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Individual differences in general intelligence correlate with brain function during nonreasoning tasks

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Abstract

Brain imaging can help identify the functional neuroanatomy of general intelligence (i.e., "*g*") and indicate how brain areas salient to *g* relate to information processing. An important question is whether individual differences in *g* among subjects are related to brain function even when nonreasoning tasks are studied. If so, this would imply that individuals with high *g* scores may process information differently even when no reasoning or problem solving is required. To further investigate this, we administered the Raven's Advanced Progressive Matrices (RAPM) test, a strong correlate of *g*, to 22 normal subjects and then measured cerebral glucose metabolic activity with PET while the subjects viewed videos on two occasions, tasks with no inherent reasoning or problem solving. Individual RAPM scores were correlated with regional brain activity using statistical parametric mapping (SPM99) conjunction analysis to combine both video conditions. Results showed greater activation in specific posterior brain areas (left BA37/19) in high RAPM scorers (P=.02, corrected for multiple comparisons). Subsequent analyses revealed a high/low RAPM group difference in functional connectivity between left BA37/19 activity and the left anterior cingulate/medial frontal gyrus. These data provide evidence that individual differences in intelligence correlate to brain function even when the brain is engaged in nonreasoning tasks and suggest that high and low *g* subjects may preferentially activate different neural circuits, especially nonfrontal areas involved in information processing.

Keywords: General intelligence; Nonreasoning task; Individual differences

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1. Introduction

Brain imaging studies using PET, fMRI, and EEG-evoked potentials are helping establish the functional neuroanatomy of general intelligence, typically defined as the "*g*" factor determined psychometrically by factor analysis of multiple tests of cognitive abilities (Spearman, 1904). Since the neural basis of *g* may well involve the integration of complex cognitive processes, one primary question is whether the neuroanatomy of intelligence is generally distributed across multiple brain areas or relatively localized in a small number of areas. So far, the data are mixed. Imaging studies that compare high versus low *g*-loaded tasks generally show a common finding of increased activation in parts of the frontal lobes during a variety of high *g* tasks (Deary et al., 2001; Duncan et al., 2000; Esposito, Kirkby, Van Horn, Ellmore & Berman, 1999; Kroger et al., 2002; Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997; Risberg & Ingvar, 1973). Other studies, however, have examined differences in *g* among subjects as they relate to brain function during the performance of tests with high *g*-loadings. These studies commonly show *inverse* correlations between some frontal lobe activity and task performance (Ghatan et al., 1995; Haier, 1993; Haier, Siegel, MacLachlan, et al., 1992; Haier et al., 1988; Haier, Siegel, Tang, Abel, & Buchsbaum, 1992; Lamm, Bauer, Vitouch, & Gstattner, 1999; Neubauer, Freudenthaler, & Pfurtsceller, 1995; Neubauer, Fink, & Schrausser, 2002; Parks et al., 1988; Reichle, Carpenter, & Just, 2000; Seidman et al., 1998; Van Rooy, Stough, Pipingas, Hocking, & Silberstein, 2001) or correlations with task performance in areas other than frontal lobes (Haier & Benbow, 1995; Larson, Haier, Lacasse, & Hazen, 1995) or an increase in cortical activity in low *g* groups (Haier et al., 1995). Typically, all neuroimaging studies of either complex task performance or of comparisons between high and low *g* groups show the involvement of multiple areas, consistent with the view that higher-order cognition involves circuits throughout the brain rather than only those localized in the frontal lobes (Carpenter, Just, & Reichle, 2000), although a case can be made for primary frontal lobe involvement (Duncan et al., 2000).

One possible approach to help clarify salient brain areas involved in *g* is to examine how individual differences in *g* among subjects correlate with brain function during the performance of nonreasoning tasks without high *g*-loadings. Boivin et al. (1992), for example, did PET with 33 subjects at "rest" (i.e., no specific *g* task) and found inverse correlations between frontal lobe activity and scores on the RAPM and the WAIS, consistent with earlier studies using high *g* tasks (Haier et al., 1988; Haier, Siegel, Tang, et al., 1992; Parks et al., 1988). They also reported other inverse and positive correlations between subject *g* differences and brain activity throughout the cortex. The findings of Boivin et al. suggest that *g* differences among subjects are related to brain function even without performing a reasoning or problem-solving task. However, the relatively uncontrolled nature of the "resting" condition for the 32 min required for the 18F-flurodeoxyglucose (FDG) technique and older anatomical localization procedures limits this interpretation.

To further test whether individual differences among subjects in *g* correlate to brain function during nonreasoning tasks, we examined whether differences in *g* among normal subjects interacted with brain function during processing of a task with no explicit reasoning or problem-solving component.

2. Methods

2.1. Subjects

Twenty-two healthy, right-handed male and female adult volunteers were recruited through campus advertisements and were paid for their participation. Their average age was 22.1 years (S.D. = 2.6). Exclusionary criteria included any major medical or psychiatric disorder, substance abuse, or history of a head injury. All gave informed consent in accord with the University of California Irvine Institutional Review Board. These subjects were part of a broader study of emotionally influenced memory processing (Cahill et al., 1996, 2001).

2.2. Materials

Raven's Advanced Progressive Matrices (RAPM; Raven, 1962) is a standard, test of abstract reasoning ability. Each of 36 items shows a group of eight symbols arranged in a 3×3 matrix on a page according to a logical progressive pattern; the ninth symbol is always missing from the lower right-hand position in the matrix. Once the logical progression or rule of the pattern is inferred, the one correct symbol to complete the matrix can be selected from eight multiple choices presented at the bottom of the page. Psychometric studies typically show this test has the highest loading on the *g* factor of intelligence (Alderton & Larson, 1990; Bors & Stokes, 1998; Marshalek, Lohman, & Snow, 1983; Snow, Kyllonen, & Marshalek, 1984). There is some disagreement as to whether performance on the test is determined by a single set of basic cognitive processes (Carpenter, Just, & Shell, 1990) or by two strategies: analytic based on propositional representations and mental imagery based on visual representation (Hunt, 1974). Deshon, Chan, and Weissbein (1995) characterized subsets of the 36 test items as largely solved by either visual–spatial or verbal–analytic processes. They concluded that the RAPM is an excellent measure of *g* because it samples from both the verbal–analytic and the visual–spatial domains that underlie performance on many cognitive tasks.

Each subject completed the 12 practice items on the RAPM (Set I) before completing the 36-item test (Set II) with a 40-min time limit on a different day than the PET scans. For the total score (all 36 items), the group mean was 24.6 (S.D. = 3.5).

The non-*g*-loaded task consisted of viewing two different 32-min video tapes (including an audio narrative) during the PET procedure. The tapes were created to contain 12 vignettes of either somewhat negative emotionality, or neutral emotionality, as described previously (Cahill et al., 1996). For the broader study of emotional memory, each subject came for two PET scans on different days. The emotional video was viewed on one day and the control video with neutral emotional content on the other (randomized and counter balanced order). Each subject watched both tapes; sessions occurred 3–5 days apart. For each tape, subjects performed no assigned mental tasks, other than just watching the video. There is no explicit reasoning or problem solving in the task but some subjects may "watch" with some additional level of cognition which, to the extent this is related to *g*, should be reflected in the results.

2.3. Procedure

A standard PET scan procedure was followed (Haier, Siegel, MacLachlan, et al., 1992). Each subject sat on a comfortable chair in a darkened, sound-attenuated room and watched the video, which began about 30 s before the subject was injected with 5 mc of FDG, a glucose analog tracer. Subjects then watched the video passively (i.e., there was no task other than to watch the video) for the 32 min while 80–90% of the FDG was taken up by the brain (Phelps et al., 1979). Following the uptake period, the injected FDG remains metabolically fixed for several hours, with the highest concentrations occurring in the brain areas that were most metabolically active during the 32 min of watching the video. Scanning was done after the 32-min uptake using a GE2048 head-dedicated scanner (full-width half-maximum resolution about 4.5 mm in-plane). Transmission scans for each subject were used for attenuation correction. Thirty overlapping axial slices parallel to the canthomeatal (CM) line were obtained at 6-mm intervals (15 slices simultaneously). Each subject wore an individually molded thermoplastic mask to locate the CM line and hold the head still during the scan acquisition. Glucose metabolic rate (GMR) was calculated following Sokoloff et al. (1977) in milligrams of glucose per 100 g of brain tissue per minute.

Image processing and statistical analysis of the scan data were performed using SPM99 (Friston et al., 1995) ⟨www.fil.ion.ucl.ac.uk/spm⟩. PET images were spatially normalized into standard stereotactic space that conforms to the Talairach and Tournoux's (1988) atlas. To account for slight misalignments of homologous anatomical regions among subjects, the transformed images were spatially smoothed with a 12-mm isotropic Gaussian filter. Global metabolic rates (defined as the mean of all intracranial voxels) were proportionally scaled to a mean value of 50. In the first level of analysis, correlations (positive and negative) were computed between RAPM scores and GMR values for each voxel throughout the brain. The SPM conjunction analysis (Price & Friston, 1997) identified all voxels where there was a significant correlation between GMR and RAPM scores in *both* the emotional and the neutral conditions ($N = 44$ scans). Results are based on relationships between GMR and RAPM scores common to *both* scanning conditions, a more stringent criterion for significance that can be regarded as a kind of replication that also minimizes any effects of video content. Consistent with other studies, inferences were made at a statistical level of $P < .05$ corrected for multiple comparisons. Additional exploratory inferences were made at the $P < .001$, uncorrected for multiple comparisons in order to aid hypothesis generation.

In the second level of analysis, we investigated how functional activity differed in the brains of the subjects in relation to the identified findings above and the subject's scores on the RAPM. This was accomplished by testing for significant factor (RAPM scores, "high" vs. "low") by covariate (cluster GMR values) interactions using the same conjunction approach as in the first analysis. The factor was defined using a median split of the RAPM scores ("high": range 27–33, mean 29.2, S.D. 1.9; these scores are in the high average range for young adults; "low": range 19–26, mean 23.6, S.D. 2.1; these subjects are in the average range; Bors & Stokes, 1998). Both groups had equal proportions of males and females. The

covariates were the first eigenvectors of all the within-cluster voxels for each significant cluster identified in the first analysis using $P < .05$ (corrected). The number of separate secondary interaction analyses to perform depended on the number of clusters found with the first level of analysis.

For all findings, specific cortical brain areas are identified using Brodmann (BA) notation and Montreal Neurological Institute (MNI) coordinates for comparisons to other studies; naming of areas is based on the Talairach and Tournoux's (1988) atlas and should be considered as best approximations, especially for smaller cluster sizes. Because PET measures the entire brain simultaneously, areas of significance are often found which are not predicted a priori. Since we did not hypothesize specific brain areas, which may be related to the RAPM under the conditions tested, this work should be regarded as hypothesis generating.

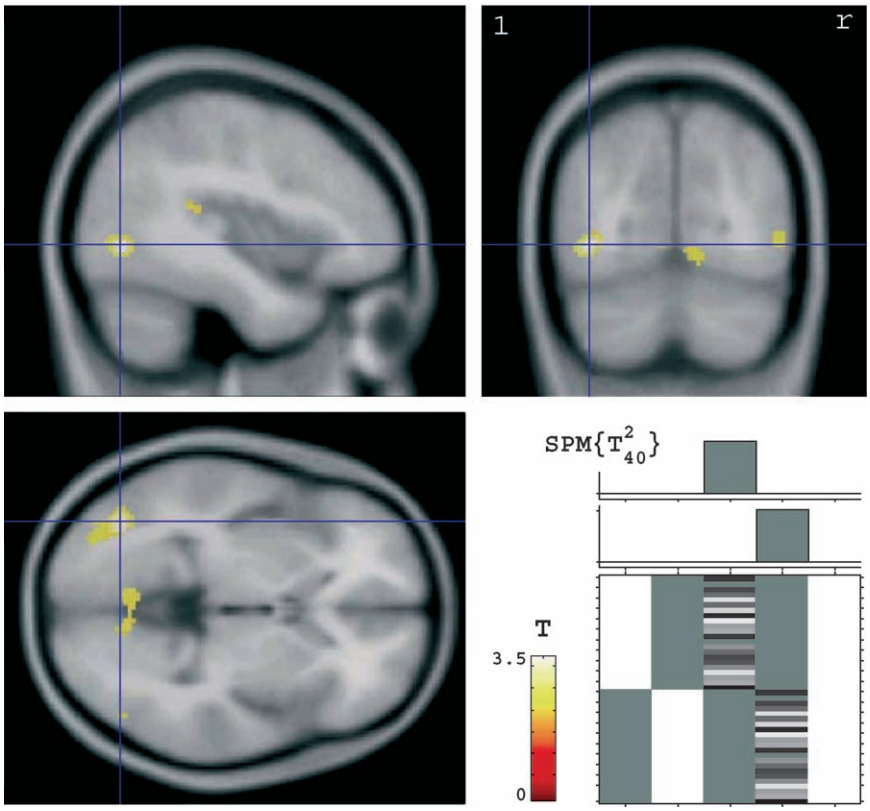

Fig. 1. The locations are shown of significant positive correlations between RAPM scores and GMR in 22 subjects watching videos with no reasoning component. Based on an SPM99 conjunction analysis of both video conditions ($N = 44$ scans), one area, BA 37/19, emerges at $P = .021$ corrected for multiple comparisons (cross hairs). This and some other areas significant at $P < .001$, uncorrected, are shown on the SPM slice templates; the SPM design matrix is shown in the lower right panel (see Table 1 for names and coordinates of each location).

3. Results

The primary analysis correlated RAPM scores to normalized GMR throughout the brains across all 22 subjects and 44 scans obtained. Using a stringent statistical correction for multiple comparisons in SPM99, RAPM scores correlated to activity only in Brodmann's Area (BA) 37/19 in the left hemisphere (MNI coordinates −40, −72, −2; cluster size 196, $T=3.20$; $P=.021$). This finding is based on the conjunction of both the emotional and the neutral conditions. For the emotional condition, the RAPM score and GMR in BA 37/19 were correlated $r=.71$ and $r=.70$ for the neutral condition. This conjunction finding is shown in Fig. 1

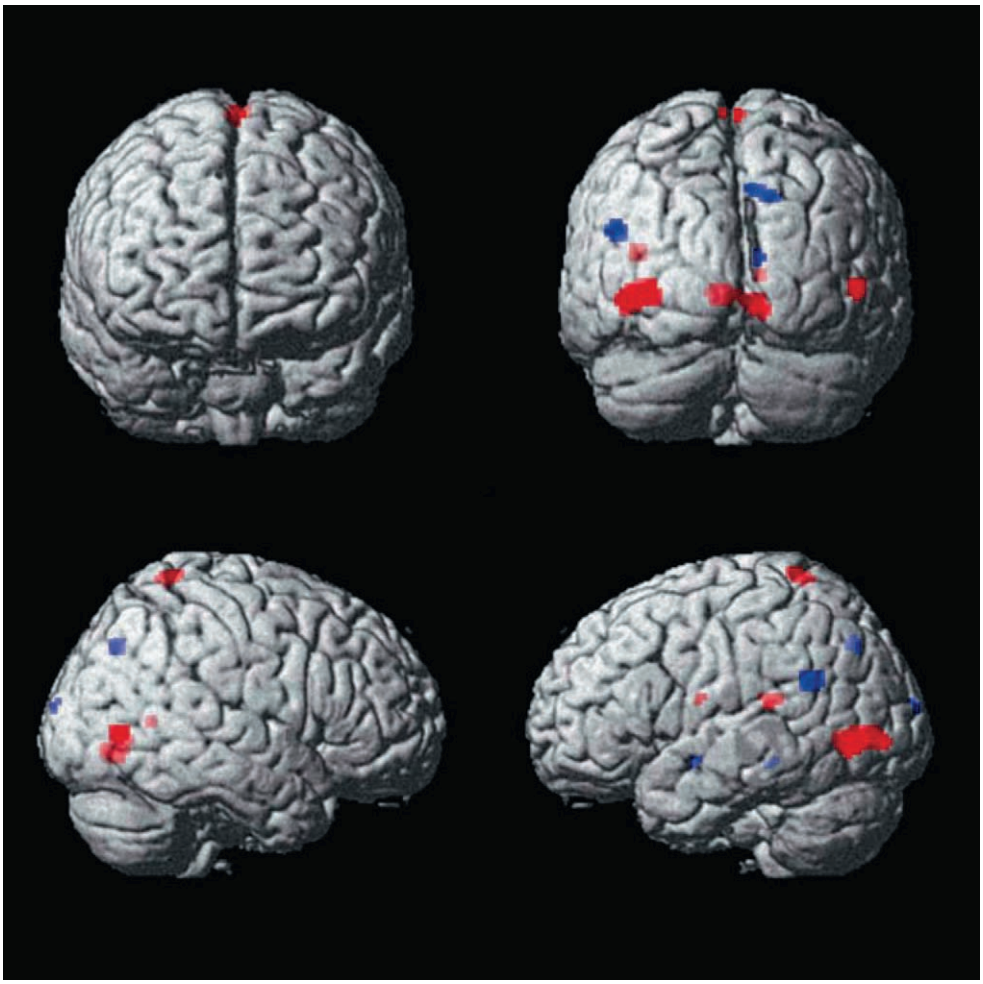

Fig. 2. The same data from Fig. 1 and Table 1 are shown on standard SPM MRI renderings for all correlations ($P<.001$, uncorrected). Red areas show positive correlations between GMR and RAPM scores; blue areas show negative correlations. The upper left view looks directly at the frontal lobes; the upper right view is directly at the occipital lobes; lower left view is the right hemisphere view; lower right is the left hemisphere view.

Table 1
Locations of significant correlations between RAPM scores and regional GMR

Brain location	*x*	*y*	*z*	Cluster size	*T* score
Positive correlations					
Left BA 37/19**	−40	−72	−2	196	3.20
Left superior temporal gyrus***	−38	−38	16	19	2.28
Right/left BA 18***	12	−72	−6	130	2.26
Right BA 37/19***	50	−70	2	30	2.23
Left/right BA 7***	−2	−48	74	40	2.20
Left insula***	−38	−6	18	3	2.02
Right BA 18***	12	−56	6	7	1.98
Negative correlations					
Left supramarginal gyrus/BA 39***	−46	−54	26	49	2.15
Right precuneus/BA 7***	8	−72	42	30	2.04
Right cuneus/BA 18***	10	−100	14	4	2.02
Left parahippocampus/amygdala***	−30	−4	−10	4	2.01
Left parahippocampus/BA 30***	−14	−38	−10	3	2.00

BA is Brodmann's area, RAPM is Raven's Advanced Progressive Matrices test. Atlas coordinates (*x*, *y*, *z*) of the most significant voxel within a cluster are in MNI space; negative *x* values are in the left hemisphere. Areas are ranked by significance.

** P=.021, corrected for multiple comparisons.

*** P<.001, uncorrected.

(see cross hairs) which includes other areas visible in the view of BA 37/19 resulting from the same analysis without the correction for multiple comparisons (P<.001). Fig. 2 shows another view of all the areas correlated positively or negatively with RAPM scores (P<.001, uncorrected). Other areas where activity is positively correlated to RAPM scores, uncorrected at P<.001, include the left superior temporal gyrus, left BA 7, left insula, right BA 18, and right BA 37/19. Negative correlations include the left supramarginal gyrus/BA 39 (Wernicke's area), right precuneus/BA 7, right cuneus/BA 18, and left areas of the parahippocampus/amygdala. The atlas coordinates and names for the areas shown in Figs. 1 and 2 are in Table 1. Note all these correlations with the RAPM are in posterior brain areas.

Table 2
Brain areas showing a significant difference in functional connectivity of the left BA 37/19 between high and low RAPM groups

Brain area	*x*	*y*	*z*	Cluster size	*T* score
Left anterior cingulate/medial frontal**	−12	46	8	77	2.70
Left BA 17**	−14	−102	−14	38	2.35
Left fusiform gyrus/BA 20**	−36	−28	−28	31	2.27
Right BA 31**	12	−42	44	3	2.00
Left superior temporal gyrus/BA 22**	−64	−6	8	1	1.95
Right parahippocampus/BA 35**	30	−26	−22	1	1.92

BA is Brodmann's area. Atlas coordinates (*x*, *y*, *z*) of the most significant voxel within a cluster are in MNI space; negative *x* values are in the left hemisphere.

** P<.001, uncorrected.

The results of the exploratory interaction conjunction analyses associated with the functional connectivity of the left area 37/19 cluster are shown in Table 2 and Fig. 3. This analysis indicates where in the brain a significant difference in functional connectivity of BA 37/19 exists between the high and low RAPM scorers for both video conditions. There are six areas where there is a correlation with the left BA 37/19 cluster that is significantly different between the high versus the low RAPM scorers ($P < .001$, uncorrected). In each of these areas, the slope of the regression was more positive in the high RAPM group compared to the low group. Table 2 shows the atlas coordinates and names of the six clusters. The strongest correlation difference with the left BA 37/19 is in the left anterior cingulate/medial frontal gyrus, a part of the prefrontal association cortex. The other areas are the left BA 17, left fusiform/BA 20, left superior temporal gyrus/BA 22, and right BA 31 and right BA 35/ parahippocampus.

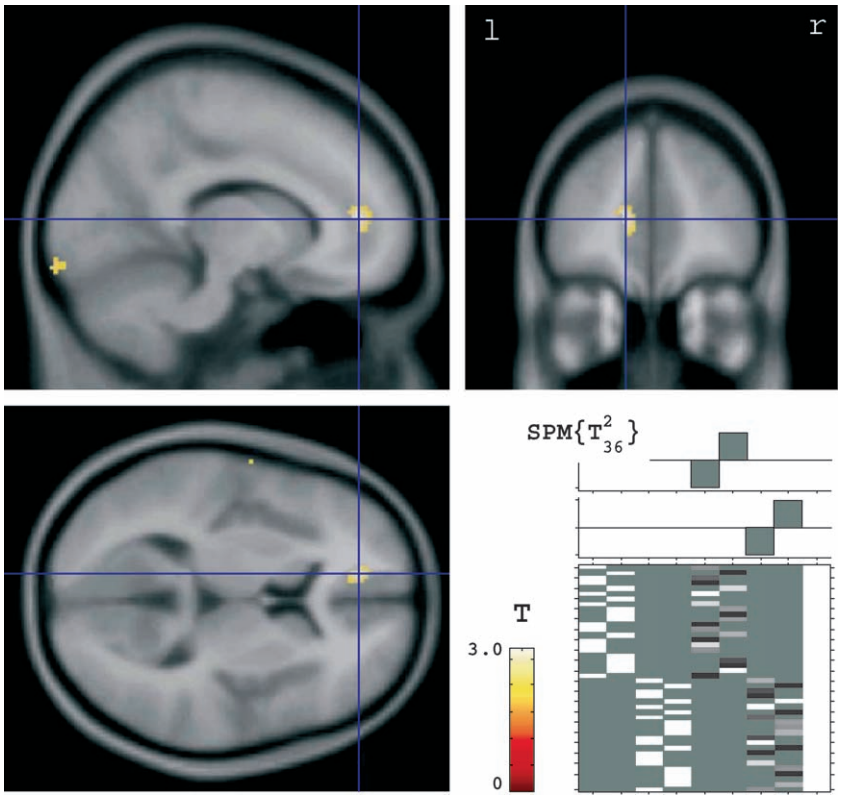

Fig. 3. The location is shown of anterior cingulate/medial frontal gyrus where there was the most significant difference ($P < .001$, uncorrected) between high and low RAPM groups (defined by median split) for correlations between GMR activity in the left BA 37/19 and other brain areas while subjects watched videos. These interaction analyses are based on the SPM99 conjunction analysis, which combines scans in both video conditions. The SPM99 design matrix is shown in lower right (see Table 2 for names and atlas coordinates of each cluster).

4. Discussion

This investigation into the neuroanatomy of what underlies individual differences in general intelligence took the approach of correlating brain function during nonreasoning tasks to differences in *g* among subjects assessed psychometrically. The most statistically robust primary finding showed only one brain region where performance on the RAPM for the 22 subjects was directly related to regional brain activity in both conditions of the study. This was the left BA 37/19 association area. Less robust positive and negative correlations ($P < .001$, uncorrected) were found with the RAPM in other posterior brain areas; none were found in frontal lobes. The exploratory interaction analyses suggested that differences in subject intelligence appear to influence how the BA 37/19 region interacts with other brain circuits and systems. The strongest finding was a correlation between the left BA 37/19 and the left anterior cingulate/medial frontal gyrus in the prefrontal cortex in subjects with higher RAPM scores compared with those subjects with lower RAPM scores. These are the main findings for discussion.

4.1. Primary correlation findings

4.1.1. RAPM correlation with BA 37/19

The left BA 37/19 is a temporal/occipital lobe association area which is especially involved with object recognition (Stewart, Meyer, Frith, & Rothwell, 2001), object memory (Smith et al., 1995), and language integration (Buchel, Price, & Friston, 1998). The integrative function of BA 37/19 appears to be that of object identification and translation into language format, processes undoubtedly engaged while watching a video. Stewart et al. (2001) showed that transcranial magnetic stimulation over the left BA 37 region blocked the ability of normal subjects to name simple objects. This finding implicates this region in generating some component of an internal language-based understanding of the external world. A connection between this specific BA and general intelligence has not been reported, but several earlier PET studies using pre-SPM segmentation methods of anatomical localization found that activity in this general region of temporal/occipital lobe was related to measures of *g* (Boivin et al., 1992; Haier, Siegel, MacLachlan, et al., 1992; Haier et al., 1988; Haier, Siegel, Tang, et al., 1992; Parks et al., 1988; Risberg & Ingvar, 1973). Moreover, GMR in parts of BA 37 bilaterally showed an inverse correlation to age in subjects performing the RPM (a simpler form of the RAPM) (Esposito et al., 1999).

There is some suggestion of an asymmetry in the importance of left and right BA 37/19 as related to *g*. We found that BA 37/19 in the right hemisphere was less robustly correlated with the RAPM scores ($P < .001$, uncorrected). Thompson et al. (2001) recently reported that gray matter in the left BA 37 is more heritable than in the right (their Fig. 3), a finding that is perhaps consistent with the inheritable nature of *g*. Also, deactivation with transcranial magnetic stimulation of the left but not the right BA 37 inhibits object naming (Stewart et al., 2001) and Smith et al. (2001) reported left but not right differences in BA 37/19 between good and poor performers on a task-switching test.

A number of speculations for why this posterior association area might emerge from this correlation analysis could be offered for hypothesis generation. Perhaps BA 37/19 mediates intelligence by serving as a brain site in which higher-order language-based concepts converge with the incoming visual information stream to which the relevant logical language-based concept is to be applied. Alternatively, perhaps the more intelligent subjects are more actively involved with identifying objects within the videotape and translating them into words. Or, perhaps the more intelligent subjects are more actively integrating the visual components of the videotape with the audio components of the tape. Attention processes also could be at work here in that the more intelligent subjects are simply more capable of paying better attention to the videotape and thus somehow comprehend it in more detail (Posner, 1994; Posner & Gilbert, 1999; Sarter, Givens, & Bruno, 2001). Gevins and Smith (2000) reported that in 80 normal subjects, high *g* was correlated with better focus and sustained attention as assessed by EEG. They also reported that low *g* subjects used cognitive strategies more reliant on frontal lobe areas. Kanwisher and Wojciulik (2000) have reviewed several mechanisms of how attention can affect neural responses.

Kastner and Ungerleider (2000) have argued that a typical visual scene contains many objects that compete for neural representation since there is limited processing capacity in the visual system. This competition is resolved within the visual cortex, especially in the ventral stream (including BA 37/19) with input from frontal and parietal areas. Individual differences in the ability to resolve competition among incoming visual stimuli may be a component of *g*. Our exploratory analyses ($P < .001$, uncorrected; Table 1) also identified RAPM correlations with BA 18, the secondary visual cortex, and BA 7, the posterior parietal association area and part of the "where" circuit of visual processing (Ungerleider & Haxby, 1994).

Of the remaining exploratory correlations with the RAPM shown in Table 1, the strongest negative correlation is with the left supramarginal gyrus/BA 39, Wernicke's area, a region involved with language comprehension. The other areas of negative correlations with the RAPM are related mostly to visual processing.

4.2. Exploratory interaction correlation findings

The difference in correlation between the left BA 37/19 and the left anterior cingulate/medial frontal gyrus suggests that high and low RAPM groups differ in how they integrate the visual processing of video viewings with frontal circuits possibly involved with attention and working memory (Posner, 1994). The other differential correlations with the left BA 37/19 between high and low RAPM groups (Table 2) all involved areas related to sensory processing, again suggesting that the high RAPM subjects integrated processing differently at these early stages than the low RAPM group.

4.3. Study limitations

The time resolution of 32 min inherent with FDG PET allows only cumulative effects to be identified. Any effects that last for only a short or intermittent time will not be seen with FDG PET. Only effects sustained for a large portion of the 32 min will be identified. FDG also

limits the usefulness of a "rest" condition for comparison since resting for 32 min is a quite uncontrolled condition compared to a resting state of 40 s in typical blood flow PET studies.

4.4. In summary

As researchers move from purely psychometric approaches to *g*, it is now widely understood that, "The highest priority in *g* research. . . is to discover how certain anatomical structures and physiological processes of the brain cause individual differences" (Jensen, 1998, p. 579). Our study demonstrates that the left BA 37/19 association area, along with other posterior areas of the temporal and occipital cortex, is associated with individual differences in *g* during processing of nonreasoning task conditions. This suggests that the *g* factor may play a more significant physiologic role in mediating early information processing than has been appreciated.

Our findings provide some evidence that more intelligent subjects may process information using different neural circuits than other subjects. Our findings also support the view that the neural basis of *g* differences among subjects may be more distributed among specific systems throughout the brain rather than localized within the frontal lobe. Functional imaging technology provides the means to test specific hypotheses about how brain areas interact with each other (like measures of coherence) during various *g*-loaded cognitive tasks and how high and low *g* individuals differ in such interactions. At minimum, our findings reinforce the view that future functional brain imaging studies consider that inherent individual variations in subject intelligence can influence regional imaging results during any kind of cognition and should be more actively taken into account.

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