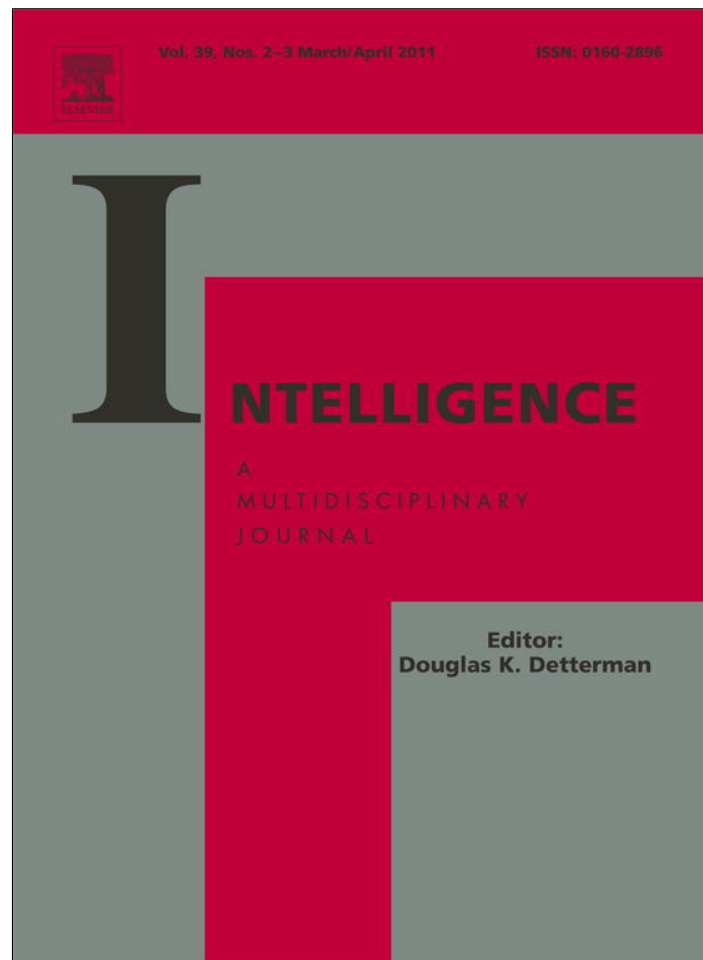


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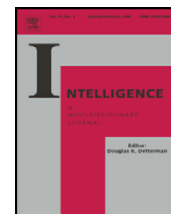
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Intelligence



Midsagittal brain shape correlation with intelligence and cognitive performance

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ABSTRACT

Brain shape might influence cognitive performance because of the relationships between functions, spatial organization, and differential volumetric development of cortical areas. Here we analyze the relationships between midsagittal brain shape variation and a set of basic psychological measures. Coordinates in 2D from 102 MRI-scanned young adult human brains were superimposed through a Procrustes approach, and the residual variation was regressed onto 21 cognitive tests performed by the same individuals. Most of the composite and specific variables (including general intelligence, working memory, attention, and executive functions) do not show meaningful correlations with midsagittal brain morphology. However, variables related to mental speed display subtle but consistent correlations with brain shape variation. Such correlations are small, suggesting that the influence of midsagittal brain geometry on individual cognitive performance is negligible. Nevertheless, this evidence can supply information on brain biology and evolution. Areas associated with the parietal cortex appear to be involved in relationships between brain geometry and mental speed. These areas have been associated with relevant endocranial differences between living and extinct humans, and are important as functional and structural components of brain organization. The limited correlation between brain geometry and mental speed among modern individuals might be more relevant when the large paleoneurological variation of the genus *Homo* is taken into account.

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1. Introduction

Brain morphology results from the integration between the evolution of neural functions and structural adjustments related to cranial organization (Bruner, 2007; Richtsmeier et al., 2006). Soft tissues (neural components, as well as vascular and connective elements) and hard tissues (bones) interact reciprocally during growth and development through structural (biomechanical) and functional (physiological and biochemical) factors. The final phenotype, both in terms of ontogeny and phylogeny, results from this morphogenetic

matrix. During morphogenesis, changes in neurocranial size are mostly due to brain growth pressure while changes in neurocranial shape are largely associated with tension distribution through the connective dura layers (Enlow, 1990; Moss & Young, 1960). This relationship is quite linear for the bone components of the cranial vault (which contact the frontal, parietal, and occipital lobes), while it is more complex in the lower cranial areas (housing the temporal and cerebellar lobes, as well as subcortical structures) where biomechanical integration with the cranial base constrains brain form (Bastir & Rosas, 2009; Bruner & Ripani, 2008; Neubauer, Gunz, & Hublin, 2009). Apart from the skull vs. brain relationships, the brain form itself is internally constrained by topological relationships linking volume, surface distribution, folding patterns, cortical thickness, and cellular organization (e.g., Hilgetag & Barbas, 2006; Hofman, 1989).

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A number of studies have explored the relationships between mental abilities and several morphological components such as overall and regional brain volumes, regional gray and white matter volumes, cortical thickness, cortical convolution, or callosal thickness (see Colom et al., 2009; Deary, Penke, & Johnson, 2010; Jung & Haier, 2007; Luders, Narr, Thompson, & Toga, 2009). When global brain volume is considered, correlation coefficients between morphology and cognitive performance range between 0.3 and 0.4. When analyzing regional volumes based on main cerebral lobes, significant correlations for frontal, parietal and temporal lobes range from 0.26 to 0.56. Significant correlations have been also found between intelligence, education, and increase in geometrical complexity of the cortical surface (Im et al., 2006). However, even when intelligence can be related to the topological properties of brain networks (Li et al., 2009), no data are currently available regarding the correlation between brain shape and cognitive performance. Taking the evidence of relationships between cognition and local differences in brain volumes into account, it must be assumed that the same volumetric differential changes will affect the spatial arrangement of the surrounding components.

Shape is intended as the geometrical relationships within a group of elements, in terms of their spatial organization. Accordingly, shape analysis is aimed at localizing and quantifying patterns of spatial relationships which have generated a given sample variation. Such patterns are necessary for ordering the sample according to these spatial rules, being also the ultimate results of the underlying biological *bauplan*. The field encompasses a number of techniques, of which Procrustes analysis and coordinate-based morphometrics are particularly outstanding (Dryden & Mardia, 1998; Bookstein, 1991; Gower & Dijksterhuis, 2004). Multivariate statistics applied to landmark data allows the identification of co-variation patterns within the anatomical system, splitting the overall morphological variation into components based on the reciprocal relationships between the anatomical elements. When cranial constraints can be ruled out, brain shape variation is supposed to be associated with differential growth of the brain parts, or local adjustment in neural circuits and internal configurations. In both cases, this implies spatial reorganization of the relationships between neural components.

Midsagittal brain sections have been widely used both in neurosciences and in human evolutionary studies, because they supply reliable and homologous anatomical references for the analyses of the morphological relationships among cranial organization, cortical brain areas, and subcortical brain elements. Recently, the patterns of covariation of the midsagittal brain morphology in adult humans have been described and quantified by means of geometric morphometrics (Bruner, Martin-Loeches, & Colom, 2010). This analysis suggested that fronto-parietal bulging may be the most patent integration scheme generating the morphological variability of the midsagittal brain.

Here we test the correlation between adult midsagittal brain shape and cognitive performance, as measured through standard psychometric tests and cognitive tasks. Procrustes superimposition and multivariate approaches were used to describe and quantify the correlation between brain geometry and scores associated with a broad set of cognitive

abilities, including intelligence, working memory, executive control, mental speed, and attention.

2. Materials and methods

2.1. Sample

The sample included 102 participants (52 females), aged between 18 and 27 years (mean age = 19.9, SD = 1.6). According to a standardized questionnaire regularly administered at the hospital, none of the participants had medical illness, brain injury, or a psychiatric history. Participants were university psychology undergraduates and their native language was Spanish. All participants gave written informed consent prior to the study. Midsagittal T1-weighted MRI brain sections were selected to investigate brain shape, by using a configuration with 20 cortical and 7 subcortical landmarks (Fig. 1; see Bruner et al., 2010 for further information on sample, MRI data, and landmarks).

2.2. Morphometrics

Coordinates were investigated by using tools from geometric morphometrics (Zelditch, Swidersky, Sheets, & Fink, 2004). Data were superimposed through a Procrustes approach (Bookstein, 1991; Rohlf & Marcus, 1993; Slice, 2004). The first step of Procrustes superimposition is the translation of all the coordinate systems to the same centroid. Then, each coordinate system is scaled to unitary centroid size, defined as the square root of the sum of squared distances of a set of landmarks from their centroid. Finally, the centered and scaled coordinate systems are rotated in order to minimize the sum of the residual squared differences at each landmark from an average configuration (*consensus*). The Procrustes approach provides a standardized and efficient method minimizing the difference between individuals, normalizing position, scale, and rotation of a set of coordinates according to a quantitative criterion. Residuals after superimposition (both in their x and y components) can be used in standard multivariate techniques. Vectors resulting from multivariate ordination approaches can be projected directly onto the original coordinates to visualize the spatial changes associated with the covariation patterns evidenced through these analyses, or visualized through interpolant functions like the *thin-plate spline* (see Zelditch et al., 2004 for a complete reference on geometric morphometrics).

Shape residuals were regressed onto scores from cognitive tests through multivariate and partial-least square regression. Multivariate regression was used to analyze the relationships between each cognitive test (independent variable) and shape residuals (dependent variables). Correlations were quantified reporting the amount of variance (V%) for which the regression accounts. Partial Least Square (PLS) regression was used for analyzing the overall correlation between shape variation and groups of psychometric variables. PLS computes latent vectors (combinations of variables) showing the relationships between two groups of multivariate dataset, by using a symmetric regression approach to quantify and describe the axes of maximum covariance between the two groups of variables (Rohlf & Corti, 2000). The Escoufier correlation coefficient (R_v) was used as an overall measure of

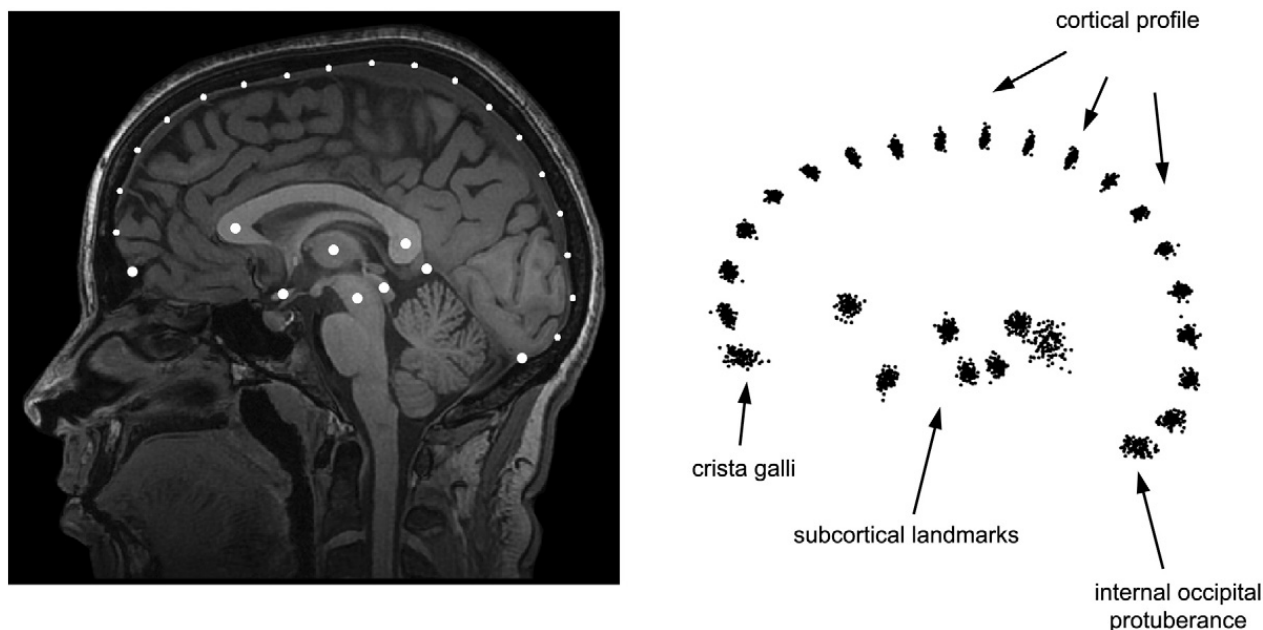


Fig. 1. Configuration of landmarks used in the analysis and scatterplot of the sample after Procrustes superimposition. The cortical profile has been sampled from the anterior border of the *crista galli* to the internal occipital protuberance, with equally-spaced landmarks. Subcortical landmarks included thalamic areas (center of the thalamus, midbrain colliculi, and center of the midbrain), the corpus callosum (centers of the genu and splenium), the optic chiasm, and the midpoint between cerebral, cerebellar, and subcortical structures.

association between the two blocks. All statistical significance values were estimated through permutation tests (10,000 replicates). Note that because of the exploratory nature of this study and because of the many relationships analyzed here, no corrections for multiple comparisons were applied. Hence, a common threshold of $p=0.05$ was used to find those correlations revealing the association between shape variation and psychometric variation. Accordingly, raw figures are reported and discussed to show the degree and strength of correlation among factors, without giving specific inferential values to the casewise results. Shape analysis was performed with Morphoj (Klingenberg, 2010). Sex differences for this shape configuration were not detected in a previous study using the same sample (Bruner et al., 2010), so the whole sample is used here with no further analysis of sex-related patterns.

2.3. Cognitive tests

We have considered 21 specific measures and seven composite scores. Each composite score is comprised by 3 measures (see Colom, Abad, Quiroga, Shih, & Flores-Mendoza, 2008, 2009; Colom et al., 2009 for details on tests and tasks). *Fluid intelligence* (Gf) is measured by the advanced progressive matrices test (APM), the inductive reasoning subtest from the Primary Mental Abilities (PMA) battery, and the abstract reasoning (AR) subtest from the Differential Aptitude Test (DAT) battery. *Crystallized intelligence* (Gc) is measured by the verbal reasoning (VR) and numerical reasoning (NR) subtests from the DAT battery, as well as by the vocabulary subtest from the PMA battery. *Spatial intelligence* (Gv) is measured by the spatial relations (SR) subtest from the DAT battery, the mental rotation (S) subtest from the PMA battery, and the rotation of the solid figures test. A further variable, general intelligence or *g* is the average of Gf, Gc, and Gv.

Working memory (WM) is measured by the reading span, computation span, and dot matrix tasks. *Executive functioning* (EF) is measured by the n-back, letter memory, and keep-track tasks. *Mental speed* (MS) is measured by the verbal, numerical, and spatial simple recognition tasks. *Attention* (ATT) is measured by the Simon Task along with verbal and numerical versions of the Flanker Task. Sex differences for these kinds of scores are already known and have been widely discussed (e.g., Deary et al., 2010; Halpern, 2000). Accordingly, such differences are not analyzed here.

3. Results

Table 1 shows the percentage of brain shape variation explained by each psychological variable (significance values are also reported). Values are given for composite and specific scores, as well as for general intelligence (*g*). Among the specific scores, a correlation with shape variation is evidenced for PMA-V (vocabulary test: $V\%=3.2$; $p=0.002$), RSPA (verbal working memory: $V\%=2.0$; $p=0.04$), and all the specific mental speed tasks (VSP, verbal speed: $V\%=2.1$; $p=0.03$; NSP, numerical speed: $V\%=2.3$; $p=0.02$; SSP, spatial speed: $V\%=2.2$; $p=0.02$). Considering the composite cognitive variables, intelligence, working memory, executive function, and attention did not show any relationship with brain shape. Mental speed (MS) showed low but significant correlation with shape variation ($V\%=3.1$; $p=0.003$).

A first PLS analysis correlating these five specific cognitive tasks with Procrustes coordinates showed that RSPA contributes mainly to a second latent vector of variation, which was not even significant. Therefore, a second PLS analysis was computed, correlating brain shape to the four remaining variables (PMA-V, VSP, NSP, SSP). The two blocks (morphological and cognitive) showed a significant overall correlation ($R_v=0.11$; $p=0.0007$). Only the first latent vector is significant

Table 1
Brain shape variation explained by each psychological score.

		% VAR	p
<i>Specific variables</i>			
APM	Advanced progressive matrices	0.50	0.890
PMA-R	Inductive reasoning	1.09	0.340
DAT-AR	Abstract Reasoning	0.55	0.850
PMA-V	Vocabulary test	3.24	0.002
DAT-VR	Verbal reasoning	0.40	0.960
DAT-NR	Numerical reasoning	0.55	0.850
SOD	Rotation of solid figures	0.42	0.950
PMA-S	Spatial rotation	1.35	0.190
DAT-SR	Spatial relations	0.89	0.500
RSPA	Reading span	1.99	0.040
CSPA	Computation span	0.42	0.950
DMAT	Dot matrix	0.42	0.950
VSP	Verbal speed	2.09	0.030
NSP	Numerical speed	2.32	0.020
SSP	Spatial speed	2.23	0.020
N_Back	2-back	1.34	0.190
LMEM	Letter memory	1.73	0.080
KTR	Keep track	0.81	0.590
VATT	Verbal attention	1.68	0.090
NATT	Numerical attention	0.72	0.680
SATT	Spatial attention	0.94	0.460
<i>Composite variables</i>			
g	General intelligence	0.70	0.700
Gf	Abstract-fluid intelligence	0.59	0.810
Gc	Verbal-crystallized intelligence	0.88	0.510
Gv	Spatial intelligence	0.56	0.840
WM	Working memory capacity	0.84	0.530
MS	Mental speed	3.15	0.003
EF	Executive functioning	0.71	0.680
ATT	Attention	1.05	0.360

($p=0.0006$), explaining most of the overall correlation between blocks (86%). In terms of psychological variation, this vector is associated with increases in both the vocabulary test score (PLS coefficient: 0.58) and the mental speed variables (smaller reaction times, RTs) (PLS coefficients: -0.45 , -0.47 , and -0.48 for VSP, NSP, and SSP, respectively—note the negative sign because reaction time was the dependent measure). This morphological latent vector is associated with relative flattening and projection of frontal and occipital lobes, bulging at the fronto-parietal junction, and relative downward shifting of the subcortical elements (Fig. 2). When the opposite pattern beyond the actual range of variation is visualized, the

source of geometrical dilation associating shape changes with increased mental speed is evidenced, showing a crease localized in the depth of the parietal area (Fig. 3). Considering this first vector of correlation between the two blocks, the psychological pattern associated with a decrease of reaction times and the morphometric pattern associated with the crease at the deep parietal areas show a correlation coefficient (r) of 0.44 ($p=0.05$).

4. Discussion

Different volumetric development of neural components and variations in the organization of the neural networks may lead to adaptive functional changes in the spatial organization of the brain. At the same time, variations in the architecture of the braincase can promote secondary changes in brain geometry which are not related to neuro-functional variations, but just to spatial constraints associated with cranial morphogenesis. Hence, the skull induces changes in the brain components, and the brain induces changes in the cranial elements, both in ontogeny (Richtsmeier et al., 2006) and phylogeny (Bruner, 2007). Of course, whenever the primary source of brain changes can be related to neural function (cognition) or to cranial adjustments, the secondary consequences may be either neutral in evolutionary terms or be involved in successive cooption between functions and characters (exaptation; Gould & Vrba, 1982). For example, the cranial base flexion in primates largely influences the whole cranial organization (Lieberman et al., 2000), and it has been proposed that it may also influence neural wiring because of its impact on brain globularity (see McCarthy, 2001). Taking the possible relationships between brain geometry and neural organization into account (Hilgetag & Barbas, 2006; Hofman, 2001), the present study aimed to quantify the degree of correlation between midsagittal brain shape variation and cognitive performance as measured through a wide range of psychological measures. We found no correlation between brain shape variation and most of the cognitive scores, except for those associated with mental speed.

Therefore, the first result concerns the lack of evidence for any association between midsagittal brain shape and most of the psychological measurements. Variables associated with intelligence and working memory show only limited and

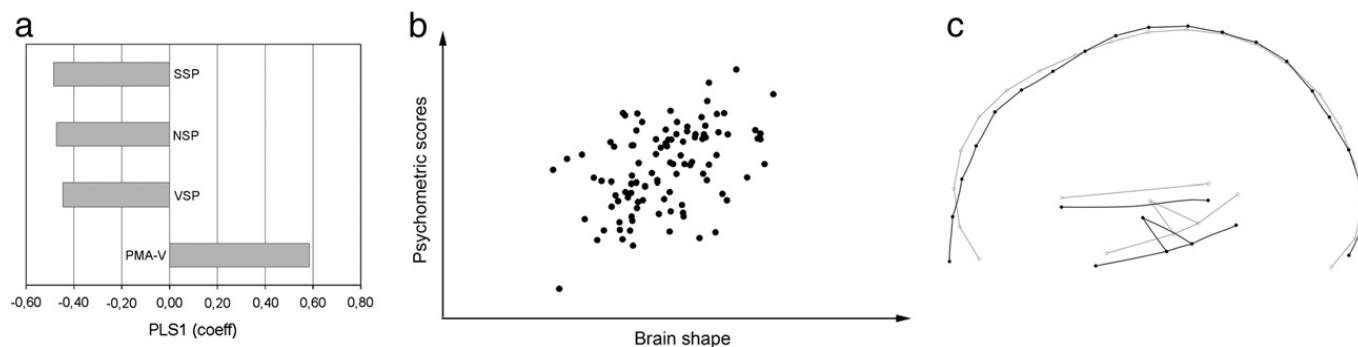


Fig. 2. Procrustes coordinates have been regressed onto PMA-V (vocabulary), VSP (verbal speed), NSP (numerical speed), and SSP (spatial speed). Increases in PMA-V and Mental Speed (lower reaction times, RTs) tasks is associated with bulging at the fronto-parietal boundary, flattening of the frontal lobe, and downward shifting of the subcortical elements: a) coefficients for each cognitive variable along the psychometric vector; b) correlation plots between brain shape vector and cognitive vector for the first axis of covariation between the two blocks; c) geometric changes associated with the morphological vector (positive values: bold links).

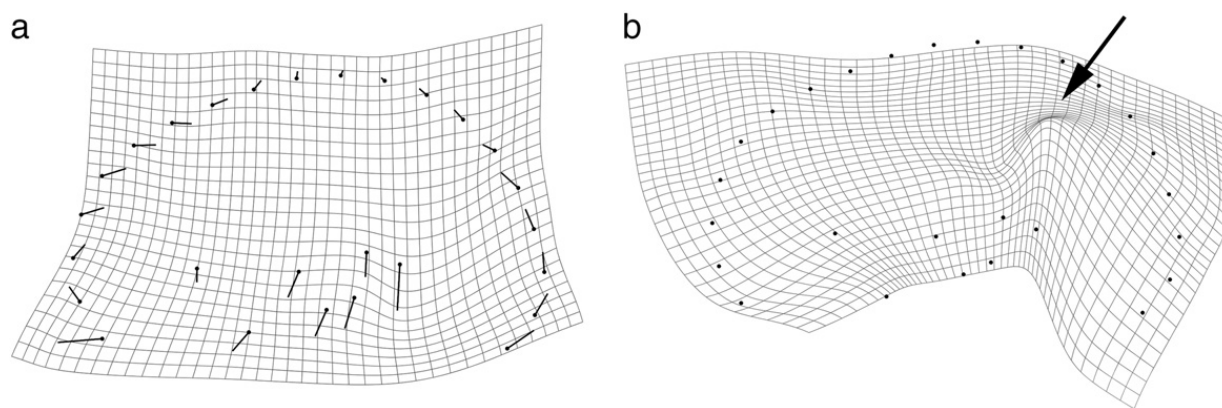


Fig. 3. The morphological pattern evidenced by PLS analysis is visualized through a thin-plate spline deformation grid to show the overall spatial changes (a). The opposite patterns, stressed beyond the actual range of variation, shows a source of geometrical dilation in the depth of the parietal volumes, largely responsible for the shape changes observed (arrow).

non-homogeneous statistical evidence which, also because of the very low percentage of variance explained (around 2–3%), cannot really be considered as biologically meaningful. Attention and executive function did not yield any correlation at all. It must be acknowledged that lack of evidence must not be interpreted as absence of relationships. Here we have considered midsagittal brain geometry, modeled by specific neural elements. We cannot discard the presence of some correlation associated with other brain components which have not been considered here, or differences beyond the statistical resolution that the present sample allows.

Interestingly, however, all the mental speed tasks showed a small but significant correlation with brain shape. Although the percentage of variance explained by these correlations is low, the fact that all variables associated with mental speed display a comparable relationship with brain morphology deserves attention. Brain shape changes accounted for only 2% of the performance on these tasks (3% when these variables are considered together as a composite factor). Hence, the present data support a certain relationship between midsagittal brain morphology and mental speed, regardless of the specific task involved (verbal, numerical, or spatial). It is noteworthy that PMA-V (a highly speeded vocabulary task) also showed a certain correlation with brain shape ($V\% = 3.2\%$). Therefore, even if the low determination coefficients suggest a scarce association between brain shape and the overall psychological response, the consistency of these different correlations deserves close attention as a possible biological signal.

As already mentioned, flexion of the cranial base is associated with neurocranial globularity in primates (Lieberman et al., 2000) and especially in modern humans (see Lieberman et al., 2002; McCarthy, 2001; Neubauer et al., 2010), and it remains to be verified whether or not this may have influenced neural wiring because of geometrical advantages. In human evolution, neurocranial shape has been often hypothesized to be related with cognitive ability, considering that the average time for neural communication may depend on brain geometry (Hofman, 2001). The basic rationale suggests that more spherical brains would have faster neural communication, because of the smaller mean connection length between cortical areas. Together with axon conduction delay, dendrite attenuation, and number of synapses, wiring length is a relevant factor in connectivity which

may have been optimized under selection pressures during evolution (Chklovskii, Schikorski, & Stevens, 2002). Furthermore, global efficiency of the brain network seems correlated with intelligence, suggesting that topological variables of the neural system may influence the velocity of information transfer according to the length of the neural path (Li et al., 2009). It is therefore interesting that in the present study the only cognitive variables related to brain shape variation were those associated with the speed of the neural response. In our analysis, faster responses are associated with brains showing outward bulging of the profile at the fronto-parietal boundary, flattening of the prefrontal areas, and subcortical elements situated in a relatively lower position. If midsagittal brain shape accounts just for 2–3% of mental speed variation in a relatively homogeneous modern human population, this value might be definitely larger when taking the much larger neurocranial variation into account, like those between different species. In particular, although within-species and between-species differences may not rely on the same factors, we wonder if these results can be extrapolated to the genus *Homo* and to topics pertaining to paleoneurology (Holloway, 2008). Actually, the main endocranial difference between modern and non-modern humans is represented by bulging of the fronto-parietal cortical profile (Bruner, 2004). Hence, a small effect on the limited variability within a single species (*Homo sapiens*) may become a relevant factor when considering the larger inter-specific degree of changes (the genus *Homo*). In this case, apart from giving some information on the possible biological relationships between brain geometry and cognition in the modern human brain, these results can introduce a tool for evaluating cognitive components in extinct species, even if only through extrapolative approaches.

The fronto-parietal network is gaining increasing attention because of its involvement in many cognitive systems (e.g., Gläscher et al., 2010; Jung & Haier, 2007). In particular, the implication of areas around the intraparietal sulcus is even more promising, taking into account the relevance of this region in neontological (Orban et al., 2006; Rushworth et al., 2001) and paleontological (Bruner, 2010; Stout & Chaminade, 2007) analyses. It is worth noting that, within the fronto-parietal system, functional changes at the parietal areas might be more influenced by the environment and less determined by genetic factors (Neubauer & Fink, 2009). These parietal regions are very relevant as the structural core of

brain organization, not only by virtue of their topological position, but also considering their patterns of neural connections (Hagmann et al., 2008). Actually, despite the low correlation between specific psychological variables and overall brain shape, the correlation between the combination of those cognitive variables and the specific morphological pattern associated with a deep parietal crease is definitely higher ($R=0.44$). The role of the parietal areas as the structural core of the cerebral geometry, the relationships between neural wiring and spatial organization, and our results associating deep parietal areas with mental speed, provide a preliminary framework to evaluate possible influences of cerebral shape on cognition. However, considering the multifactorial nature of these variations, the subtle relationships between anatomy and intelligence, and the limited degree of correlation between shape changes and psychometric scores, we prefer not to provide further neuroanatomical or neuropsychological interpretations for the observed morphological changes associated with mental speed. Future analyses might be focused on these specific variations, allowing tentative interpretations which must rely also on other kinds of information (anatomy, functional imaging, etc.). However, what is really important is that such convergence of different results suggests possible links between brain evolution, cognition, and morphogenetic integration.

The present analysis represents a starting point for future studies into the relationship between brain shape, neural wiring, and cognitive functions. Further studies should be focused on specific brain areas, as well as 3D analyses of brain morphology, or using different kinds of morphometrics approaches. However, morphometric modeling must be interpreted as an exploratory tool, and direct interpretation of these brain shape patterns is largely speculative, needing the support of neuro-functional evidence. If these correlations suggest a possible biological relationship between brain shape and cognition, the low determination coefficients nonetheless evidence a large individual component, in which factors other than morphology contribute to cognitive performance. Strictly considering neural efficiency, apart from neural geometry and the consequent brain topological properties, there are many other factors influencing the brain component placement and spatial arrangement. Efficiency could be associated with the number of processing steps more than with wiring length (Kaiser & Hilgetag, 2006), or with energy management and neural activation parameters (Deary et al., 2010; Neubauer & Fink, 2009). Nevertheless, the existence of this morphological signal must be taken into consideration, to provide new perspectives in brain functional anatomy and for assessing hypotheses in human brain evolution within a paleoneurological context.

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