscript{d} University of California at Irvine, USA
\textsuperscript{e} Universidad Pompeu Fabra, Barcelona, Spain
\textsuperscript{f} Montreal Neurological Institute (MNI), Canada

\textbf{A B S T R A C T}

Evidence from neuroimaging studies suggests that intelligence differences may be supported by a parieto-frontal network. Research shows that this network is also relevant for cognitive functions such as working memory and attention. However, previous studies have not explicitly analyzed the commonality of brain areas between a broad array of intelligence factors and cognitive functions tested in the same sample. Here, fluid, crystallized, and spatial intelligence, along with working memory, executive updating, attention, and processing speed were each measured by three diverse tests or tasks. These twenty-one measures were completed by a group of one hundred and four healthy young adults. Three cortical measures (cortical gray matter volume, cortical surface area, and cortical thickness) were regressed against psychological latent scores obtained from a confirmatory factor analysis for removing test and task specific variance. For cortical gray matter volume and cortical surface area, the main overlapping clusters were observed in the middle frontal gyrus and involved fluid intelligence and working memory. Crystallized intelligence showed an overlapping cluster with fluid intelligence and working memory in the middle frontal gyrus. The inferior frontal gyrus showed overlap for crystallized intelligence, spatial intelligence, attention, and processing speed. The fusiform gyrus in temporal cortex showed overlap for spatial intelligence and attention. Parietal and occipital areas did not show any overlap across intelligence and cognitive factors. Taken together, these findings underscore that structural features of gray matter in the frontal lobes support those aspects of intelligence related to basic cognitive processes.

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\textbf{Introduction}

Evidence from neuroimaging studies suggests that intelligence differences among individuals may be supported by a parieto-frontal network (PFIT model; Jung and Haier, 2007) that also is related to basic cognitive processing. There is a large set of published articles analyzing the behavioral relationships between intelligence and cognitive measures (see Sternberg, 2000 for a summary). However, the number of studies addressing the simultaneous correlation among several diverse intelligence and cognitive constructs is much smaller (Ackerman et al., 2002; Colom et al., 2004, 2008; Krumm et al., 2009; Martínez et al., 2011; Oberauer et al., 2005). This state of affairs provides an uncertain general picture regarding their overlap. Thus, for instance, as noted by Nisbett et al. (2012) there are largely different estimations of the 'true' correlation between intelligence and working memory capacity. Variations from study to study might be attributed to the specific measures administered, the way latent factors are defined, the nature of the samples, and so forth. The heterogeneity of findings and lack of consensus may be behind the relative neglect of this particular topic in the review of intelligence research in the last 10 years recently published by Deary (2012).

In the comprehensive behavioral study reported by Martínez et al. (2011) fluid intelligence, short-term memory, executive updating, and working memory were hardly distinguished at the latent variable level. In this study, twenty-four measures were analyzed tapping eight intelligence and cognitive factors (three measures for each factor): fluid, crystallized, and spatial intelligence, along with short-term memory, working memory capacity, executive updating, attention, and processing speed. Their main findings supported the view that fluid intelligence can be largely identified with basic short-term storage processes, namely, encoding, maintenance, and retrieval. This was in keeping with neuroimaging evidence suggesting
that fluid intelligence shares relevant brain structural (Colom et al., 2007) and functional (Gray et al., 2003) correlates with working memory capacity (Halldor et al., 2007). This was also seen as possibly consistent with behavioral studies suggesting that intensive training on executive updating, using the n-back task, might improve fluid intelligence, even when cognitive requirements of these two constructs are superficially very different (Jaege et al., 2008, 2010, 2011).

There are few neuroimaging studies comprehensively measuring several intelligence and cognitive factors with the same sample of participants, as discussed by Haier et al. (2009). They suggested several guidelines for a proper estimation of the constructs of interest with respect to the neuroimaging analysis of intelligence. The key one was the use of three or more varied measures to define each group factor. This guideline should be generalized to other cognitive variables as well, as underscored by Colom and Thompson (2011).

Here we apply this basic guideline for defining several relevant intelligence and cognitive factors: fluid intelligence, crystallized intelligence, spatial intelligence, working memory capacity, executive updating, attention, and processing speed. The behavioral relationships among the considered constructs were analyzed by confirmatory factor analysis for obtaining scores, as representative as possible, removing variance specific to each test and task. These psychological scores were then submitted to different imaging analysis protocols quantifying cortical gray matter volume (GMV), cortical surface area (CSA), and cortical thickness (CT).

These brain indices are considered separately because previous research shows that they should be distinguished. Sanabria-Diaz et al. (2010) have demonstrated that CSA and CT quantify largely distinguishable brain properties. These indices are supported by substantially different cellular mechanisms of different genetic origins (Panizzon et al., 2009; Winkler et al., 2010). Individual differences in CSA depend upon the number of columns, while individual differences in CT depend on the number of cells within a given column. Cortical gray matter volume (GMV) is a composite of CSA and CT, but individual differences in cortical GMV show a greater association with differences in CSA than for CT when considering individual differences in higher cognitive processes.

Abstract-fluid intelligence (Gf) was measured by the Raven Advanced Progressive Matrices Test (RAPM) (Raven et al., 2004), the abstract reasoning subtests from the Differential Aptitude Test (DAT-AR) battery (Bennett et al., 1990), and the inductive reasoning subtests from the Primary Mental Abilities (PMA-R) battery (Thurstone, 1938). The RAPM comprises a matrix figure with three rows and three columns. Among eight possible alternatives the one completing the 3 × 3 matrix figure must be chosen. The screening version comprising odd items only was administered (max. score = 18). DAT-AR is a series test based on abstract figures. Successive figures follow a given rule, so the one continuing the series must be chosen from several alternatives. The screening version comprising odd items only was administered (max. score = 20). PMA-R comprises letters’ series items. The rule (or rules) underlying a given sequence must be extracted for selecting the correct alternative (max. score = 30).

Verbal-crystallized intelligence (Gc) was measured by the verbal and numerical reasoning subtests from the DAT (VR and NR), along with the vocabulary subtest from the PMA (V). DAT-VR is based on sentences stated like an analogy. The first and last words from the sentence are missing, and a pair of words completing the sentence must be selected. The screening version comprising odd items only was administered (max. score = 20). PMA-V is a synonym test based on the meaning of words that must be evaluated against a given model word (max. score = 50). DAT-NR consists of quantitative reasoning problems. The screening version comprising odd items only was administered (max. score = 20).

Spatial intelligence (Gv) was measured by the spatial relations subtest from the DAT (SR), the spatial rotation subtest from the PMA (S), and the rotation of solid figures test (Yela, 1969). Items from the rotation of solid figures test are based on a 3D model figure and several 3D rotated alternatives (max. score = 21). PMA-S includes a model figure and six alternatives, some of which are simply rotated versions of the model figure, whereas the remaining figures

**Method**

**Participants and neuroimaging data**

The sample comprised 104 young adults (59 females and 45 males) with a mean age of 19.9 (SD = 1.6). Exclusion criteria included neurological or psychiatric illness, considering a history of serious head injury and substance abuse. Informed consent was obtained following the Helsinki guidelines.

MRIs were obtained with a 3 T scanner (GEHC Waukesha, WI, 3 T Excite HDX) 8–channels coil. 3D: FSPGR with IR preparation pulse (TR 5.7 ms, TE 2.4 ms TI 750 ms, flip angle 12). Sag acquisition 0.8 mm thickness, full brain coverage (220 slices), matrix 266×266 FOV 24 (isotropic voxels 0.7 cm³).1

**Psychological measures**

Twenty-one cognitive tests and tasks were administered for measuring the psychological constructs of interests. Fluid-abstract intelligence (Gf) assesses the complexity level that subjects can handle in situations for which previous knowledge is not relevant, whereas crystallized-abstract intelligence (Gc) relies in the ability to cope with academic types of skills and knowledge, such as reading or math (Cattell, 1971). Spatial intelligence (Gv) implicates the construction, temporary retention, and manipulation of mental images (Lohman, 2000). Working memory can be defined as the ability for simultaneous storage and processing of varied amounts of information (Colom et al., 2006). Executive control implicates the ability for regulating mental processes. Inhibition, shifting and updating are key components of this type of control (Friedman et al., 2006). Attention is a broad cognitive function for focusing available mental resources (Baddeley, 2002). Here we consider the control of automatic responses (inhibition). Finally, processing speed is usually measured by reaction time tasks (Sheppard and Vernon, 2008), so simple verification tasks are administered in the present study. All these constructs were estimated by three different measures for obtaining theoretically representative scores using a latent variable approach.

1 We have previously published some reports using this sample (Bruner et al., 2010, 2011, 2012; Bregla et al., 2012; Colom et al., 2009; Martin-Loeches and Bruner, in press). However, only Colom et al. (2009) applied a VBM approach and the analyses were focused on g and residualized Gc (crystallized-abstract intelligence) and Gv (spatial intelligence). Further, (a) only sex was controlled for, (b) the cerebellum was removed from the brain images, and (c) a p level of 0.005 uncorrected was employed.
are mirror imaged. Only rotated figures are to be selected and there could be several correct options for each item. The score is the total number of correct responses (appropriately selected figures – simply rotated) minus the total number of incorrect responses (inappropriately selected figures – mirror imaged) (max. score = 54). DAT-SR is a mental folding test. One unfolded figure is shown at the left, whereas figures at the right depict folded versions. The folded figure matching the unfolded figure at the left must be chosen. The screening version comprising odd items only was administered (max. score = 25).

Working memory (WM) was measured by the reading span, computation span, and dot matrix tasks (Colom et al., 2010). In the reading span task participants verify if a set of sentences sequentially displayed make or make no sense. Each display includes a sentence and a to-be remembered capital letter. Sentences are 10–15 words long. At the end of a given set, participants recall, in their correct serial order, each letter from the set. Set sizes range from 3 to 6 sentence/letter pairs per trial, for a total of 12 trials (4 levels × 3 trials = 12 trials total). The computation span task includes a verification task and a recall task. 6 s is allowed to see the math equation without a time limit for verifying its accuracy. The displayed solution, irrespective of its accuracy, must be serially remembered at the end of a given set. Each math equation includes two operations using digits from 1 to 10. The solutions are always single-digit numbers. Trials range from three to seven equation/solutions (5 levels × 3 trials each = 15 trials total). In the dot matrix task, a matrix equation must be verified and a dot location displayed in a five × five grid must be retained. The matrix equation is presented during a maximum of 4.5 s for adding or subtracting simple line drawings. Once the response is given, the grid comprising the to-be remembered dot is displayed for 1.5 s. After a given set of equation-grid pairs, the grid spaces that contained dots must be recalled clicking with the mouse on an empty grid. Trials increase in size from two to five equations and dots (4 levels × 3 trials = 12 trials total). The score for these three WM tasks is the number of hits in the verification and recalling tasks.

Executive control (updating, UPD) was measured by the 2 back, keep track, and letter memory tasks (Colom et al., 2008). In the 2-back task upper and lower case letters are presented in one of eight equidistant spatial locations around the center of a computer screen. Stimuli are presented for 200 ms and 1300 ms are given for responding. There are 75 experimental stimuli of which 25 are match stimuli. Participants press the space bar of the keyboard to make a match response (a letter presented in the same spatial location 2 positions back in the sequence). The score is the number of hits. In the keep track task participants see several categories at the bottom of the computer screen. Fifteen items, including two or three exemplars from each of the six possible categories (Odd, even, vowel, consonant, lowercase pairs of letters, and uppercase pairs of letters) are then presented serially and in random order for 1500 ms each, with the target categories remaining at the bottom of the screen. The last item presented for each target category must be retained. Therefore, items must be monitored for updating memory representations for the appropriate categories. After the practice trials, participants complete three trials with four target categories, and three trials with five target categories, recalling a maximum of 27 items. In the letter memory task several letters are presented serially for 1000 ms per letter. The last four letters presented in the list must be remembered. Instructions require and emphasize rehearsing the last four letters by mentally adding the most recent letter and deleting the fifth letter back. Participants perform three practice trials, and there are six experimental trials of varying length (15, 17, 19, 21, 23, 25) randomly presented, for a total of 24 letters recalled.

Attention (ATT) was measured by verbal and numerical versions of the flanker task, along with a spatial variant of the Simon task (Colom et al., 2010). The verbal and quantitative tasks require deciding, as fast as possible, if the letter/digit presented in the center of a set of three letters/digits is vowel/odd or consonant/even. The target (e.g. vowel/odd) can be surrounded by compatible (e.g. vowel/even) or incompatible (e.g. consonant/even) letters/digits. The spatial task requires deciding if an arrow (horizontally depicted) points to the left or to the right of a fixation point. The target arrow pointing to a given direction (e.g. to the left) can be presented at the left (e.g. compatible) or at the right (e.g. incompatible) of the fixation point. There are a total of 32 practice trials and 80 experimental trials. Half of the trials are compatible and they are randomly presented across the entire session. The mean reaction time for the incompatible trials is the dependent measure.

Finally, processing speed (PS) was measured by simple recognition verbal, numerical, and spatial tasks (Colom et al., 2008). In these speed tasks one or two items (letter, digit, or arrows) are sequentially displayed for 650 ms. each. Those items define a memory set that can comprise (a) uppercase and lowercase letters, (b) digits, or (c) arrows with different shapes. After the last displayed item, a fixation point appears for 500 ms. Finally, the probe item appears in order to have the participant decide, as quickly and accurately as possible (a) if it has the same meaning as one of the letters, (b) if the number can be divided by one of the digits, or (c) if it has the same orientation of one of the arrows, presented within the memory set. Experimental trials range from one to two items (2 levels × 30 trials each = 60 trials total). The score is the mean RT for the correct answers.

The intelligence tests were administered, following instructions given by the tests’ manuals, in two separate sessions. Session 1 was devoted to the RAPM (20 min), inductive reasoning (PMA-R, 6 min), vocabulary (PMA-V, 4 min), and abstract reasoning (DAT-AR, 10 min), while session 2 was comprised by verbal reasoning (DAT-VR, 10 min), Rotation of solid figures (5 min), numerical reasoning (DAT-NR, 10 min), mental rotation (PMA-S, 5 min), and spatial relations (DAT-SR, 10 min). The cognitive tasks were administered in two separate sessions. Session 1 included the working memory and processing speed tasks, whereas session 2 was comprised by the executive and attention tasks.

Imaging analyses

VBM analyses

These analyses were performed with SPM8 (Statistical Parametric Mapping 8, 2009). Volumes for each participant were first manually aligned to the AC-PC for maximizing registration accuracy. These realigned images were bias-corrected and segmented into gray matter, white matter, and CSF using default tissue probability maps (TPMs) provided with the software. Gray matter partitions were finally 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 (Ashburner and Friston, 2005). The design matrix for statistical analyses was based on a t test ($p<0.001$, uncorrected). Sex, age, and handedness were nuisance variables.

Cortical surface area and cortical thickness analyses

We used surface-based morphometry methods providing independent local information about cortical surface area and cortical thickness. As noted above, these indices deliver distinct information about the genetic and cellular underpinnings of cortical morphology (Chenn and Walsh, 2002; Panizzon et al., 2009; Rogers et al., 2010). Cortical surface area is related to the number and spacing of mini-columnar units of cells in the cerebral cortex, whereas cortical thickness evaluates the number of neurons per column, or neuron density (Chance et al., 2008; Fougeré et al., 2011; Lyttelton et al., 2009; Rakic, 1988, 1995) as well as glial support and dendritic connections (Chklovskii et al., 2004; Sur and Rubenstein, 2005; Thompson et al., 2007). This surface-based technique was implemented in the CIVET pipeline, developed at the Montreal Neurological Institute (MNI, Ad-Dabagh et al., 2006). Three are the basic analytic steps. First, CIVET applies a tissue classification algorithm that segments a structural MRI into gray matter, white matter, and cerebro-spinal fluid. Secondly, it creates a
Results

First, the following confirmatory model was tested: (1) fluid abstract intelligence (Gf) was defined by the Raven Advanced Progressive Matrices Test (RAPM), the inductive reasoning subtest from the PMA (PMA-R), and the abstract reasoning subtest from the DAT (DAT-AR). (2) Crystallized- verbal intelligence (Gc) was defined by the vocabulary subtests from the PMA (PMA-V), the verbal reasoning subtest from the DAT (DAT-VR), and the numerical reasoning subtest from the DAT (DAT-NR). (3) Spatial intelligence (Gv) was defined by the rotation of solid figures test, the mental rotation subtest from the PMA (PMA-S), and the spatial relations subtest from the DAT (DAT-SR). (4) Working memory capacity (WMC) was defined by the reading span, computation span, and dot matrix tasks. (5) Executive updating (UPD) was defined by the 2 back, letter memory, and keep track tasks. (6) Processing speed was defined by verbal, numerical, and spatial short-term recognition speed tasks. (7) Attention was defined by the verbal and numerical flanker tasks, along with the Simon task.

Two main statistical indices were considered for evaluating the fit of this theoretical model to the data. First, the \( \chi^2/DF \) (chi square/degrees of freedom) index is considered as a rule of thumb because it corrects the high sensitivity of the chi-square statistic (Jöreskog, 1993). Values smaller than 2 indicate a very good fit. Secondly, RMSEA (root mean square error of approximation) is usually recommended because it estimates the discrepancy between the model and the data per degree of freedom for the tested model. Values between 0 and 0.05 indicate good fit values, between 0.05 and 0.08 represent acceptable errors, and values greater than 0.10 are indicative of poor fit (Ackerman et al., 2002; Byrne, 1998; Jöreskog, 1993).

Results showed that the latent factors for working memory capacity and executive updating were perfectly correlated, so they were collapsed into the same factor. Supplementary Fig. 1 depicts the final model showing correlations among the resulting six latent factors—fluid intelligence (Gf), crystallized intelligence (Gc), spatial intelligence (Gv), working memory capacity (WMC), processing speed, and attention (ATT)—along with the regression weights for the specific measures attached to each factor.

The final model showed appropriate fit indices: \( \chi^2 = 249.6, \text{df} = 174, \chi^2/\text{DF} = 1.4, \text{RMSEA} = .065 \). Non-significant correlations were omitted. Note that (a) Gf was correlated with WMC (.74), but not with processing speed and attention, and (b) Gc was correlated with WMC (.67) and processing speed (−.37), but not with attention, and (c) Gv was correlated with WMC (.55) and processing speed (−.35), but not with attention. Therefore, considering the simultaneous relationships among all these intelligence and cognitive factors, attention was unrelated to the three intelligence factors, whereas working memory capacity was related to all the intelligence factors, and processing speed was related to Gc and Gv but not to Gf.

Secondly, general scores for the intelligence and cognitive factors were computed for capturing reliable shared variance among the specific measures of each construct. This was done by means of the imputation function of the AMOS program (Arbuckle, 2007). Because this imputation method takes into account the simultaneous relationships among all the considered variables within the model, correlations among the resulting imputed latent scores are a bit higher (see Fig. 1, values in parenthesis). Afterwards, statistical parametric maps (SPMs) were computed separately for the six latent intelligence and cognitive factor scores. The results are depicted in Fig. 1, keeping the correlations among the corresponding factors obtained from the confirmatory model for clarity. Specific information regarding brain regions, \( x \ y \ z \) coordinates, and cluster sizes is reported in Table 1.

The obtained SPMs reveal more findings for attention and processing speed than for working memory capacity and the three intelligence factors. Frontal, temporal, and occipital clusters were detected for attention, whereas frontal and occipital regions were relevant for processing speed. Only frontal clusters were relevant for Gf and Gc, whereas Gv also was related to the temporal fusiform gyrus and the caudate. Working memory capacity was related to frontal and parietal clusters.

Thirdly, brain correlates for cortical surface area and cortical thickness were computed. Significant results were found for cortical surface area only (Fig. 2). The middle frontal gyrus showed significant results for fluid intelligence (\( x \ y \ z \) coordinates 44, 37, 14, BA 46) and working memory capacity (\( x \ y \ z \) coordinates 44, 36, 15, BA 46). For crystallized intelligence, the significant cluster was located in the inferior frontal gyrus (\( x \ y \ z \) coordinates 41, 33, 11, BA 46). Note that a significant cluster was also detected in the left hemisphere for working memory capacity (\( x \ y \ z \) coordinates −47, 37, 6, BA 46).

In the fourth step, SPMs for the intelligence factors, as well as for the cognitive factors, were simply overlapped using the display function of the SPM8 software (Fig. 3). It might seem appropriate to compute conjunction analyses for reaching this goal. However, (a) as noted in the SPM-8 Manual, “SPM checks whether the contrasts are orthogonal and, if not, makes them so. Contrasts are orthogonalized with respect to the first contrast specified” (page 282), and (b) Friston et al. (2005) indicates that “in reporting subsequent conjunction analyses, it might be good practice to describe the inference with something like the following: we performed a conjunction analysis using SPMs of the minimum T-statistic over n orthogonal contrasts. Inference was based on P values adjusted for the search volume using random field theory” (page 667). Therefore, conjunction analyses are appropriate for orthogonral data. This happens when you have different samples and you are interested in finding common activated regions (Haier et al., 2005). It is also relevant for comparing activations across conditions in fMRI experiments (Fehr et al., 2007; Karama et al., 2011a). But, as expected, here the computed latent scores representing the psychological constructs of interest are substantially correlated and, therefore, it seems reasonable to rely in one-sample t-tests for each latent score using the same threshold and, afterwards, report their common clusters. This approach avoids an arguable manipulation of the psychological data (Karl Friston, personal communication).

Fig. 3 shows that Gf and Gc show an overlapping cluster in the right middle frontal gyrus (BA 8), whereas Gc and Gv show an overlapping cluster in the right inferior frontal gyrus (BA 10). Working memory capacity does not show any overlap with processing speed (PS) or attention (ATT), whereas these two latter factors overlap in the right inferior frontal gyrus (BA 47) and the left occipital lingual gyrus (BA 18).

Because these findings were obtained using a \( p < 0.001 \) uncorrected, we computed small volume corrections (SVCs). Importantly, the center of the sphere is selected independent of the data using the closest BA included within the framework of the PHT model (Jung and Haier, 2007) using a radius of VOI = 20 mm and a FWE of \( p < 0.05 \) (Salgado-Pineda et al., 2003). Results for Gf ad Gc at BA 8 survived FWE (\( p = .033 \) and .019, respectively; the center of the sphere was in BA 9). For Gc and Gv at BA 10, \( p \) values were .033 and .019, respectively (the center of the sphere was in BA 10). For PS and ATT at BA 47, \( p \) values were .016 and .064 (the center of the sphere was in BA 47). Finally, for PS and ATT at BA 18, \( p \) values were .035 and .002 (the center of the sphere was in BA 18).

Finally, SPMs for each of the three intelligence factors were overlapped with each of the three cognitive factors (Fig. 4). There are three main results here: (a) fluid intelligence (Gf), crystallized intelligence (Gc), and working memory capacity (WMC) share a cluster in the middle frontal gyrus (BA 8), (b) crystallized intelligence (Gc), spatial intelligence (Gv), attention (ATT), and processing speed (PS)
are consistent with this reading of the available evidence. The general factor of intelligence (g) may be too general for...
Table 1

Coordinates obtained from the SPMs for the psychological constructs of interest (p < 0.001, uncorrected, controlling for sex, age, and handedness).

<table>
<thead>
<tr>
<th>Construct</th>
<th>Brain region</th>
<th>x, y, z coordinates</th>
<th>Cluster size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fluid intelligence (Gf)</td>
<td>Right middle frontal gyrus (BA 8)</td>
<td>32 14 40</td>
<td>15</td>
</tr>
<tr>
<td>Crystallized intelligence (Gc)</td>
<td>Right middle frontal gyrus (BA 8)</td>
<td>32 16 40</td>
<td>20</td>
</tr>
<tr>
<td>Spatial intelligence (Gs)</td>
<td>Right inferior frontal gyrus (BA 10)</td>
<td>34 41 3</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Caudate body</td>
<td>12 16 7</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Temporal fusiform gyrus (BA 37)</td>
<td>44 −37 −10</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Left caudate head</td>
<td>−14 20 5</td>
<td>38</td>
</tr>
<tr>
<td>Working memory (WM)</td>
<td>Right middle frontal gyrus (BA 8)</td>
<td>30 14 40</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Right parietal postcentral gyrus (BA 3)</td>
<td>22 −33 72</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td>Left superior frontal gyrus (BA 6)</td>
<td>−2 −5 65</td>
<td>10</td>
</tr>
<tr>
<td>Attention (ATT)</td>
<td>Left occipital lingual gyrus (BA 18)</td>
<td>−18 −76 −5</td>
<td>375</td>
</tr>
<tr>
<td></td>
<td>Left cerebellar tonsil</td>
<td>−16 −46 −33</td>
<td>708</td>
</tr>
<tr>
<td></td>
<td>Right inferior frontal gyrus (BA 47)</td>
<td>24 19 −11</td>
<td>123</td>
</tr>
<tr>
<td></td>
<td>Right frontal precentral gyrus (BA 6)</td>
<td>34 5 72</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>Right pyrarnis</td>
<td>16 −60 −27</td>
<td>297</td>
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<tr>
<td></td>
<td>Right cerebellar tonsil</td>
<td>16 −43 −35</td>
<td>23</td>
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<tr>
<td></td>
<td>Left frontal subcallosal gyrus (BA 47)</td>
<td>−20 17 −11</td>
<td>40</td>
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<td></td>
<td>Left inferior frontal gyrus (BA 47)</td>
<td>−24 23 −8</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Left putamen</td>
<td>−22 6 9</td>
<td>23</td>
</tr>
<tr>
<td>Processing speed (PS)</td>
<td>Right inferior temporal gyrus (BA 37)</td>
<td>42 −66 −5</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Left occipital lingual gyrus (BA 18)</td>
<td>−16 −56 3</td>
<td>10</td>
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<td></td>
<td>Left inferior frontal gyrus (BA 47)</td>
<td>24 21 −13</td>
<td>62</td>
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<td></td>
<td>Left declive</td>
<td>−36 −61 −9</td>
<td>64</td>
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<td></td>
<td>Left occipital lingual gyrus (BA 18)</td>
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<td></td>
<td>Left occipital lingual gyrus (BA 18)</td>
<td>24 −70 2</td>
<td>85</td>
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providing a fine approach to the brain correlates of key intelligence components. In other words, a neuro-g may not exist (Haier et al., 2009).

In a recent fMRI study, Prabhakaran et al. (2011) analyzed two key components of working memory, namely, capacity and speed. Their findings can be seen as consistent with the main conclusion achieved here. Across two different studies testing working memory capacity and working memory processing speed respectively, they found significant increased activity in very specific right prefrontal regions for both experimental conditions (BA 46/10). It was suggested that these right prefrontal areas might be a common region connecting the capacity and speed components of the working memory system. Further, these authors also suggest that this brain region may connect working memory with complex mental processes such as reasoning, a key facet of fluid intelligence: “individual differences in the ability to implement binding or chunking strategies in working memory may underlie performance differences between individuals in both their capacity and speed (…) the brain basis of this capacity construct involves flexible recruitment of domain-independent regions (in right DLPC) to effectively expand the storage capacity of domain-dependent regions (in a left-hemisphere network for verbal material). Determination of the true capacity limits of short-term storage has been considered essential to understanding human mental processes” (p. 7).

Secondly, the latent scores derived for attention and processing speed showed overlaps with crystallized and spatial intelligence also in specific frontal regions. However, in this case, these regions were located within BAS 10 and 47. BAS 10 corresponds to the frontopolar region and it supports strategic processes related to memory retrieval and executive processes (Gilbert et al., 2006). BA 47 is related to language processing. BAS 10 and 47 are not far away from BA 46 and are all considered relevant for stage 3 (hypothesis testing) within the parieto-frontal integration theory (P-FIT) of intelligence (Jung and Haier, 2007). Therefore, this main result supports the theory in this regard. Nevertheless, overlap in parietal regions was not detected here with structural parameters. Perhaps the integration role usually attributed to the parietal lobes is redundant for capturing and manipulating relevant information from the environment.

Finally, a specific overlap was observed for spatial intelligence and attention in the temporal fusiform gyrus (BA 37). This region was interpreted as relevant for stage 1 (processing of sensory information) within the P-FIT model. It is relevant for general recognition processes (face, body, words, numbers, etc.) and it is activated more in high g subjects during a non-reasoning task (Haier et al., 2003). Together with the frontal results found for fluid intelligence, crystallized intelligence, and working memory capacity, this suggests that the documented relationships between intelligence and cognitive factors are supported by gray matter features in temporal and frontal brain regions, but not in occipital and parietal areas.

Of note is that we found significant associations for cortical gray matter volume (GMV) and cortical surface area (CSA) but not for cortical thickness (CT). Variance for the former indices seems relevant for the behavioral differences computed for the analyzed intelligence and cognitive factors. CT might be important for intelligence and cognition (as it is shown by Karama et al., 2011b) but the current findings show that CT variance for the analyzed sample is unrelated to individual differences in the considered intelligence and cognitive latent factors. Given that cortical GMV is more highly correlated with CSA than with CT (Winkler et al., 2010) the results reported in the present study suggest that individual differences in the number of columns of the cortical mantle (but not the number of cells within columns) may contribute substantially to variations in intelligence and cognition. As noted above, CSA and CT can be distinguished by their genetic underpinnings, and, therefore, genes contributing to variations in CSA could be also nice candidates for intelligence and cognitive variations.

Perhaps the main inference might be that key intelligence and cognitive factors are related, at least in part, because they are supported by shared specific regions in the brain. From this perspective, the separate analysis of distinguishable intelligence and cognitive factors shows that mainly (but not exclusively) individual differences in frontal and parietal areas are relevant. However, we did show here that their

For the sample analyzed in the present study (N = 104) the correlation between cortical gray matter volume and cortical surface area was .35, whereas the correlation between cortical gray matter volume and cortical thickness was .65. The correlation between cortical surface area and cortical thickness was .39. All these correlations were statistically significant at p < .01. These correlation values are highly consistent with results reported by Karama et al. (2011b) with a different sample of 207 children and adolescents.
commonality is generally circumscribed to individual differences in the frontal lobes. This happens for cortical gray matter volume and cortical surface area, but not for cortical thickness. It is important to distinguish between results for each intelligence-cognitive factor and results for the overlap among the considered factors. Further, as underscored here, the analyzed intelligence and cognitive functions are obtained from a latent variable analysis capturing the common variance among the specific tests and tasks theoretically tapping the constructs of interest (and, consequently, partialling out specific/error variance).

The identified clusters within the frontal lobes might be key hubs shared by central cognitive functions. These hubs might change for different samples, but we endorse the view that they will be located within the frontal lobes. The inclusive framework provided by the P-FIT model is based on varied imaging studies, both structural and functional. For most of the considered research, too global (such as IQ) or very specific measures (such as the advanced progressive matrices test) represent the intelligence-cognitive function of interest. However, as noted before, this sort of scores combines variance shared with other measures and variance specific for the particular measure. Our approach here was aimed at capturing the shared variance for several varied measures for defining a giving psychological construct. The removal of the specific variance may be behind the lack of significant findings in the parietal lobes for some of the considered intelligence-cognitive functions.

Fig. 2. Significant correlations ($p<0.001$, uncorrected, controlling for sex, age, and handedness) between cortical surface area and Gf (fluid intelligence)/Gc (crystallized intelligence)/WMC (working memory capacity).
In summary, whereas some research has underscored the relevance of a parieto-frontal network for general intelligence (Barbey et al., 2012; Colom et al., 2009, 2010; Gläscher et al., 2010; Jung and Haier, 2007, Karama et al., 2011b, Woolgar et al., 2010) and cognitive functions such as working memory capacity (Colom et al., 2007; Halford et al., 2007; Jonides et al., 2008; Marois and Ivanoff, 2005; Wager and Smith, 2007; Wager and Smith, 2008), others have suggested that intelligence and cognitive functions may be subserved by different brain regions. For example, recent studies have reported that working memory capacity, a cognitive function that is highly correlated with intelligence, is associated with activity in the prefrontal cortex (Colom et al., 2007; Halford et al., 2007; Jonides et al., 2008; Marois and Ivanoff, 2005; Wager and Smith, 2007; Wager and Smith, 2008). These findings suggest that the brain regions associated with intelligence and cognitive functions may be distinct, and that the relationship between intelligence and cognitive functions may be mediated by different brain regions.

**Fig. 3.** Top panel, overlapping SPMs for the three intelligence factors. Bottom panel, overlapping SPMs for the three cognitive factors. N = 104 (p < 0.001, uncorrected, controlling for sex, age, and handedness).

**Fig. 4.** Top panel, overlapping SPMs among the three intelligence factors and working memory capacity. Middle panel, overlapping SPMs among the three intelligence factors and attention. Bottom panel, overlapping SPMs among the three intelligence factors and processing speed. N = 104 (p < 0.001, uncorrected, controlling for sex, age, and handedness).
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