Cortical Structure in Nodes of the Default Mode Network predicts General Intelligence

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Abstract

A growing number of studies implicate functional brain networks in intelligence, but it is unclear if network nodal structure relates to intelligence. Using MRI, we studied the relationship of the general intelligence factor (g) with cortical thickness (CT), local gyrification index (LGI) and voxel-based morphometry in the nodes of the Default Mode Network (DMN) and Task-Positive Network (TPN) in a cohort of 44 young, healthy adults. Employing a novel strategy, we performed repeated analyses with multiple sets of g estimates to remove false positives. CT and LGI in medial and temporal nodes of the DMN were reliably correlated with g ($P < 0.05$; $r: 0.31-0.41$). A linear regression model developed with these parameters (adj. $R^2: 0.15-0.40$) could predict individual g scores. Cortical thickness and gyrification in key nodes of the Default Mode Network correlate with intelligence and can predict g in individual subjects.

Introduction

The study of intelligence has generated much interest, but its neural basis is yet to be fully elucidated. With the discovery of intrinsic or resting-state networks in the brain, cerebral functioning has come to be increasingly viewed in terms of networks. The Default Mode Network (DMN) is a functional brain network that exhibits activity during the resting state (1, 2), while the Task Positive Network (TPN) exhibits increased activity in response to cognitive tasks, particularly those requiring attention (3, 4). There is growing evidence that the properties of these networks are correlated with intelligence.

The global efficiency of the DMN (5) and nodal efficiency in the TPN (6) have been found to correlate with intelligence. Segregation between the DMN and other resting-state networks is associated with higher intelligence both in older adults and in children (7, 8). The strength, stability and variability of connectivity spatial patterns in multiple networks including the DMN and dorsal attention network among others, predict cognitive performance (9). Intelligence may be reflected in structural characteristics as well. Cortical thinning and increased surface area of the DMN nodes were observed in mathematically gifted adolescents (10). We therefore hypothesized that cortical structure in the nodes of the DMN and TPN would reflect differences in intelligence in healthy adults.

The general intelligence (' g ') factor - a construct put forth by Spearman in 1904 - has been defined as the common intelligence that underlies cognitive abilities across multiple domains (11-13). It is calculated by factor analysis of a set of test scores spanning multiple cognitive domains (11-13). The quality of g depends on the diversity of the test scores used, but by definition, is robust to the specific combination of tests used (11, 14, 15) - a property known as the positive manifold of g . The neurophysiological substrates of g are believed to include nerve conduction velocity, genes, and brain size (16). IQ, on the other hand, is a summation of standardized scores, and may be understood as a combination of g plus specific cognitive abilities and skills (17).

Lack of reproducibility is a concern with much of experimental science, including neuroimaging (18–20). False-positive results may in part underlie the lack of clear consensus among imaging studies of intelligence. We took advantage of the positive manifold property of g in a novel analysis strategy to exclude false-positive results. We reasoned that a true neural correlate of the g factor would correlate with g estimates derived from different combinations of test scores due to its positive manifold property. Hence, in a cohort of healthy young adults, we derived multiple g estimates using different combinations of test scores from a test battery, and identified network nodes that showed structural correlation with a majority of these g estimates.

Methods

Participant recruitment

This study was approved by the Institutional Ethics Committee of the Institute of Stem Cell Science and Regenerative Medicine, and performed in accordance with relevant guidelines and regulations. All subjects were enrolled only after obtaining informed consent with an explanation of the nature of the study.

Healthy individuals between the ages of 22 and 35 years were recruited for cognitive assessment. Participants had to be fluent in English (the language of the test battery). As our test battery was developed and tested on advanced undergraduate and graduate students, we required participants to have at least three years of a college education. Intelligence is known to correlate with years of education although reverse causality does not appear to be a major factor. (21) The relatively homogenous education level of our subjects mitigated any influence of education on g. Those with any history of psychiatric or neurological disorders were excluded.

A subset of willing participants aged between 25 and 35 years of age, without contraindications to MRI, underwent scanning. Their handedness was assigned a rank based on the Edinburgh Handedness Inventory (<http://www.brainmapping.org/shared/Edinburgh.php>).

Behavioral Assessment

A battery consisting of tests of cognitive and behavioral function spanning multiple cognitive domains, was administered over two separate sessions to participants. Domains traditionally used for g factor or IQ estimation i.e. math/logic, language, executive function, and fluency, encompassing 9 tests (Table 1), were used to estimate the g factor for this study. We ensured by questioning, that participants were not sleep-deprived or fatigued prior to being tested.

Table 1
Tests used to assess subjects' cognitive abilities in this study

Domain	Function	Test	Short Description / Reference
Executive	Attention, Switching, Response inhibition	Modified Trail Making test	Modified version of the trail making test (22) using coloured circles with numbers. The task was to alternate between two colours while selecting numbers sequentially; numbered circles of a third colour served as a distractor.
	Attention, Mental speed	Symbol Digit Modalities test	Substitution for a set of symbols with the digits 1 to 9, using a conversion chart (23).
	Response Inhibition	Stroop test	Three-coloured English version of the classic Stroop test (24).
Language	Vocabulary	Word puzzles	Single word puzzles, anagrams and word analogies.
	Comprehension	Comprehension	Timed passage reading followed by questions to test comprehension.
Verbal Fluency	Phonemic fluency	F-A-S test	Freelisting as many words as possible starting with 'F', 'A', or 'S' in 1 minute. (25)
	Semantic fluency	Category fluency	Freelisting as many words as possible from the following categories - animals and birds - in 1 minute. (26, 27).
Math-Logic	Mathematics	Mathematical puzzles	Test of mathematical ability.
	Logic	Logical reasoning	Test of logical deduction.

MRI

MRI scans were acquired using a 20-channel RF head coil at a SIEMENS SKYRA 3 Tesla MR scanner located in HCG Hospital, Bangalore. High-resolution T1-weighted images (TE 3.9 ms, TR 8.3 ms, No. of slices 192, FOV 240*240, Slice thickness 1 mm) were obtained initially, followed by fMRI and diffusion tensor images (DTI). This report focuses exclusively on the structural (T1-weighted) images.

Analysis

Cognitive data - g factor estimation

We used the Cattell-Horn-Carroll model (28, 29) to calculate the g factor. The Math, Logic, Symbol Digit Modalities, Stroop, and Trail Making test scores were weighted by time to finish. The test scores were

then tested for normality using the Shapiro-Wilks test. Scores that had a non-normal distribution were log-transformed to approximate a normal distribution.

The g factor was calculated by performing factor analysis (without rotation) of a subset of the test scores. For each round of g factor estimation, we performed factor analysis on a combination of 4 test scores, one from each of the 4 cognitive domains. Using the 24 (3x2x2x2) such unique combinations of tests possible, 24 sets of g score estimates were obtained.

Voxel-based morphometry, Cortical thickness, and gyrification

FSL (<https://fsl.fmrib.ox.ac.uk>) was used to perform voxel-based morphometry (VBM) (30, 31). Images were pre-processed by brain extraction, segmentation, linear registration, normalization, and smoothing. These images were then correlated with each of the 24 sets of g scores using the general linear model (GLM), regressing out gender and handedness. Significance levels were set for this voxel-based comparison by permutation testing and cluster-wise thresholding with family-wise error rate correction for multiple comparisons ($p_{\text{corrected}} < 0.05$).

Cortical thickness (CT) and local gyrification index (LGI) were estimated using Freesurfer (<https://surfer.nmr.mgh.harvard.edu>). Each T1 image was reconstructed using standard pre-processing (brain co-registration, segmentation, surface extraction), and surface vertices were generated (32–35). Before the group level analysis, each surface was resampled and smoothed at 10 mm FWHM. A white matter surface was created at the white-gray matter interface, while two more surfaces were created over the gray matter: an outer surface that tightly enveloped the cortical surface visible from the outside, and the pial surface that followed the actual contours of the pia mater into the depths of sulci and over the gyri. CT at each vertex was measured as the shortest distance from the white matter to the pial surface. LGI quantifies the amount of cortex folded within the sulci as compared with the visible cortex on the outer surface *i.e.* the ratio between the pial surface and the outer surface (36).

We used a region of interest (ROI)-based approach to identifying the nodes of the DMN and TPN from the Destrieux Atlas (37). Each of the 24 sets of g scores derived was then used in GLM analyses, separately with CT and LGI (cluster-wise corrected for multiple comparisons, ($p_{\text{corrected}} < 0.05$). Gender and handedness were regressed out as nuisance covariates in all the group-level analyses.

For each ROI, we tabulated which g factors (out of 24) it showed a significant correlation with. We then accepted as significant those ROI's that correlated in > 50% *i.e.* at least 13 out of the 24 GLM analyses. ROIs that did not correlate with at least 50% of the g score estimates were rejected as possible false positives.

ROI's included for -

DMN : (1) Dorsal and (2) Ventral posterior cingulate gyri, (3) Precuneus, (4) Subparietal Sulcus, (5) Angular gyrus, (6) Straight gyrus, (7) Subcallosal gyrus, (8) Suborbital Sulcus, (9) Superior frontal gyrus, (10) Inferior, (11) Middle and (12) Planum polare of superior temporal gyri, (13) Superior temporal sulcus, (14) Temporal pole, (15) Collateral sulcus and (16) Lingual and medial occipito-temporal sulcus, and (17) Parahippocampal gyrus

TPN : (1) Supramarginal gyrus, (2) Superior and (3) Inferior frontal sulci, (4) Triangular inferior frontal gyrus, (5) Middle-anterior cingulate gyrus and sulcus, (6) Marginal cingulate sulcus, (7) Long insular gyrus and central sulcus of the insula, (8) Short insular gyri

Regression Model and Leave one out analysis

The CT and LGI values for ROIs that were significantly correlated in the group analysis were then regressed against the g score to create a multiple linear regression model.

Using the parameters of the optimized linear regression model, we performed a validation of the model using a leave-one-out (LOO) approach.

Results

We enrolled 98 subjects (22–35 years; 45 female; 71 with advanced (post-graduate) degrees; 88 right-handed) and assessed them using a cognitive test battery. Scores from 9 tests representing 4 cognitive domains - executive function, math/logic, language, and word generation fluency - were used to derive g scores by factor analysis. 24 sets of g scores were obtained using all possible test combinations covering the 4 domains. The 24 g scores were mutually highly correlated (Pearson's coefficient: median 0.86; range: 0.71–0.98), as predicted by the positive manifold phenomenon (Suppl. Figure 1).

Of the above cohort, 44 subjects (25–35 years; 16 female; 36 with post-graduate degrees; 36 right-handed) also underwent MRI scans. Voxel-based morphometry (VBM), cortical thickness (CT), and local gyrification index (LGI) maps of the brain were created and used in ROI-based general linear modeling (GLM) analyses with each of the 24 sets of g scores. Only those ROI's that correlated with > 12/24 g scores were considered true positives.

Cortical Thickness and g factor

The CT in three nodes of the DMN – Inferior temporal gyrus, Ventral posterior cingulate, and Parahippocampal gyrus in the right hemisphere significantly correlated with 24, 23, and 20 g scores respectively (Fig. 1A), with correlation values ranging from -0.52 to -0.25 (median -0.41, -0.34 and -0.38 respectively, Fig. 1B). Clusters in the left Inferior temporal gyrus and right Collateral and Lingual sulci correlated with < 12 g estimates and were rejected.

Local Gyrification Index and g factor

The LGI in five nodes of the DMN significantly correlated with > 12/24 g estimates (Fig. 2A). The right Ventral and Dorsal posterior cingulate gyri, right Middle temporal gyrus, right and left Collateral, and Lingual sulci correlated with 24, 20, 19, 18, and 16 g scores respectively, with correlation values ranging from 0.22 to 0.41 (median 0.34, 0.32, 0.32, 0.32 and 0.31; Fig. 2B). The left Ventral and Dorsal posterior cingulate gyri, right Parahippocampal gyrus, right Temporal pole, right Subparietal, and Inferior temporal sulci, and left Superior temporal sulcus did not cross the threshold of 12 g-estimates.

Some nodes of the TPN showed correlations, but with fewer than half the g score estimates. Similarly, the VBM analysis did not identify any nodes that crossed the 12 g score threshold.

Regression model and predictability of DMN nodes and g factor

Multiple linear regression of g scores with the CT/LGI of the brain regions identified in the previous step (3 regions for CT and 5 regions for LGI) identified the CT of right Parahippocampal gyrus and right Inferior temporal gyrus, and LGI of right Dorsal posterior cingulate gyrus and right Middle temporal gyrus as being significant parameters in the model of g. The regression model consisting of these 4 parameters could explain a median of 27% of the variance in g scores (Adjusted R^2 : 0.15–0.40).

We tested how well this regression model could predict the g factor using Leave-One-Out (LOO) analysis. We calculated predicted g scores, and these have been plotted against actual scores in Fig. 3 (Adjusted R^2 : 0.16).

(A): DMN ROIs where CT correlated with g: (T1) Right Inferior Temporal Gyrus, (T2) Right Parahippocampal Gyrus, and (T3) Right Ventral Posterior Cingulate Gyrus ($p < 0.05$).

(B): Median correlation plots of CT vs g scores. Pearson's r for T1 = -0.41, T2 = -0.38, T3 = -0.34

(A): DMN ROIs where LGI correlated with g: (G1) Right Collateral and Lingual Sulcus, (G2) Ventral and (G3) Dorsal Right Posterior Cingulate Gyrus, (G4) Right Middle Temporal Gyrus and (G5) Left Collateral and Lingual Sulcus ($p < 0.05$).

(B) Median correlation plots of LGI vs g scores. Pearson's r for: G1 = 0.32, G2 = 0.34, G3 = 0.32, G4 = 0.32, and G5 = 0.31.

Discussion

In a cohort of young adults, we show that cortical thickness and gyrification index in key nodes of the DMN are not only reliably correlated with intelligence, but also able to predict the general intelligence factor in individual subjects. Our linear regression model, combining CT and LGI of four nodes of the DMN, could explain 15–40% of the variance in *g*.

Viewed in light of previous evidence that DMN properties such as global efficiency, segregation from other networks, strength, stability, and variability of connectivity, are related to intelligence (5, 7–9), our results emphasize the pivotal role of the DMN in intelligence. The variance explained by our DMN-based model using CT and LGI is higher than the 11.5% previously reported in healthy adults using LGI alone (38). In line with previous findings in adolescents (10), we found that cortical thinning and greater gyrification correlated with higher intelligence in adults also.

We employed the positive manifold property of *g* to ensure our results were reliable. We derived multiple sets of *g* estimates and accepted only regions that showed correlation with more than half of these. Had we used a single *g* estimate as most studies do, we may have reported some of the regions that we rejected, as significant.

We found a correlation of cortical morphology with *g* primarily in the temporal and medial nodes of the DMN. A growing body of evidence points to the importance of medial and temporal areas such as the parahippocampus, precuneus, fusiform, Broca's and Wernicke's areas in intelligence (39–42). The posterior cingulate is a key functional hub of the DMN, especially in attention (43), and is thought to act as an integrator of information represented in the medial and lateral temporal lobes (44). The parahippocampal gyrus is also an important node that connects the DMN to the memory system of the medial temporal lobe (45). Functional interactions between the DMN and hippocampal – parahippocampal areas have been found to correlate with the speed of accurate responses (46).

Correlations with *g* have been previously reported for LGI in the cingulate cortex and medial temporo-occipital junction among other areas (38). A study that included both children and young adults found significant correlations of CT with *g* in left frontal and parietal areas, right frontal, lateral occipital, and precuneus (41). However, there is evidence that at least some of the CT-cognition correlation in age-heterogeneous samples may be attributable to the influence of age on either (47). It is not clear if statistical methods can completely abrogate this confounding effect. Therefore, we used a sample of young adults with a narrow age range to exclude such confounding. In line with what we found, VBM has previously shown no correlation with *g* (21).

Our study has some limitations. Our cohort was relatively small in size. Therefore we used a Leave-One-Out analysis to investigate the predictability of *g* using CT and LGI in the DMN. Validating this in an independent test cohort would be an important next step. Second, our reproducibility criterion of at least 50% of *g*-score estimates may have been too stringent: it is possible we rejected some true correlates of '*g*'. This was a tradeoff we made to ensure a high degree of confidence in the results obtained.

In conclusion, we show for the first time that cortical structure in key medial and temporal nodes of the DMN is reliably associated with intelligence, and can predict the general intelligence factor in individual subjects. The DMN appears to play a pivotal role in intelligence.

Declarations

Acknowledgment

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Data and Code Availability Statement:

The data of this study are expected to form the basis for a few other publications. Once these have been published, the data will be made available to individual researchers on request, subject to the approval of the Institutional Ethics Committee that approved the initial study. [\[1\]](#)

Declaration of Interest

No competing interest.

Remove unless required by the journal

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Figures

B

Figure 1

(A): DMN ROIs where CT correlated with g: (T1) Right Inferior Temporal Gyrus, (T2) Right Parahippocampal Gyrus, and (T3) Right Ventral Posterior Cingulate Gyrus ($p < 0.05$).

(B): Median correlation plots of CT vs g scores. Pearson's r for T1 = -0.41, T2 = -0.38, T3 = -0.34

A

B

Figure 2

(A): DMN ROIs where LGI correlated with g : (G1) Right Collateral and Lingual Sulcus, (G2) Ventral and (G3) Dorsal Right Posterior Cingulate Gyrus, (G4) Right Middle Temporal Gyrus and (G5) Left Collateral and Lingual Sulcus ($p < 0.05$).

Figure 3

Results of Leave-One-Out analysis to predict the g factor using a linear model based on CT of right Parahippocampal and Inferior temporal gyri and LGI of right Dorsal posterior cingulate and Middle temporal gyri (Adj. $R^2 = 0.16$)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [DMNnodalstructureandgSupp.pdf](#)