Neural correlates of superior intelligence: Stronger recruitment of posterior parietal cortex

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General intelligence (g) is a common factor in diverse cognitive abilities and a major influence on life outcomes. Neuroimaging studies in adults suggest that the lateral prefrontal and parietal cortices play a crucial role in related cognitive activities including fluid reasoning, the control of attention, and working memory. Here, we investigated the neural bases for intellectual giftedness (superior-g) in adolescents, using fMRI. The participants consisted of a superior-g group ($n = 18$, mean RAPM = 33.9 ± 0.8, >99%) from the national academy for gifted adolescents and the control group ($n = 18$, mean RAPM = 22.8 ± 1.6, 60%) from local high schools in Korea (mean age = 16.5 ± 0.8). fMRI data were acquired while they performed two reasoning tasks with high and low g-loadings. In both groups, the high g-loaded tasks specifically increased regional activity in the bilateral fronto-parietal network including the lateral prefrontal, anterior cingulate, and posterior parietal cortices. However, the regional activations of the superior-g group were significantly stronger than those of the control group, especially in the posterior parietal cortex. Moreover, regression analysis revealed that activity of the superior and intraparietal cortices (BA 7/40) strongly covaried with individual differences in g ($r = 0.71$ to 0.81). A correlated vectors analysis implicated bilateral posterior parietal areas in g. These results suggest that superior-g may not be due to the recruitment of additional brain regions but to the functional facilitation of the fronto-parietal network particularly driven by the posterior parietal activation.
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Introduction

General intelligence, or psychometric g, refers to a single factor (specifically, the first principal component) that influences performance in diverse forms of cognitive abilities, especially reasoning and novel problem solving (Gustafsson, 1984; Johnson et al., 2004). It was originally proposed by Spearman (1904) on the basis of factor analysis and has been firmly established as a good predictor of academic and job relevant performance (Jensen, 1991; Schmidt and Hunter, 1998). Over several decades, psychometric research on g has largely focused on the assessment of individual differences (Neisser et al., 1996) and has converged on the conclusion that Raven's Advanced Progressive Matrices (RAPM) measures cognitive ability that is central to g (Marshalek et al., 1983; Snow, 1989). The RAPM, designed as a nonverbal measure of Spearman's g, is broadly accepted as an essential test of fluid reasoning (Alderton and Larson, 1990; Anastasi, 1988; Bors and Strokes, 1998). For these reasons, the reasoning ability is thought to be responsible for individual performance in a broad variety of cognitive and learning tasks (Cattell, 1963; Neisser et al., 1996).

Recently, functional neuroimaging studies have tried to reveal the neural basis of general intelligence using g-relevant cognitive tasks such as reasoning or working memory tasks (Gray and Thompson, 2004). Both functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) experiments provide evidence that lateral prefrontal and posterior parietal cortices are involved in fluid reasoning (Haier et al., 1988; Houdé and Tzourio-Mazoyer, 2003; Kroger et al., 2002; Prabhakaran et al., 1997) and working memory (Cabeza and Nyberg, 2000; Cohen et al., 1997; Smith and Jonides, 1998), especially when interpreted in light of studies of patients with brain damage to these areas (Duncan et al., 1995, 1996; Gray and Thompson, 2004). The activation level of these cortical areas exhibited moderate correlation with task difficulty (Braver et al., 1996; Klingberg et

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al., 1997) and individual differences in *g* (Gray et al., 2003; Haier et al., 2003). In parallel, both structural data from anatomical MRI and biochemical data from MR spectroscopy further confirmed the positive relationship between the brain areas and the intelligence (Haier et al., 2004; Jung et al., 1999). These observations suggest that the *g* factor depends on a broad bilateral fronto-parietal network.

Although imaging and patient studies have considerably extended our understanding of the neurobiology of intelligence, it is still unclear which nodes in the fronto-parietal network play a crucial role in individual differences. This obscurity may be attributable to the dearth of neurobiological data on individual differences in *g*. In addition, the previous studies were performed on a population with a relatively normal range of intelligence (Gray et al., 2003; Haier et al., 2003) or patients with cortical damages who have some deficits in cognitive function (Duncan et al., 1995, 1996; Waltz et al., 1999). To clarify the functional anatomy of *g*, people with extremely good performance on *g*-relevant tasks should be explored. Such an effort could provide important insights into the neural mechanism of human intelligence. Furthermore, understanding the neural basis of superior-*g* may be helpful in devising interventions to improve cognitive ability and performance.

The goal of the current study is to address the nature of the neurobiological basis underpinning superior intelligence. From the perspective of resource theories, more accurate and rapid performance requires additional resources in the brain (Bunge et al., 2000). Additional resources could be achieved from newly recruited brain areas for superior intelligence or from enhanced activation of common brain areas such as the fronto-parietal network. Still, the origin of the additional resource is not, as yet, clear.

Here, we showed that the neural substrates for fluid reasoning resulted in a widely distributed fronto-parietal network and that the superiority in general intelligence was driven not by the engagement of an additional cortical activation but by the increased activation of the posterior parietal cortex, including the superior parietal lobule (SPL) and intraparietal sulcus (IPS).

Methods

Subjects

Half of the participants were students of the national academy for gifted adolescents (Busan, Korea) who had been selected as the gifted students through the three-step screening process: they should (1) be awarded the first or second prize in the nationwide Olympiad for science and mathematics, (2) be recommended by their school principal and teacher in charge, and (3) pass the entrance test assessing novel problem solving ability. As a joint research and education program with the academy, we recruited 25 volunteers among the gifted students (for superior-*g*). Additionally, equal number of the matched control subjects was volunteered from local regular high schools (for average-*g*).

The RAPM and the Wechsler Adult Intelligence Scale-Revised (WAIS-R) were administered to all participants (*n* = 50) for assessing their *g*-level and diverse cognitive ability. Ten volunteers were excluded from the fMRI experiment because their physical and psychometric backgrounds were not suitable for the experimental design. Four participants moved their heads excessively

during the scanning and so were excluded from the data analysis. The remaining 36 right-handed male students (aged 16.5 ± 0.8, *M* ± SD) were divided into two groups (*n* = 18 each) on the basis of their RAPM scores (superior-*g* group: ≥33; average-*g* group: <33), (cf. Haier and Benbow, 1995; Larson et al., 1995). The superior-*g* group scored 33.9 ± 0.8 (*M* ± SD) on the RAPM test, while the average-*g* group scored 22.8 ± 6.6. All participants gave their written informed consent with the agreement of their parents. This study was approved by the Ethics Committees of the Catholic University of Korea and the Korea Institute of Brain Science.

Psychometric tests

All participants underwent both the RAPM Set II and the WAIS-R (Korean version). The RAPM, a standard test for general fluid intelligence, is one of the purest measures of psychometric *g* (Raven et al., 1988). It contains 36 nonverbal items requiring fluid reasoning ability. Each item consists of a 3 × 3 matrix with a missing piece to be completed by selecting the best of 8 alternatives. The RAPM score (number correct in 40 min) was used as an index of individual *g*-level. The WAIS-R is the standard intelligence quotient (IQ) test which consists of 11 subtests with different *g*-loadings (Marshalek et al., 1983; Wechsler, 1981). For entry into the fMRI study, we selected the participants who had a WAIS-R full scale score of 85 or greater to eliminate potential participants who might display excessively poor performance on the experimental tasks because it is difficult to readily distinguish performance deficits that are related to the ability from those that arise from a lack of effort or compliance with task demands.

fMRI tasks

We developed the two behavioral tasks for the fMRI experiment (the simple *g*-task and the complex *g*-task) to differ in *g*-loading and difficulty without any significant differences in surface contents. The simple *g*-tasks were designed to have minimal *g*-loading by following the rule "Constant in a Row," while the complex *g*-tasks were designed to have high *g*-loading by following complicated rules such as "Quantitative Pair-wise Progression," "Figural Addition or Subtraction," and "Distribution of Three Values" (Carpenter et al., 1990). A scanning session consisted of four simple *g*-task blocks and three complex *g*-task blocks, which were alternated every 30 s. Four task items (7.5 s each) were presented in a simple *g*-task block, and one task item (30 s) was presented in a complex *g*-task block. Subjects were instructed to choose an answer during the last 3 s of each task item. For this period, the remaining time was indicated in the top right-hand corner of the presentation screen. The presentation time for a task was tightly restricted to eliminate any lapses of concentration during the tasks: the time span for solving each task type was set short enough for more than half of the participants to complete the task entry, based on the results from the behavioral study for task validation.

Behavioral study

To validate the *g*-loading and the difficulty of the behavioral tasks (simple and complex *g*-tasks), we administered the computerized behavioral tasks to a sample group (*n* = 82; aged 15.9 years ± 0.29, *M* ± SD) with a normal distribution of RAPM scores

(23.8 ± 4.4). The participants were instructed to respond as quickly as possible while avoiding errors. Their response times were measured and used to decide the presentation time for each task type. The g-loading of each task was represented by the correlational coefficient of the RAPM score, and the difficulty was indicated by the correct response rate in the sample.

Image acquisition

Images were acquired using a 3.0 T MR scanner (Forte, Isol Technology, Korea). Visual stimuli were presented on a 12-cm (visual angle = 13.7°) LCD monitor (IFIS-SA, MRI Devices, FA, USA) mounted on the head coil, and behavioral responses made on a right hand button response unit were recorded by custom-made software on a PC. Head movement was minimized using foam padding. To be familiarized with the test environment, all participants completed task examples for more than 10 min in the MR scanner before the fMRI experiment. Imaging included both T1-weighted structural images and gradient echo, echo-planar T2*-weighted images with blood oxygen level-dependent (BOLD) contrast (Ogawa et al., 1990). Twenty-four axial slices (5 mm thick, no gap) including the entire brain volume (TR = 3000 ms, TE = 35 ms, flip angle = 80°, 64×64 matrix) were acquired.

MRI data analysis

Data were processed using statistical parametric mapping SPM 99 (Wellcome Department of Cognitive Neurology, London). Functional images were motion-corrected using the 6-parameter rigid-body transformation (Friston et al., 1995). Images were then spatially normalized to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain in Talairach and Tournoux space by applying a 12-parameter affine transformation followed by nonlinear warping using basis functions (Ashburner and Friston, 1999). Images were resampled into 3-mm cubic voxels and smoothed by a Gaussian kernel of 9 mm FWHM. Individual contrast images (activation levels for complex g-tasks minus those for simple g-tasks) were generated using the general linear model. Group-based analysis and individual-differences-based analysis were performed sequentially using random effects analysis and regression analysis as follows. First, g-task-related brain regions specifically involved in high g-loaded tasks were determined using one-sample t test with height ($P < 0.0001$ corrected for multiple comparisons) and extent ($P < 0.0001$ uncorrected) thresholds. Second, to identify the group-specific activations, a two-sample t test was conducted between the superior- and average-g groups with less conservative height and extent thresholds ($P < 0.001$ uncorrected). Third, the g-level-related activation, which is an activation map dependent on individual g differences, was generated using simple regression with individual g-level (RAPM score) as a covariate. Significant clusters of g-level-related activation that occurred within the mask area from the first step were determined by using height ($P < 0.001$ uncorrected) and extent ($P < 0.001$ uncorrected) thresholds. Finally, the functional activation clusters from the two previous random effects analyses were used as the region of interest (ROI) for regression analysis. The activated voxel rates corresponded to the percentages of voxels activated in each ROI with a specific height threshold ($P < 0.05$, corrected), while the peak t scores were the highest t scores observed in each ROI (Kwon et al., 2002).

Results

Subjects and tasks (g-level and IQ; g-loading and accuracy)

As shown in Table 1, the superior-g group had an exceptional g-level (RAPM = 33.9 ± 0.8, >99%), while the average-g group had an ordinary g-level (RAPM = 22.8 ± 6.6, 60%). The mean WAIS-R full scale IQ of each group further confirmed the subject differences in general cognitive ability (superior-g, IQ = 137 ± 12, 99%; average-g, IQ = 105 ± 17, 63%).

To isolate the brain regions involved in g-related processes, we developed complex g-tasks and simple g-tasks that were similar in shape but contrasted in g-loading (Fig. 1 and Methods). Both were validated in g-loading by a separate behavioral study with a large number of subjects whose mean age and g-level were equivalent to the average participants of the experimental group ($n = 82$; mean age = 15.9 ± 0.29; RAPM = 23.8 ± 4.4). The complex and simple g-tasks exhibited a sharp contrast in g-loading (complex, $r = 0.62$; simple, $r = 0.20$) and difficulty (complex, 40% correct; simple, 94% correct; $t > 13.90$, $df = 42$, $P < 0.001$) (Fig. 1B).

g-related neural substrates

We first identified the entire network of cortical regions involved in the g-related neural processes regardless of individual differences. Using a random effects analysis (one-sample t test), the activation map of the whole group (all participants, $n = 36$) was created by subtracting the brain activity during the simple g-task from that of the complex g-task. As shown in Fig. 1C, the sharp g-contrast between complex and simple g-tasks elicited the robust bilateral activations ($P < 0.0001$ corrected) in the lateral prefrontal (PFC), the anterior cingulate (ACC), and the posterior parietal cortices (PPC). These g-task-related neural substrates were most likely to be the fronto-parietal network that was previously reported to constitute the neural bases for fluid reasoning and working memory (Ghatan et al., 1995; Gray et al., 2003; Newman et al., 2003; Prabhakaran et al., 1997). A more detailed description of the regions of activation is provided in Table 2.

Superior-g group versus average-g group

To explore differences in regional activation between the superior-g and average-g groups, we performed random effect analysis using a two-sample t test. Neither the superior-g group nor the average-g group recruited any additional brain areas, although we used a less conservative threshold ($P < 0.001$ uncorrected)

Table 1
Subject information and behavioral data

	Average-g ($n = 18$)	Superior-g ($n = 18$)
Age	16.6 ± 0.9	16.5 ± 0.6
Psychometric tests		
RAPM score (rank)	22.8 ± 6.6 (60%)	33.9 ± 0.8 (99%)
WAIS-R full scale IQ (rank)	105 ± 17 (63%)	137 ± 12 (99%)
Accuracy on fMRI tasks		
Complex g-task	49.1% ± 21.0	65.7% ± 18.5
Simple g-task	88.3% ± 19.6	97.8% ± 1.8

Rank represents the percentile rank of mean RAPM score or WAIS-R IQ. All data present in M ± SD.
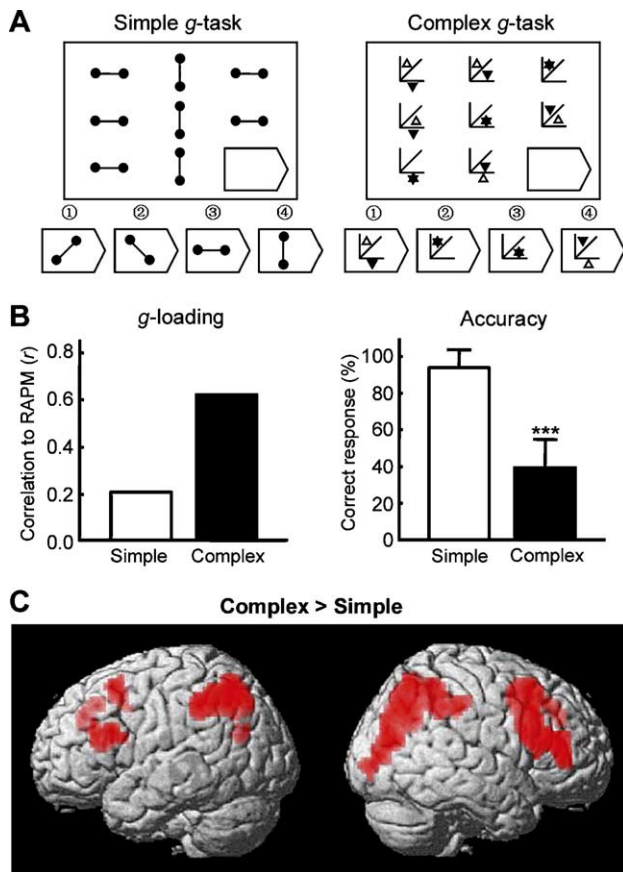
Fig. 1. Behavioral tasks and *g*-related neural network. (A) Example task items represent simple and complex *g*-tasks for the fMRI experiment. (B) *g*-loading and difficulty of each task type were validated by a behavioral study performed before the fMRI experiment (see Methods). Difference of *g*-loading (left panel) and difficulty (right panel) between simple (white bar) and complex *g*-tasks (black bar) were indicated by each task's correlations to RAPM scores and correct response rate, respectively. Error bars denote SD. ***$P < 0.001$, two-tailed *t* test. (C) *g*-related neural substrates were revealed by the contrasting of complex *g*-task versus simple *g*-task in a random effects analysis of the whole group ($n = 36$; one-sample *t* test, $P < 0.0001$ corrected). See Table 2 for the standard stereotaxic coordinates.

(data not shown). However, the superior-*g* group was much greater than the average-*g* group in the percent signal changes of the regions of interest (ROIs), which were defined as the activation clusters obtained from the whole group analysis (Fig. 2F). These differences in regional activity were statistically significant in all ROIs except the left PFC (Figs. 2A–E). Intriguingly, the most significant gap in the regional activation was not in the prefrontal cortex but in the posterior parietal region (right PPC, $P < 0.001$; left PPC, $P < 0.01$; ACC and right PFC, $P < 0.05$).

Given the strong group difference in subject *g*-level ($P < 0.001$) indicated by the RAPM scores (Fig. 2G), the behavioral performance of the complex *g*-task was expected to show a striking difference between the two groups. However, the difference in accuracy on complex *g*-tasks was not very remarkable, although it was statistically significant ($P < 0.05$) and greater than that of the simple *g*-task (Figs. 2H and I). It might be the reflection of the stringent task condition because the presentation time for the complex *g*-task (30 s per a test item) was tightly controlled to eliminate any lapses of concentration during the task performance which could have generated extraneous brain activations.

Correlation between individual g-level and regional brain activity

The group comparison in brain activity revealed that a higher *g*-level was linked to greater regional activity. To examine whether this positive relation is still valid on an individual level, the correlations between individual *g* differences and regional activities were analyzed using the same ROIs as in the group difference analysis described above. The regional brain activity was calculated by the peak *t* score and the activated voxel rate within the ROIs (see Methods). The correlation data in Table 2 indicated that the right and the left PPC had the highest correlation coefficients for the activated voxel rate ($r_v = 0.76$, $P < 0.001$) and the peak *t* score ($r_t = 0.74$, $P < 0.001$), respectively. The other ROIs also showed a moderate correlation, and most of them were statistically significant. These observations are consistent with the results from the group analysis and provide further evidence supporting the fact that individual *g*-level was associated with regional activity in the *g*-related neural substrates, particularly in the PPC.

Relationship between task modality and regional brain activity

In terms of surface features, our fMRI tasks largely belong to the category of visuo-spatial tasks. The PPC region exhibiting the highest correlation with subject differences in *g* is also known to play an important role in visuo-spatial working memory (Kwon et al., 2002; Pessoa et al., 2002; Vogel and Machizawa, 2004). To assess the possibility that the task modality could significantly influence the regional brain activation induced by the *g*-tasks, we performed a correlated vectors analysis (Jensen, 1998), a procedure devised to discover non-psychometric (e.g., biological) correlates of *g*, using two vectors: (1) the correlation coefficients of the activity in each foci of the group-based activations to the WAIS-R subtest and RAPM scores and (2) the standard *g*-loadings of both tests which were validated using a hierarchical model in a large-sample study ($n = 241$) (Marshalek et al., 1983).

As shown in Table 3, this analysis has demonstrated that the left and right PPC activations were significantly associated with the *g* factor: the left PPC activation showed statistical significance in both the Pearson and Spearman correlations ($r = 0.68$ and 0.65, respectively, $P < 0.05$), while the right PPC activation exhibited statistical significance in the Pearson correlation ($r = 0.66$, $P < 0.05$) and almost reached statistical significance in the Spearman correlation ($r = 0.57$, $P = 0.054$). Irrespective of the test modality, the correlation coefficients of the bilateral PPC activations to the WAIS subtest scores were more parallel with the standard *g*-loadings of the tests than those of any other activation clusters. Additionally, the correlational data between WAIS-R IQ scores and the ROI activations driven by the RAPM-like task demonstrated that, in all the ROIs (ACC, bilateral PFC, and bilateral PPC), the verbal IQ revealed a stronger correlation with the brain activations than the nonverbal (performance) IQ, although our fMRI task was nonverbal. In consideration of the *g*-loading of each IQ, this also increased the possibility that the ROI activations may be due, not to the task modality, but to the *g*-loadedness.

Individual-differences-related neural substrates

To identify specific brain areas whose functions are associated with individual differences in *g*-level, a linear regression analysis was performed using RAPM score as a covariate, with the cortical

Table 2
Brain regions related with g

Anatomical area		Brodmann area	g-correlation		Cluster size	Peak activation			
			r_t	r_v		t score	x	y	z
Group-based activations (complex g-task > simple g-task)									
	ACC, medial frontal gyrus	6, 9, 8, 32	0.54***	0.43**	102	10.07	−6	36	30
Left	PFC (SFG, MFG)	8, 6	0.66***	0.51**	57	9.76	−27	15	51
Left	PFC (IFG, MFG)	46, 9, 45	0.45	0.13	115	9.80	−39	24	18
Right	PFC (MFG, SFG, IFG)	46, 8, 6, 9, 45	0.53***	0.46**	532	12.01	36	15	30
Left	PPC (IPL, IPS, SPL, PCu, SMG)	7, 40, 39, 19	0.74***	0.70***	551	13.71	−36	−51	45
Right	PPC (IPL, IPS, SPL, PCu, AnG, SMG)	7, 40, 39, 19	0.73***	0.76***	749	13.62	39	−75	21
Individual difference-based activations (correlated with individual g-level)									
Left	SPL	7	0.71***	0.76***	120	4.86	−15	−66	57
Right	SPL, IPS	7, 40, 19	0.78***	0.81***	244	4.93	15	−66	54

These data resulted from random effects group analyses of all subjects ($n = 36$; Upper: one-sample t test, threshold, $P < 0.0001$ corrected, size > 20; Lower: simple regression analysis, threshold, $P < 0.001$ uncorrected, size > 100). r_t, correlation coefficient of g and peak t score; r_v, correlation coefficient of g and activated voxel rate. Cluster size: number of voxels ($3 \times 3 \times 3$ mm^3). ACC, anterior cingulate cortex; PFC, prefrontal cortex; MFG, middle frontal gyrus; SFG, superior frontal gyrus; PPC, posterior parietal cortex; IPL, inferior parietal lobule; IPS, intraparietal sulcus; SPL, superior parietal lobule; PCu, precuneus; AnG, angular gyrus; SMG, supramarginal gyrus.

** $P < 0.01$.
*** $P < 0.001$.

brain activity (complex g-task > simple g-task) as the dependent variable. This cross-subject comparison revealed bilateral activation clusters in the posterior parietal region ($P < 0.001$): bilateral SPL and right IPS (Fig. 3A, Table 2). There was no negatively correlated area at the same threshold. Using these clusters as ROIs, we then correlated brain activity with g scores (Figs. 3B and C). This showed a strong linear increase in both cluster size and magnitude of peak activation within the ROI as a function of individual g-level (right SPL/IPS, $r_v = 0.81$, $r_t = 0.78$; left SPL, $r_v = 0.76$, $r_t = 0.71$, $P < 0.001$). To explore the possibility that other factors could affect the SPL activities, we assessed the relative contributions of g-level, accuracies on simple and complex g-tasks, and age to the bilateral SPC activities using multiple linear regression analysis. Only individual g differences were a significant predictive variable of the bilateral SPC activities ($P < 0.001$). The other variables did not show statistical significance ($P > 0.05$).

Discussion

Although there are several studies on prodigies in domain-specific ability such as chess, semantic memory, and mental calculation (Amidzic et al., 2001; Maguire et al., 2003; Pesenti et al., 2001), little is known about the neural basis of exceptional intellectual ability. The present study is the first neuroimaging study to examine a large number of people with exceptional g to address the nature of the neurobiological basis underpinning superior general intelligence. We first identified the entire neural network engaged in the high g-loaded reasoning task independent of individual differences and then determined the impact of individual g differences on activation patterns of this network by examining the differences in activation nodes and its BOLD signal intensity between the subjects with superior-g and ordinary-g. The group-based analysis suggested that the neural basis of superior-g was characterized not by engagement of extra network components unique to the superior-g group but by robust activation of the entire fronto-parietal network, particularly in the posterior parietal cortex. Furthermore, the linear regression analysis revealed that the

parietal activation encompassing bilateral SPL (BA 7) and right IPS (BA 40) was strongly correlated with individual differences in g ($r = 0.71$ to 0.81).

Apparently, the present results and a previous event-related fMRI study (Gray et al., 2003) have demonstrated a positive correlation between individual difference in g and cortical activations during fluid reasoning or working memory tasks. These findings appear to conflict with an early PET study suggesting that higher g is associated with lower brain activity, namely the neural efficiency hypothesis (Haier et al., 1988). This discrepancy could be attributed to the differences in experimental design (i.e. task presentation time) and imaging modality. In general, high-ability subjects tend to spend less time on performing the task compared to low-ability subjects (Poldrack, 2000; D'Esposito et al., 1997). Under the block-designed experiments, therefore, higher intelligence with faster response time could lead to lower averaged cortical activation over the task time, although the cortical activation is greater for shorter duration. In this regard, the event-related fMRI study is intrinsically free from the averaging effect, and the present study also could avoid that effect because the task presentation time is tightly controlled for maximizing the proportion of time spent on the task.

The present results converge strongly with an event-related fMRI study of individual differences (Gray et al., 2003) in implicating parietal areas in supporting intelligence. Taken together, the two studies implicate parietal regions (especially BA 40) about as strongly as it is possible to do on the basis of imaging data (which are intrinsically correlational) for having not merely the strongest correlations, but also implicated by a correlated vectors analysis (here) and mediational analyses (Gray et al.). The two studies diverge somewhat in the degree to which they implicate lateral prefrontal cortex (less strongly here). There are several potentially important methodological differences (e.g., the tasks that the subjects performed during scanning and the distribution of individual g-level), making the differences between the studies harder to interpret than the similarities.

Recently, there has been a large trend to invoke the construct of working memory to address the cognitive and neural bases
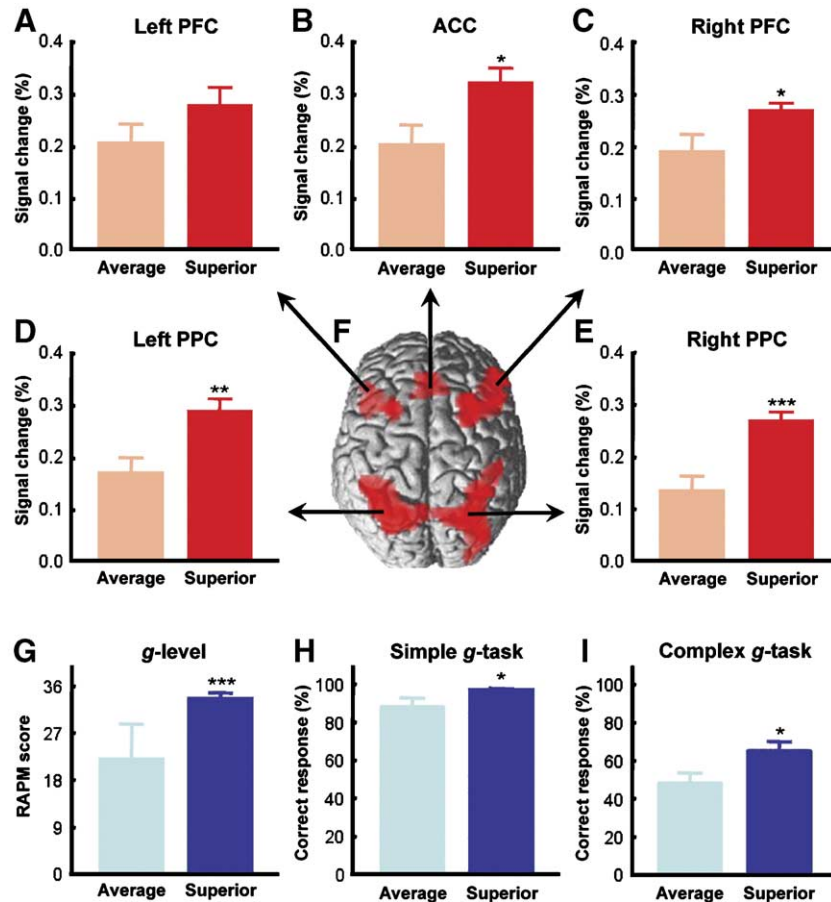
Fig. 2. Differences in regional activation and behavioral performance between the superior- and average-g groups. (A–E) Activation levels of the regions of interest (ROIs) are indicated by changes in BOLD signals in both groups (average-g group, pink bar; superior-g group, red bar); PFC, prefrontal cortex; ACC, anterior cingulate cortex; PPC, posterior parietal cortex. (F) Each ROI stands for the g-related activation region in the whole group analysis (see Table 2). (G–I) Behavioral differences between the average-g and superior-g groups are presented by RAPM scores and correct response rates on simple and complex g-tasks. Error bars denote SD. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$, two-tailed t test.

underlying individual differences in psychometric g. The general conclusion drawn from extensive psychometric studies was that working memory capacity is significantly associated with g (reasoning) ability ($r = 0.58$ to 0.65) but is not the same construct as reasoning ability (Ackerman et al., 2002; Conway et al., 2002; Engle et al., 1999). Similar conclusions have been drawn from accumulating neurobiological evidence (Gray et al., 2003; Marko-witsch and Kessler, 2000). For example, Gray et al. (2003) have shown that the dorsolateral PFC (DLPFC) and the PPC regions may mediate the relation between g and behavioral performance. In that study, subjects ($n = 48$) performed RAPM to assess individual differences in g and were then scanned during a working memory task (n-back). Importantly, significant correlations were observed between individual differences in g and the regional activity across a wide neural network including the lateral prefrontal, the parietal, and the temporal cortices during the trials with high interference. These findings are reconcilable with our present results as well as the previous studies that showed a broad fronto-parietal network during performance of reasoning tasks (Acuna et al., 2002; Esposito et al., 1999; Prabhakaran et al., 2001).

The notion of the neural network for g, however, appears to be in conflict somewhat with previous PET data suggesting that the DLPFC (BA 46) plays a unique role in g because it is the only region that is consistently involved in the three different types of reasoning tasks with high g-loadings (Duncan et al., 2000). To isolate the neural substrates of g, Duncan and colleagues compared brain activity during high g-loaded tasks ($r = 0.55$ to 0.67) and low g-loaded control tasks ($r = 0.37$ and 0.41). Taking into account that the experimental paradigm is based on the task differences in g-loading irrespective of individual differences, the g-contrast between the two tasks does not seem to be very significant. Particularly, the statistically more significant activation foci ($P < 0.05$, corrected) were drawn from the tasks with the lower g-contrasts (difference in g-loading, $\Delta r^2 = 0.13$ or 0.21). Thus, it is possible that greater g-contrast between active and control tasks could elicit more activation foci. In addition, individual variations in g-level would influence regional imaging results (Habeck et al., 2003; Haier et al., 2003). Indeed, our data resulting from a sharp g-contrasting condition (difference in task g-loading, $\Delta r^2 = 0.34$) demonstrated that ordinary people exhibited more robust and stable activation in the prefrontal regions including the DLPFC than the posterior regions but exceptional people did not (Fig. 2).

Another class of evidence supporting an important role of the PFC in problem solving (g) was provided from the studies on patients with brain injury. For example, patients with PFC damage performed poorly on the reasoning tasks requiring relational integration, whereas patients with temporal lobe damage exhibited

Table 3
Correlated vectors analysis of g-related neural network

	Standard g-loading	Group-based activation area				
		ACC	Left PFC	Right PFC	Left PPC	Right PPC
WAIS-R IQ						
Full scale	0.73	0.27	0.54***	0.30	0.47**	0.63***
Performance	0.61	0.15	0.33*	0.13	0.40*	0.57***
Verbal	0.74	0.30	0.61***	0.35*	0.48**	0.63***
WAIS-R subtest						
Digit span	0.49	0.22	0.58***	0.26	0.52***	0.56***
Picture completion	0.49	−0.08	0.00	−0.08	−0.20	−0.10
Similarities	0.54	0.28	0.44**	0.44**	0.46**	0.61***
Comprehension	0.56	0.12	0.53***	0.30	0.32	0.41*
Digit symbol	0.57	0.20	0.11	0.08	0.33*	0.44**
Object assembly	0.63	0.05	0.20	0.12	0.41*	0.48**
Picture arrangement	0.66	0.17	0.36*	0.28	0.39*	0.52***
Information	0.61	0.31	0.55***	0.43**	0.53***	0.64***
Block design	0.65	0.11	0.48**	0.28	0.61***	0.70***
Arithmetic	0.66	0.21	0.69***	0.31	0.57***	0.66***
Vocabulary	0.66	0.22	0.60***	0.46**	0.53***	0.59***
RAPM	0.80	0.45**	0.53***	0.48**	0.74***	0.79***
Correlation of vectors						
Pearson correlation		0.55	0.38	0.53	0.68*	0.66*
Spearman correlation		0.26	0.39	0.56	0.65*	0.57

The correlation of vectors is a Pearson correlation or Spearman rank order correlation between two vectors: (1) g-loadings of WAIS-R subtests and RAPM and (2) correlations of each area's activity (activated voxel rates) with the tests. The standard g-loadings of the subtests and RAPM were adopted from Marshalek et al. (1983). All data were corrected for attenuation. ACC, anterior cingulate gyrus; PFC, prefrontal cortex; PPC, posterior parietal cortex.

    * $P < 0.05$.
    ** $P < 0.01$.
    *** $P < 0.001$.

normal performance (Waltz et al., 1999). In addition, Duncan et al. (1995) suggest that brain damage to the frontal lobe caused a considerable deficit in fluid intelligence but not in crystallized intelligence. They also showed that fluid intelligence was impaired more by damage to the frontal than to the posterior region (Duncan et al., 1996). The latter two studies, however, do not exclude the possibility that the PPC region may be critically involved in fluid reasoning because a greater proportion of posterior patients had temporal and occipital damage rather than parietal damage. Notably, patients with parietal damage also showed significant impairment in fluid intelligence, although they were only a small portion of the whole posterior patients.

The main finding of the current study emphasized the role of the posterior parietal region (specifically, bilateral SPL and right IPS (BA 7/40)) among the entire network components of g. These regions were cross-validated by high g-contrasting in terms of both task and subject. This notion is further supported by previous EEG and PET data on individual differences in g. Using EEG-evoked potentials, it has been found that high-ability subjects were correlated with relatively greater use of parietal regions when they develop problem solving strategies, whereas low-ability subjects

relied more exclusively on the frontal region (Gevins and Smith, 2000). A previous study using PET also has reported that several posterior regions including the bilateral SPL (BA 7) revealed significant positive correlation with individual differences in g during performance of non-reasoning tasks (Haier et al., 2003). Intriguingly, these findings are in harmony with a previous anatomical data demonstrating that Albert Einstein had an extraordinary parietal cortex: his parietal cortex was relatively wider than that of controls (Witelson et al., 1999).

What is a possible role of the PPC in fluid reasoning and new problem solving? Although the PPC region is well known to be involved in the visuo-spatial short-term memory (Todd and Marois, 2004), it is difficult to postulate that the PPC activation in our experiment is sustained merely by domain-specific visual processes since the PPC regions were significantly high in the g-correlation ($r = 0.71$ to 0.81) and the correlation of the vectors analysis ($r = 0.65$ to 0.68), and our behavioral tasks require both visuo-spatial and verbal–analytic processes (Deshon et al., 1995). As mentioned above, high-ability people showed greater use of parietal regions while developing problem solving strategies (Gevins and Smith, 2000). Nevertheless, these findings do not exclude the possibility that the PPC may play a crucial role in visuo-spatial working memory capacity. Indeed, it has previously been demonstrated that increased brain activity in frontal and posterior regions including the PPC underlies the improvement of
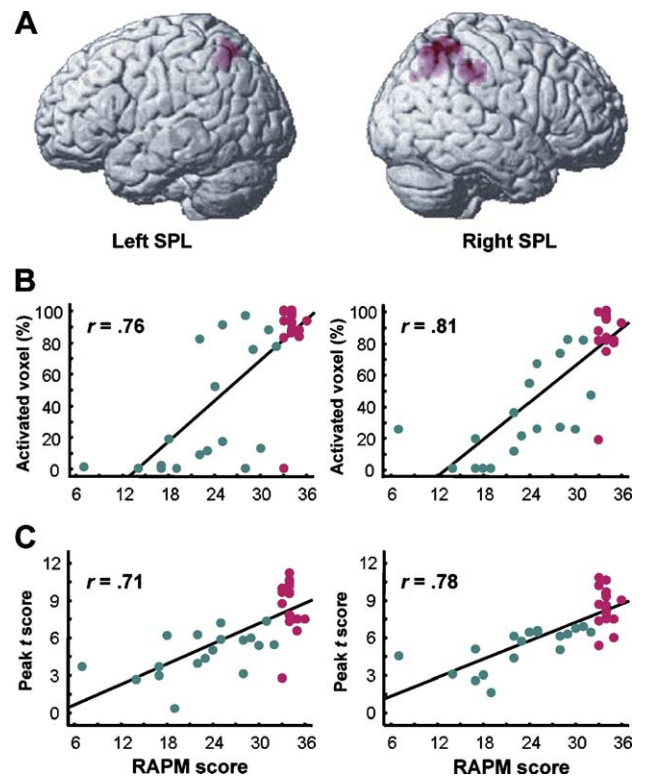

Fig. 3. g-level-related neural substrates and correlation of their activations with individual differences in g. (A) Activation clusters related to g-level in the left and right SPLs were defined by a simple regression analysis with RAPM score as a covariate, $n = 36$, $P < 0.001$ uncorrected; SPL, superior parietal lobule. (B and C) Regression plots showing correlations (r) of RAPM scores with the activated voxel rate and the peak t score in both the activation clusters (left panel, left SPL; right panel, right SPL/IPS; blue circle, average-g individual; red circle, superior-g individual).

visuo-spatial working memory performance throughout childhood and adolescence into young adulthood (Klingberg et al., 2002; Kwon et al., 2002). Consistent with this, increased BOLD activity of the fronto-parietal network, particularly right IPS, predicted successful performance on the working memory tasks (Pessoa et al., 2002). Furthermore, adaptive and intensive training of working memory induced an increase in both working memory capacity and the cortical activations including superior and inferior parietal cortices (Olesen et al., 2004). In that study, all subjects, during the training period, have used or changed to chunking as an encoding strategy. Thus, one important role of the PPC could be the development of problem solving strategies such as chunking to find rules in diverse figural elements in our fluid reasoning task.

In conclusion, we suggest that higher order cognitive functions, such as general intelligence, may be processed by the coordinated activation of widely distributed brain areas and that exceptional g ability may be attributable to the functional facilitation rather than the structural peculiarity of the neural network for g. In addition, our results demonstrated that the posterior parietal regions including bilateral SPL and right IPS could be the neural correlates for superior general intelligence. These findings would be the early step toward the development of biological measures of g which leads to new perspectives for behavior interventions improving general cognitive ability.

Acknowledgments

References

Ackerman, P.L., Beier, M.E., Boyle, M.O., 2002. Individual differences in working memory within a nomological network of cognitive and perceptual speed abilities. J. Exp. Psychol. Gen. 131, 567–589.

Acuna, B.D., Eliassen, J.C., Donoghue, J.P., Sanes, J.N., 2002. Frontal and parietal lobe activation during transitive inference in humans. Cereb. Cortex 12, 1312–1321.

Alderton, D.L., Larson, G.E., 1990. Dimensionality of Raven's Advanced Progressive Matrices items. Educ. Psychol. Meas. 50, 887–900.

Amidzic, O., Riehle, H.J., Fehr, T., Wienbruch, C., Elbert, T., 2001. Pattern of focal gamma-bursts in chess players. Nature 412, 603.

Anastasi, A., 1988. Psychological Testing. Macmillan Publishing Co., New York.

Ashburner, J., Friston, K.J., 1999. Nonlinear spatial normalization using basis functions. Hum. Brain Mapp. 7, 254–266.

Bors, D.A., Strokes, T.L., 1998. Raven's Advanced Progressive Matrices: norms for first-year university students and the development of a short form. Educ. Psychol. Meas. 58, 382–399.

Braver, T.S., Cohen, J.D., Nystrom, L.E., Jonides, J., Smith, E.E., Noll, D.C., 1996. A parametric study of prefrontal cortex involvement in human working memory. NeuroImage 5, 49–62.

Bunge, S.A., Klingberg, T., Jacobsen, R.B., Gabrieli, J.D., 2000. A resource model of the neural basis of executive working memory. Proc. Natl. Acad. Sci. U. S. A. 97, 3573–3578.

Cabeza, R., Nyberg, L., 2000. Imaging cognition II: an empirical review of 275 PET and fMRI studies. J. Cogn. Neurosci. 12, 1–47.

Carpenter, P.A., Just, M.A., Shell, P., 1990. What one intelligence test measures: a theoretical account of the processing in the Raven Progressive Matrices Test. Psychol. Rev. 97, 404–431.

Cattell, R.B., 1963. Theory of fluid and crystallized intelligence: a critical experiment. J. Educ. Psychol. 54, 1–22.

Cohen, J.D., Perlstein, W.M., Braver, T.S., Nystrom, L.E., Noll, D.C., Jonides, J., Smith, E.E., 1997. Temporal dynamics of brain activation during a working memory task. Nature 386, 604–608.

Conway, A.R.A., Cowan, N., Bunting, M.F., Therriault, D.J., Minkoff, S.R.B., 2002. A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. Intelligence 30, 163–183.

Deshon, R.P., Chan, D., Weissbein, D.A., 1995. Verbal overshadowing effects on Raven's Advanced Progressive Matrices: evidence for multidimensional performance determinants. Intelligence 21, 135–155.

D'Esposito, M., Zarahn, E., Aguirre, G.K., Shin, R.K., Auerbach, P., Detre, J.A., 1997. The effect of pacing of experimental stimuli on observed functional MRI activity. NeuroImage 6, 113–121.

Duncan, J., Burgess, P., Emslie, H., 1995. Fluid intelligence after frontal lobe lesions. Neuropsychologia 33, 261–268.

Duncan, J., Emslie, H., Williams, P., Johnson, R., Freer, C., 1996. Intelligence and the frontal lobe: the organization of goal-directed behavior. Cogn. Psychol. 30, 257–303.

Duncan, J., Seitz, R.J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., Newell, F.N., Emslie, H., 2000. A neural basis for general intelligence. Science 289, 399–401.

Engle, R.W., Tuholski, S.W., Laughlin, J.E., Conway, A.R., 1999. Working memory, short-term memory, and general fluid intelligence: a latent-variable approach. J. Exp. Psychol. Gen. 128, 309–331.

Esposito, G., Kirkby, B.S., Van Horn, J.D., Ellmore, T.M., Berman, K.F., 1999. Context-dependent, neural system-specific neurophysiological concomitants of ageing: mapping PET correlates during cognitive activation. Brain 122, 963–979.

Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.B., Heather, J.D., Frackowiak, R.S.J., 1995. Spatial registration and normalization of images. Hum. Brain Mapp. 2, 165–189.

Gevins, A., Smith, M.E., 2000. Neurophysiological measures of working memory and individual differences in cognitive ability and cognitive style. Cereb. Cortex 10, 829–839.

Ghatan, P.H., Hsieh, J.C., Wirsen-Meurling, A., Wredling, R., Eriksson, L., Stone-Elander, S., Levander, S., Ingvar, M., 1995. Brain activation induced by the perceptual maze test: a PET study of cognitive performance. NeuroImage 2, 112–124.

Gray, J.R., Thompson, P.M., 2004. Neurobiology of intelligence: science and ethics. Nat. Rev. Neurosci. 5, 471–482.

Gray, J.R., Chabris, C.F., Braver, T.S., 2003. Neural mechanisms of general fluid intelligence. Nat. Neurosci. 6, 316–322.

Gustafsson, J.E., 1984. A unifying model for the structure of intellectual abilities. Intelligence 8, 179–203.

Habeck, C., Hilton, H.J., Zarahn, E., Flynn, J., Moeller, J., Stern, Y., 2003. Relation of cognitive reserve and task performance to expression of regional covariance networks in an event-related fMRI study of nonverbal memory. NeuroImage 20, 1723–1733.

Haier, R.J., Benbow, C.P., 1995. Sex differences and lateralization in temporal lobe glucose metabolism during mathematical reasoning. Dev. Neuropsychol. 11, 405–414.

Haier, R.J., Siegel, B.V., Nuechterlein, K.H., Hazlett, E., Wu, J., Paek, J., Browning, H., Buchsbaum, M.S., 1988. Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. Intelligence 12, 199–217.

Haier, R.J., Nathan, S.W., Alkire, M.T., 2003. Individual differences in general intelligence correlate with brain function during nonreasoning tasks. Intelligence 31, 429–441.

Haier, R.J., Jung, R.E., Yeo, R.A., Head, K., Alkired, M.T., 2004. Structural brain variation and general intelligence. NeuroImage 23, 425–433.

Houdé, O., Tzourio-Mazoyer, N., 2003. Neural foundations of logical and mathematical cognition. Nat. Rev. Neurosci. 4, 507–514.

Jensen, A.R., 1991. Spearman's g and the problem of educational equality. Oxford Rev. Educ. 17, 169–187.

Jensen, A.R., 1998. The g Factor: The Science of Mental Ability. Praeger, Westport, CT.

Johnson, W., Bouchard, T.J., Krueger, R.F., McGue, M., Gottesman, I.I., 2004. Just one g: consistent results from three test batteries. Intelligence 32, 95–107.

Jung, R.E., Yeo, R.A., Chiulli, S.J., Sibbitt, W.L.J., Weers, D.C., Hart, B.L., Brooks, W.M., 1999. Biochemical markers of cognition: a proton MR spectroscopy study of normal human brain. NeuroReport 10, 3327–3331.

Klingberg, T., O'Sullivan, B.T., Roland, P.E., 1997. Bilateral activation of fronto-parietal networks by incrementing demand in a working memory task. Cereb. Cortex 7, 465–471.

Klingberg, T., Forssberg, H., Westerberg, H., 2002. Increased brain activity in frontal and parietal cortex underlies the development of visuospatial working memory capacity during childhood. J. Cogn. Neurosci. 14, 1–10.

Kroger, J.K., Sabb, F.W., Fales, C.L., Bookheimer, S.Y., Cohen, M.S., Holyoak, K.J., 2002. Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. Cereb. Cortex 12, 477–485.

Kwon, H., Reiss, A.L., Menon, V., 2002. Neural basis of protracted developmental changes in visuo-spatial working memory. Proc. Natl. Acad. Sci. U. S. A. 99, 13336–13341.

Larson, G.E., Haier, R.J., LaCasse, L., Hazen, K., 1995. Evaluation of a "Mental Effort" hypothesis for correlations between cortical metabolism and intelligence. Intelligence 21, 267–278.

Maguire, E.A., Valentine, E.R., Wilding, J.M., Kapur, N., 2003. Routes to remembering: the brains behind superior memory. Nat. Neurosci. 6, 90–95.

Markowitsch, H.J., Kessler, J., 2000. Massive impairment in executive functions with partial preservation of other cognitive functions: the case of a young patient with severe degeneration of the prefrontal cortex. Exp. Brain Res. 133, 94–102.

Marshalek, B., Lohman, D.F., Snow, R., 1983. The complexity continuum in the radex and hierarchical models of intelligence. Intelligence 7, 107–127.

Neisser, U., Boodoo, G., Bouchard, T.J.J., Boykin, A.W., Brody, N., Ceci, S.J., Halpern, D.F., Loehlin, J.C., Perloff, R., Sternberg, R.J., et al., 1996. Intelligence: knowns and unknowns. Am. Psychol. 51, 77–101.

Newman, S.D., Carpenter, P.A., Varma, S., Just, M.A., 2003. Frontal and parietal participation in problem solving in the Tower of London: fMRI and computational modeling of planning and high-level perception. Neuropsychologia 41, 1668–1682.

Ogawa, S., Lee, T.M., Kay, A.R., Tank, D.W., 1990. Brain magnetic resonance imaging with contrast dependent on blood oxygenation. Proc. Natl. Acad. Sci. U. S. A. 87, 9868–9872.

Olesen, P.J., Westerberg, H., Klingberg, T., 2004. Increased prefrontal and parietal activity after training of working memory. Nat. Neurosci. 7, 75–79.

Pesenti, M., Zago, L., Crivello, F., Mellet, E., Samson, D., Duroux, B., Seron, X., Mazoyer, B., Tzourio-Mazoyer, N., 2001. Mental calculation in a prodigy is sustained by right prefrontal and medial temporal areas. Nat. Neurosci. 4, 103–107.

Pessoa, L., Guitierrez, E., Bandettini, P.A., Ugerleider, G.L., 2002. Neural correlates of visual working memory: fMRI amplitude predicts task performance. Neuron 35, 975–987.

Poldrack, R.A., 2000. Imaging brain plasticity: conceptual and methodological issues—a theoretical review. NeuroImage 12, 1–13.

Prabhakaran, V., Smith, J.A.L., Desmond, J.E., Glover, G.H., Gabrieli, J.D.E., 1997. Neural substrates of fluid reasoning: an fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. Cogn. Psychol. 33, 43–63.

Prabhakaran, V., Rypma, B., Gabrieli, J.D., 2001. Neural substrates of mathematical reasoning: a functional magnetic resonance imaging study of neocortical activation during performance of the necessary arithmetic operations test. Neuropsychology 15, 115–127.

Raven, J.C., Court, J.H., Raven, J., 1988. Manual for Raven's Progressive Matrices and Vocabulary Scales. Lewis, London.

Schmidt, F.L., Hunter, J.E., 1998. The validity and utility of selection methods in personnel psychology: practical and theoretical implications of 85 years of research findings. Psychol. Bull. 124, 262–274.

Smith, E.E., Jonides, J., 1998. Neuroimaging analyses of working memory. Proc. Natl. Acad. Sci. U. S. A. 95, 12061–12068.

Snow, R.E., 1989. Toward assessment of cognitive and conative structures in learning. Educ. Res. 18, 8–14.

Spearman, C., 1904. General intelligence, objectively determined and measured. Am. J. Psychol. 15, 201–293.

Todd, J.J., Marois, R., 2004. Capacity limit of visual short-term memory in human posterior parietal cortex. Nature 428, 751–754.

Vogel, E.K., Machizawa, M.G., 2004. Neural activity predicts individual differences in visual working memory capacity. Nature 428, 748–751.

Waltz, J.A., Knowlton, B.J., Holyoak, K.J., Boone, K.B., Mishkin, F.S., de Menezes Santos, M., Thomas, C.R., Miller, B.L., 1999. A system for relational reasoning in human prefrontal cortex. Psychol. Sci. 10, 119–125.

Wechsler, D., 1981. WAIS-R Manual. Psychol. Corp, New York.

Witelson, S.F., Kigar, D.L., Harvey, T., 1999. The exceptional brain of Albert Einstein. Lancet 353, 2149–2153.