Differential Patterns of Cortical Activation as a Function of Fluid Reasoning Complexity

Bernardo Perfetti,^{1,2,3,4*} Aristide Saggino,⁵ Antonio Ferretti,^{3,4}
Massimo Caulo,^{3,4} Gian Luca Romani,^{3,4} and Marco Onofri^{1,2}

¹Department of Oncology and Neurosciences, University of Chieti-Pescara, Chieti, Italy

²Center of Excellence on Aging, Ce.S.I., Fondazione Università G. d'Annunzio, Chieti, Italy

³Department of Clinical Sciences and Bioimaging, University of Chieti-Pescara, Chieti, Italy

⁴ITAB, Fondazione Università G. d'Annunzio, Chieti, Italy

⁵Department of Biomedical Sciences, Laboratory of Psychometrics,
University of Chieti-Pescara, Chieti, Italy

Abstract: Fluid intelligence (gf) refers to abstract reasoning and problem solving abilities. It is considered a human higher cognitive factor central to general intelligence (g). The regions of the cortex supporting gf have been revealed by recent bioimaging studies and valuable hypothesis on the neural correlates of individual differences have been proposed. However, little is known about the interaction between individual variability in gf and variation in cortical activity following task complexity increase. To further investigate this, two samples of participants (high-IQ, $N = 8$; low-IQ, $N = 10$) with significant differences in gf underwent two reasoning (moderate and complex) tasks and a control task adapted from the Raven progressive matrices. Functional magnetic resonance was used and the recorded signal analyzed between and within the groups. The present study revealed two opposite patterns of neural activity variation which were probably a reflection of the overall differences in cognitive resource modulation: when complexity increased, high-IQ subjects showed a signal enhancement in some frontal and parietal regions, whereas low-IQ subjects revealed a decreased activity in the same areas. Moreover, a direct comparison between the groups' activation patterns revealed a greater neural activity in the low-IQ sample when conducting moderate task, with a strong involvement of medial and lateral frontal regions thus suggesting that the recruitment of executive functioning might be different between the groups. This study provides evidence for neural differences in facing reasoning complexity among subjects with different gf level that are mediated by specific patterns of activation of the underlying fronto-parietal network. *Hum Brain Mapp* 30:497–510, 2009. © 2007 Wiley-Liss, Inc.

Key words: fMRI; intelligence; mental effort; prefrontal cortex; intelligence tests; attention; individual differences

INTRODUCTION

The first reliable definition of intelligence was proposed by Spearman [Spearman, 1904] who, on the basis of factor analysis, individuated a latent dimension (the g factor) common to a large variety of cognitive tests which could account for the tendency of most human cognitive abilities to be positively correlated. Recently, neuroscientists have focused on this topic aiming at establishing the neural underpinnings of intelligence and addressing the mecha-

*Correspondence to: Perfetti Bernardo, CeSI Fondazione G. d'Annunzio, Unità Neurologia Comportamentale e Disordini del Movimento, via Colle dell'Ara 31, Chieti Scalo 66013 (CH), Italy. E-mail: perfetti@inwind.it

Received for publication 31 July 2007; Revised 24 October 2007; Accepted 26 October 2007

DOI: 10.1002/hbm.20519

Published online 19 December 2007 in Wiley InterScience (www.interscience.wiley.com).

nistic models of the specific brain activity related to intelligent behavior [Gray and Thomson, 2004]. As Sternberg [Sternberg, 2000, 2005] pointed out, this growing field of data has some important limitations since it focuses on a specific factor, namely fluid intelligence (gf factor), which may not be identifiable with human general intelligence [Blair, 2006; Carroll, 2003; Kaufman and Kaufman, 2006; but Cattell, 1987; Horn, 1998].

From a psychometric perspective, human cognitive abilities can be assumed to exist at three principal levels (specific, broad, and general) which are organized in a hierarchical structure. Fluid intelligence belongs to the second broad stratum and is strictly involved with higher cognition together with other 8–10 factors such as comprehension-knowledge and mathematics. In cognitive psychology, gf refers to analytic reasoning and problem solving abilities which are mostly evident in novel context. It is strongly associated with working memory and with the capability to maintain and manipulate goals and information relevant to the task. [Carpenter et al., 2000; Deary, 2000; Kane et al., 2005].

Anatomically, both functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies have revealed patterns of activation focused in medial and lateral prefrontal cortices and in posterior parietal areas associated with fluid intelligence [Haier et al., 1988; Kroger et al., 2002; Lee et al., 2006; Prabhakaran et al., 1997]. Overall, the individuated cortical activations are organized in a functional fronto-parietal network similar to the one associated with working memory tasks [Gray et al., 2003; Kane et al., 2005] and “cognitive control” [Hon et al., 2006]. Although there is a sort of consensus on the nodes composing the network, it is still under debate whether these regions provide a different contribution to fluid intelligence and in which way their activity is related to individual differences in gf.

To clarify these topics, two different and complementary approaches have been implemented, namely task- and individual differences-based studies, respectively. The first approach aimed at highlighting the specific contribution of each region composing the network as a function of task complexity and as something independent from people’s intellectual ability. In general, subjects with similar gf-level performed versions of the same fluid task with increasing difficulty. Their corresponding brain activities were compared. Dorsolateral prefrontal cortex (DLPFC) has been indicated as a crucial for fluid intelligence because of its neural activity enhancement in response to increasing reasoning difficulty [Kroger et al., 2002; Prabhakaran et al., 1997]. Complementary, the second approach focused on variability in neural activation associated with fluid reasoning across participants with differences in gf-level. Recent fMRI investigations have suggested that people with higher gf, when asked to perform high demanding WM or gf task, show greater activation of the entire functional network [Gray et al., 2003], that in some cases is stronger for the posterior regions [Lee et al., 2006].

Although these two approaches have strengthened our understanding of the biological underpinnings of intelligence, they provided less information about the interaction between task complexity and individual gf variability. Do higher and lower gf subjects present specific patterns of neural activity variation in response to increasing difficulty? In general, when reasoning task complexity increases people with similar intellectual ability show an enhancement of the signal in lateral prefrontal cortex—that is in those areas mostly involved with executive attention [Christoff et al., 2001; Kroger et al., 2002]. Similarly, an increment of WM load can result in a specific linear increase of activity in the same cortical areas [Braver et al., 1997]. But, when cognitive demand is excessive, some regions of prefrontal cortex may show an unchanged or even reduced activation, especially in presence of interference [Fletcher et al., 1998; Weinberger et al., 1986].

Considering the abovementioned findings, one might expect that manipulation of gf task complexity may induce differential variation in cortical activities among subjects with different resources which might be likely associated with differences in performance. Specifically an increment of the overall cognitive load might yield unchanged or even a decreased signal across the entire fronto-parietal network in people with low fluid ability. By contrast, high gf individuals are expected to go through an opposite pattern.

Hence, this study sought to address these issues. Our first goal was verifying the probable presence of differential patterns of activation in response to increasing fluid difficulty which might depend on gf variability among individuals. Then, we aimed at clarifying which regions of the network underlying fluid intelligence do neurally express these suspected differences. In light of a previous study which showed that slower individuals may require more executive control than faster participants to perform successfully [Rypma et al., 2006], we expect that prefrontal cortex might play an important role in differencing between and within low- and high-IQ participants’ activations. To do so, we recruited two samples of volunteers with significant differences in gf. Then, using fMRI we analyzed the signal variation associated with moderate and complex reasoning items between and within the two samples. Task complexity was manipulated by selecting adequate problems from the Standard and Advanced Raven Progressive Matrices [RSPM, Raven, 1976; RAPM, Raven, 1965]. The selected problems were characterized by different type and number of rules governing the relations among stimuli.

MATERIALS AND METHODS

fMRI Subjects Selection

To select 20 subjects with significant differences in gf level we first conducted a behavioral testing session, in which 69 volunteers were sequentially divided into five

Figure 1.

Distribution of intelligent quotient scores obtained by the 69 subjects at scale 3 of culture fair test. The two grey rectangles show the extreme tails of the curve from which the 18 fMRI volunteers were selected.

groups (the number of subjects ranged from 12 to 16) and were administered a test of Fluid intelligence [Culture Fair; Scale 3; Form A and B; Cattell and Cattell, 1973]. The whole sample (6 males) consisted of students aged between 19 and 30 years (males, $M = 22.3$ and $SD \pm 3.1$; females, $M = 21.3$ and $SD \pm 2.3$) and recruited from the University of Chieti-Pescara. They had a mean of 13.37 ($SD \pm 1.07$) years of education. The intelligence test was administered to all participants in a suitable setting room at our institute. Before starting the testing session, subjects were informed about the whole experimental procedure and asked for the consensus to eventually take part to an fMRI paradigm. A trained experimenter administered the two forms (A and B) composing Scale 3 of the Culture Fair test [for a detailed description of the test see the original manual; Cattell and Cattell, 1973]. To avoid floor effect of IQ scores that might be caused by the high level of education of participants to the study, we choose Scale 3 of Culture Fair which is considered appropriate for this type of subjects [Cattell and Cattell, 1973]. Intelligence Quotients (IQs) were calculated for all volunteers based upon published norms [Cattell and Cattell, 1981] and the resulting frequency distribution was normally shaped. For the fMRI session, 20 subjects belonging to the normal range (between 70 and 130) were selected from the two extreme tails of the IQ scores distribution in order to maximize differences in gf-level and have comparable gf intragroup variability (see Fig. 1).

Two participants excessively moved their head during functional acquisition, hence were excluded from data analysis. The remaining 18 right-handed subjects were sorted in two groups as follows: the low-gf group consisted of 8 participants (all female) who scored $87.37 \pm$

5.57 at Culture Fair. Their mean age was 21.3 years ($SD \pm 1.38$) and they had a mean of 13.4 years of education ($SD \pm 1.0$). The high-gf group consisted of 10 subjects (4 males) with a mean IQ score of 118.8 ($SD \pm 5.73$). Their mean age was 21.2 (± 2.44) and they had a mean of 13.5 years of education ($SD \pm 1.6$). Exclusionary criteria included any major medical or psychiatric illness, substance abuse, or history of head injury. All the 20 participants gave their written informed consent and received a reward to take part to the scanning session. The experimental procedure was approved by the Ethics Committees of the University of Chieti-Pescara and was in accordance with the Declaration of Helsinki British Medical Journal, 1996.

fMRI Task and Procedure

For the fMRI session, we developed a computerized behavioral task composed by a total of 32 fluid reasoning and 32 control problems adapted from both the RSPM [Raven, 1976] and RAPM [Raven, 1965]. As showed in Figure 2, each reasoning problem consisted of a 3×3 matrix placed on the left visual field of the subject in which the bottom right entry was missing (we refer with the word entry to each of the nine cells composing the matrix). Each of the eight filled entries of the matrix contained one or more figural elements. On the right, eight different alternatives were presented among which participants were asked to choose the one that best completed the matrix with the missing cell. The correct solution could be achieved by educing the relation ruling the elements disposition inside the filled entries of the matrix. The computerized task was kept more similar as possible to the original paper test. Only the arrangement of the alternatives was changed with the original being positioned below the matrix. Additionally, 32 control problems were used in the task, consisting of 3×3 matrices with all the entries containing figural elements devoid of any logical relations. As showed in Figure 2, the matrix was positioned in the left visual field of the subject while a series of eight pseudo-alternatives were arranged on the right.

Even though all reasoning problems shared a similar format, stimuli difficulty was manipulated according to the complexity and number of the rules (or relations) necessary to achieve the correct solution. As showed by Carpenter [Carpenter et al., 1990], Raven Progressive Matrices can be classified on the basis of the relations ruling the displacement of the figural elements inside the entries. The authors individuated five different types of rules some of which were characterized by perceptually based algorithms (i.e. they require visuo-spatial processing to be abstracted) while others loaded on more abstract thinking (namely analytic reasoning). The number and the type of rules characterizing the matrices have been shown to be fundamental for the degree of problems complexity.

For the fMRI behavioral task we selected the reasoning problems as follows: from the two original tests we first selected only those problems with a 3×3 matrix facet

Figure 2.

Three examples of item (figural, analytical, and control) used in the fMRI paradigm and adapted from the advanced and standard Raven matrices. Lower right: a time line showing the sequence of stimuli inside a single trial.

which were sequentially classified according to the five rules reported by Carpenter [Carpenter et al., 1990; see the original article for a detailed description of all the rules]. Those matrices in which the relation among the entries followed a single rule ("Constant in a Row" or "Quantitative Pair-wise Progression") with perceptually based algorithms were considered "figural". Problems requiring the abstraction of more than a rule or of a single rule ("distribution of three values") based on analytic reasoning were considered "analytic" [Carpenter et al., 1990; Hunt, 1974; Prabakaran et al., 1997]. Successively, 16 "figural" and 16 "analytic" matrices were randomly extracted and adapted for a computerized presentation with the intent to keep the original increasing difficulty within each type of problems [Forbes, 1964]. Number and types of rule governing the fMRI task items were different between figural and analytic matrices. For the 32 control problems we randomly selected from RSPM and RAPM single entries that were assembled in matrices in which the figural elements were devoid of any logical relation. The control format was kept similar to that of the reasoning problems.

A scanning session consisted of two different runs (for a total of 32 trials), each made up of 8 figural, 8 analytic, and 16 control items. The order of presentation of the

figural and analytic problems was pseudo-randomized within the whole task and a control matrix followed each reasoning. Key presses on two different two-button pads (Lumina LSC-400 controller, Cedrus, California, USA), one for each of the two hands indicated responses. As shown in Figure 2, a single trial consisted of a reasoning problem followed by a control item. The reasoning problems presentation was self-paced with a maximum of 120 s. The subject was instructed to take all the time necessary for generating the solution and when ready to press the button beneath his/her left index finger. A "match" period of maximum 1,500 ms followed, in which a red cross overlapped one of the eight alternatives and the participant had to match the generated response with the one suggested by the computer. Half the highlighted choices were correct answers and half were incorrect answers. For each reasoning matrices, the "not correct" alternative was selected among "distracter" entries, i.e. those entries similar to correct one, and were kept consistent for all participants. If the solution was consistent with the suggested alternative the subject might press the button beneath the right index finger, if not he/she might press the button beneath the right middle finger. The "match" period was kept little to avoid any additional reasoning process.

Control matrices were presented for a fixed period of 15 s permitting attenuation of the blood oxygen level dependent (BOLD) signal associated with fluid reasoning whereupon a next reasoning stimulus followed. To elicit saccadic movements, when presented with a control problem, participants were asked to look across the rows and down the columns composing the matrix and then to look at the eight pseudo-alternatives as well. Reasoning and control matrices were always preceded by the instruction “solve” for the former and “watch” for the latter, each instruction lasting for 1,200 ms. The two runs were balanced within and between groups.

Presentations of the stimuli were controlled by means of the E-Prime software, v.1.1.1, Psychology Software Tools running on a PC placed in the scanner console room. Button responses and reaction times were recorded online for each stimulus. Visual stimuli were projected on a translucent glass placed on the back of the scanner bore by means of an LCD projector. A mirror fixed to the head coil inside the magnet allowed the subjects to view the translucent glass. Before the functional imaging acquisition, all participants underwent a practice set comparable to the stimulus set presented in the scanner. They seated in front a computer placed inside the scanner console room and were instructed on the task by a trained experimenter. Given the moderate percentage of chance performance (50%), they were also explicitly taught not to guess the solution. Instead guessing subjects were told to miss the response when necessary.

Image Acquisition

BOLD contrast functional images were acquired with a SIEMENS MAGNETOM VISION scanner at 1.5 T by means of T2*-weighted echo planar imaging (EPI) free induction decay (FID) sequences with the following parameters: TR 3,000 ms, TE 60 ms, matrix size 64×64 , FOV 256 mm, in-plane voxel size $4 \text{ mm} \times 4 \text{ mm}$, flip angle 90° , slice thickness 6 mm, and no gap; functional volumes consisted of 16 transaxial slices and were acquired in two runs for each functional session. The number of volumes acquired during a single run varied across subjects between 146 and 260. Finally, a high resolution structural volume was acquired at the end of the session via a 3D MPRAGE sequence with the following features: sagittal, matrix 256×256 , FoV 256 mm, slice thickness 1 mm, no gap, in-plane voxel size $1 \text{ mm} \times 1 \text{ mm}$, flip angle 12° , TR = 9.7 ms, TE = 4 ms.

Image Analysis

Data were analyzed by means of the Brain Voyager QX software (Brain Innovation, The Netherlands). Because of the T1 saturation effects, the first three scans of each run were discarded from the analysis. Preprocessing of functional scans included motion correction and removal of linear trends from voxel time series. The motion correction

was performed by means of a three-dimensional rigid body transformation to match each functional volume to the reference volume (the fourth volume). The estimated translation and rotation parameters for each volume in the time course were inspected to check that the movement was not larger than approximately half a voxel for each functional run and that no stimulus-correlated movement had occurred [Friston et al., 1996; Hajnal et al., 1994]. Pre-processed functional volumes of a subject were coregistered with the corresponding structural data set. Since the 2D functional and 3D structural measurements were acquired in the same session, the coregistration transformation was determined using the Siemens slice position parameters of the functional images and the position parameters of the structural volume. Structural and functional volumes were transformed into the Talairach space [Talairach and Tournoux, 1988] using a piecewise affine and continuous transformation. Functional volumes were resampled at a voxel size of $3 \text{ mm} \times 3 \text{ mm} \times 3 \text{ mm}$.

The statistical analysis was performed for individual subjects using the general linear model [GLM; Friston et al., 1995] with correction for temporal autocorrelation [Bullmore et al., 1996; Woolrich et al., 2001], considering as predictors of interest the correct analytic, error analytic, correct figural, and error figural conditions. The control task was used as baseline whereas the “instruction” and “match” conditions were included in the model as predictors of no interest. To account for the hemodynamic delay, the boxcar waveform representing the rest and task conditions was convolved with an empirically founded hemodynamic response function [Boynton et al., 1996].

The GLM parameters (beta values) estimated in individual subject analysis were entered in a second level voxel-wise random effect analysis, in order to search for activated areas that were consistent for the whole group ($N = 18$). In this analysis a percent signal change normalization of the time series from each subject was performed. Activation maps were created considering the contrast between predictors of interest (correct analytic, error analytic, correct figural, and error figural) and the control task. The contrast between the analytic (correct and error) and figural (correct and error) conditions was considered as well. The resulting group activation maps were thresholded at $P < 0.05$ (corrected for multiple comparisons by means of the Bonferroni method) and superimposed on the Talairach transformed structural scan of one of the subjects.

A second step analysis considered only the brain activity during reasoning problems for which a correct response was given. To assess differences in BOLD signal change related to g-level, we performed the random effect analysis separately for the low-gf and high-gf groups. Activation maps were created considering the contrast between predictors of interest (correct analytic, correct figural) and the control task. A direct contrast between the two groups (low-gf vs. high-gf) was considered as well. Regions of interest (ROIs) were determined by considering the mask

Figure 3.

(A) Differences between low- and high-gf groups on correct response rate (lower), reaction time in the match period (upper), and reasoning time on correct responses (middle) at analytic and figural reasoning. (B) Differences between performances at moderate and difficult matrices of the whole fMRI sam-

ple ($N = 18$). Correct and incorrect response rate (lower), the corresponding reasoning time (middle), and reaction time in the match period (upper) are displayed (trials in which the response was missing are not reported). * $P < 0.005$; ** $P < 0.0001$.

obtained from voxels activated in any condition of interest and group.

Signal time course in the defined ROIs was derived for each subject and analyzed in order to characterize the fMRI response during the different conditions. The fMRI BOLD response was evaluated as the percent signal change with respect to the control condition. These values were used as the dependent variable in analysis of variance (ANOVA for repeated measures) with the following factors: "ROI," indicating the region of activations; "hemisphere," indicating the side of activations; "condition," specifying the type of problems; "groups," standing for low- and high-g samples. All the results obtained from the ANOVA tests were corrected for multiple comparisons (Bonferroni).

RESULTS

fMRI Subject Selection and Behavioral Task

The distribution of IQ scores obtained from the 69 volunteers sample is presented in Figure 1. Similarly to the

distribution of the g factor in the general population [Jensen, 1998], the curve is normally shaped (Skewness = 0.338 SE = 0.289; Kurtosis = -0.302 SE = 0.570) and has a mean value of 102.3 and standard deviation of ± 11.27 . The screening procedure for selecting subjects for the fMRI session engendered two groups with significant differences in fluid intelligence. The low-gf sample had a mean value of IQ scores ($IQ = 87.37 \pm 5.57$) that was almost two standard deviations lower than the one exhibited by the high-gf group ($IQ = 118.8 \pm 5.73$).

Figure 3 summarizes the result obtained in the fMRI gf task. Reasoning times (i.e. the time necessary to generate a solution and to make the initial button press for calling the match period), the number of correct responses, error rates, and percentages of missing responses were calculated for each participant and in both figural and analytic conditions. Our results revealed small differences between the groups with the high-gf subjects always showing better performances than the low-gf group. Independent sample *t*-tests on the behavioral variables did not reach statistical

Figure 4.

Significant clusters of activation from the group ($N = 18$) random effect analysis and superimposed on MRI image in Talairach space of a representative subject. The statistical map was obtained by subtracting the brain activity recorded during control task from that of moderate and complex (respectively figural and analytic) fluid reasoning. Corrected cluster significance $P < 0.05$.

significance. Nonetheless, within the whole sample and for the two groups separately, we found evidence for significant differences in reasoning difficulty between analytic and figural matrices. All of the 18 participants needed a longer reasoning time when dealing with analytic respect to the figural stimuli for both correct (dependent sample t -test; $P < 0.0001$) and incorrect responses (dependent sample t -test; $P < 0.005$) and showed higher rates of errors in the analytic condition (dependent sample t -test; $P < 0.0001$) as well. Moreover, we did not observe any significant differences in the reaction times recorded in the match period neither between the groups nor the types of problem. In addition, consistent with the initial instructions (the subject was asked not to guess the solution, but to miss the response when necessary), we obtained the following mean percentages of missing responses: 16.4% for the analytic items and 2.5% for the figural problems (data not reported in the figure).

Neural Networks Subservicing Fluid Reasoning

To identify the neural network subserving fluid reasoning, we first performed the random effect analysis on the whole sample ($N = 18$) ignoring any differences in gf-level within the group and disregarding of stimuli complexity and accuracy of responses. Figure 4 shows the resulting statistical map created by subtracting brain activity during control task from that of moderate and complex (respectively, figural and analytic) reasoning. We found a strong bilateral recruitment of lateral prefrontal cortices, with activations spreading from the premotor areas to the anterior parts of inferior frontal gyri, a bilateral activation of the pre-supplementary motor area, the recruitment of the anterior parts of the left and right insula and broad activities evident on the posterior parietal cortices. A detailed description of sites of activation is given in Table I.

To assess the possible cortical region selective for the two different reasoning problems, we created distinct acti-

TABLE I. Anatomical descriptions, Brodmann areas, centroids (in Talairach coordinates, mm), and maxima t score of the significant fMRI activations obtained from the whole group ($N = 18$)

ROI	Anatomical regions	Brodmann areas		Talairach coordinates			n voxel	Peak t score
				x	y	z		
Pre-SMA	Superior frontal gyrus	6, 8, 32	Left/right	-1	11	49	291	10.90
PM	Precentral sulcus	6	Left	-29	-14	52	149	10.97
			Right	24	-11	52	83	11.86
DLPFC	Inferior frontal gyrus	9, 6	Left	-46	-2	33	61	9.88
			Right	45	8	30	57	11.35
INS	Anterior insula	45, 13	Left	-30	18	8	176	11.15
			Right	33	18	8	102	9.63
TEMP	Posterior aspect of the inferior temporal gyrus	37	Left	-46	-62	-8	463	14.94
			Right	49	-53	-14	57	9.22
PPL	Precuneus, intraparietal sulcus	7, 40, 19	Left	-33	-53	43	1098	13.2
			Right	29	-62	46	1031	12.53

Pre-SMA, pre-supplementary motor area; PM, pre-motor area; DLPFC, dorsolateral prefrontal cortex; INS, anterior insula; TEMP, posterior temporal; PPL, posterior parietal lobe.

vation maps considering the contrasts analytic versus control and figural versus control. These maps were comparable in terms of number and sites of activation and both were characterized by the recruitment of the broad bilateral fronto-parietal network previously described. A direct contrast of these predictors (analytic vs. figural) did not result in activation of any specific area beyond those previously reported, thus suggesting a fluid neural network independent from complexity. Nonetheless, when using a more lenient voxel threshold ($P_{\text{uncorrected}} < 0.01$) the direct contrast between analytic and figural conditions yielded to some activations involving the aforementioned cortical sites which were considered not remarkable.

Functional Differences Between High-gf and Low-gf Samples

To explore the BOLD signal variation associated with individual differences in gf-level across subjects, we analyzed the brain activity on reasoning problems for which a correct responses was made (that is 64.2% of task). This resulted in comparable amounts of fMRI data for the two conditions since the longer reasoning time on the analytic problems was counterbalanced by a higher rate of accuracy for the figural items.

To identify the ROI for further analysis, two distinct random effect analysis were performed on low- and high-gf samples independently, comparing the signal of moderate and complex gf task to that of control task. The resulting maps ($P < 0.05$) were comparable between the groups in terms of number and sites of activation. The direct contrast (low-gf vs. high-gf, $P < 0.05$) did not reveal any specific area in addition to those of the fronto-parietal network previously described. Thus, we obtained comparable cortical sites of activation among the analysis performed on the whole sample ($N = 18$) and independently for each gf-group.

Then, we defined six ROIs as the activation clusters obtained from the whole group analysis and the individual BOLD responses in each of the above regions were entered in a $6 \times 2 \times 2 \times 2$ analysis of variance for repeated measure (see methods under image analysis section). We obtained that low- and high-gf groups showed different brain activities in two specific regions of the cortex during figural reasoning (interaction among "ROI," "condition," and "group" factors, $F_{[5,80]} = 4.17$; $P = 0.002$; observed power = 0.95; partial η -squared = 0.21). We report on top of Figure 5 the two resulting plots (analytic and figural conditions) displaying the percentage of signal change of the six ROIs for the two groups.

Regional brain activities elicited by reasoning on analytic (complex) matrices are comparable across individuals with different gf-level. By contrast, when dealing with figural (moderate) problems, participants with higher level on the gf-factor seemed to show a smaller intensity of fMRI signal in pre-SMA and DLPFC regions compared to those with lower IQs. Given that the use of extreme groups can inflate

Type I error for the interaction between gf variability and the level of complexity [Conway et al., 2005], we screened in detail individual BOLD signals within each group and no outliers were found. Moreover, we observed homogeneous variability between groups (Levene statistic) for each dependent variable (% signal change of each ROI). A one-way ANOVA between the two groups was performed on the figural BOLD signal recorded in each of the ROIs and revealed significant differences in the pre-SMA bilaterally ($F_{[1,16]} = 7.06$; $P = 0.017$; observed power = 0.70; partial η -squared = 0.31) and in the right DLPFC ($F_{[1,16]} = 17.22$; $P = 0.001$; observed power = 0.97; partial η -squared = 0.52) regions, with the low-gf group having greater brain activity (see Fig. 6).

To exclude the possibility that the observed different activations between the groups were caused by unbalanced gender ratio we performed the very same analysis including the female subjects only (8 females for the low- and 6 females for the high-IQ sample, respectively). The results were similar to the ones obtained from the all participant analysis. Specifically, we had a significant interaction among "ROI," "condition," and "group" factors ($F_{[5,60]} = 3.39$; $P = 0.009$; observed power = 0.88; partial η -squared = 0.22). The two resulting plots (analytic and figural conditions) reported at the bottom of Figure 5 indicated clear differences between the activities of the two groups in two specific regions during figural reasoning. When these differences were directly tested by means of a one-way ANOVA between the two groups, a significant P value was obtained only for the right DLPFC ($F_{[1,12]} = 10.75$; $P = 0.007$; observed power = 0.85; partial η -squared = 0.47) during figural reasoning. The different activity seen bilaterally in pre-SMA on the whole group was smaller for the female sample and did not reach statistical significance ($F_{[1,12]} = 2.15$; $P = 0.168$; observed power = 0.27; partial η -squared = 0.15).

To exclude the possibility that the reduced difference observed in pre-SMA between low- and high-IQ samples was ascribable to differences associated with gender, we also performed for the high-IQ group (4 males, 6 females) a one-way ANOVA with "sex" as factor and the individual BOLD responses of each ROI as dependent variables. The data did not reveal significant differences related to gender.

Increasing Difficulty and Individual Differences

We investigated whether the increasing difficulty between the two types of problem was related to specific patterns of regional BOLD response variation within each sample. Our analysis revealed two opposite patterns of neural activity variation for the two groups as a function of task difficulty. On the whole, an increment of stimuli complexity induced an enhancement of signal intensity in some frontal and parietal areas for the high-gf subjects and a decrement in the same cortical areas for the low-gf subjects. Of note the differences between the two types of

Figure 5.

Profile plots from the ANOVA test for repeated measure showing the interaction among “ROI,” “condition,” and “group” factors. **(A)** On the top ANOVA test was performed on the whole group ($N = 18$; $F_{[5,80]} = 4.17$; $P = 0.002$). **(B)** On the bottom ANOVA test was performed on female participants only ($N =$

14; $F_{[5,60]} = 3.39$; $P = 0.009$). PM, premotor cortex; pre-SMA, pre-supplementary motor area; TEMP, temporal; PPL, posterior region of parietal lobe; INS, insula; DLPFC, dorsolateral prefrontal cortex.

problem were obtained by comparing activities estimated on the bases of a common reference baseline (control matrices). Specifically we performed for high- and low-IQ volunteers separately, paired sample t -test between figural and analytic neural activities recorded in the six ROIs and obtained the following results: the high-gf group revealed stronger activation in the right DLPFC and pre-SMA bilaterally, when solving complex versus moderate items ($T_{[9]} = 2.86$, $P = 0.02$; $T_{[9]} = 2.37$, $P = 0.04$, respectively). By contrast, the low-gf group showed decrease brain activity in the DLPFC bilaterally (right DLPFC, $T_{[7]} = -2.8$; $P = 0.03$; left DLPFC, $T_{[7]} = -3.16$; $P = 0.02$), and in the left posterior parietal ($T_{[7]} = -4.8$; $P = 0.002$) when stimuli complexity increased (see Fig. 6).

DISCUSSION

In the last decade neuroscientists have revealed important details on the neurobiology of intelligence, making

clear which regions of the cortex are involved in gf [a broad cognitive factor belonging to the second stratum of human abilities and highly correlated with general intelligence; Carroll, 1993, 2003] and suggesting some plausible hypothesis on the neural correlates of individual differences. The present investigation sought at integrating two different methods largely employed in studying this topic: task- and individual differences-based approaches. The positive feature of our paradigm lied on the concomitant analysis of the differences in cortical activations related to fluid reasoning difficulty between and within groups of subjects with different gf-level.

Our data first confirmed a distributed fronto-parietal network subserving fluid intelligence which is common to moderate and complex reasoning items and is independent from subjects ability level. Furthermore, even if low- and high-IQ samples presented similar behavioral performances inside the scanner, they differed in terms of neural activity modulation among the entire fronto-parietal network

Figure 6.

Differences in activations of the ROIs between and within low- and high-g samples and expressed as changes in BOLD signals during moderate (figural) and difficult (analytic) reasoning. Pre_SMA, pre-supplementary motor area; PPL, posterior parietal lobe; DLPFC, dorsolateral pre-frontal cortex. $^{\circ}P < 0.05$; $*P < 0.02$; $**P < 0.001$.

when dealing with different level of fluid complexity. In particular, two opposite patterns of signal variation occurred in response to increasing difficulty, entailing some specific nodes of the network (that is DLPFC and Pre-SMA for the high-gf subjects; DLPFC and posterior parietal regions for the low-gf subjects) which have been often involved in attentional control. In addition, when directly compared, the activities of the same frontal areas were also the ones that best predicted differences between the two groups with the low-ability sample having greater activations during performance on moderate task compared to the high-ability sample.

The fronto-parietal network observed in this study has been largely indicated as the neural substrate of intelligence [Gray and Thomson, 2004; Jung and Haier, 2007]. It have been also associated with many different tasks [Duncan and Owen, 2000], such as shifts of attention between location [Corbetta et al., 2000] or sensory modalities [Shomstein and Yantis, 2004], where executive control

was the main common feature. This strong common activation of the network across a large variety of tasks, led to an interesting proposal which emphasizes its adapting function to task demands and describes it as a sort of facilitating system which attends, in many contexts, to relevant information and supports its processing in specific brain systems [Duncan, 2001, 2005; Miller and Cohen, 2001].

An unforeseen result was that, despite the significant variability among participants IQs, we did not find sharp differences between sample behavioral performances at the fMRI task. At both figural and analytic problems, the high-gf group performed slightly better than the low-gf but these differences were not statistically significant. Even if unexpected this phenomenon can be related to the somewhat tight and stressing condition in which the participants had to perform their task. This condition might have affected the cognitive abilities involved with fluid intelligence. Another reasonable explanation could be ascribed to the selection of the Raven items, since a set of matrices

randomly selected (the fMRI task used in the current study) might not have a progressive variability of difficulty, especially for complex problems. This could be somewhat related to the finding of a reduced percentage of overall accuracy in analytic reasoning (around 40% which is near to chance performance) with respect to those revealed by some other authors [around 70%; e.g. Prabhakaran et al., 1997]. The missing response analysis suggested that subjects followed the initial instructions and that the correct solutions during the analytic problems were provided by reasoning on the matrices instead guessing the results. Actually, in a recent fMRI investigation Lee et al. [2006] reported behavioral data partly similar to those presented in the current study both in terms of differences between groups and of accuracy rates. Superior- and average-gf groups performed simple and complex fluid reasoning problems inside the scanner which were previously validated with a behavioral experiment on a different sample. Regardless of the extreme variability in gf-level they did not obtain very remarkable differences in task accuracy even if they reached statistical significance (note the good number of participants in the investigation of Lee et al., 2006; $N = 36$). Moreover, in the complex task (the one comparable to analytic problems of the current study), the validating sample obtained 40% of correct responses while the average g group achieved the 50%.

Even if unexpected the comparable performance between the two groups might represent an important advantage for the interpretation of the fMRI results and can extend our knowledge on the neural underpinnings of intelligence. A comparison of brain activation between groups which differ in task performance can be confounded by the performance differences. In the current study, the obtained BOLD variation patterns could be disentangled from the performance in the scanner and could be related to substantial differences in fronto-parietal neural modulation which likely depended on individual differences in gf-level.

In our study, subjects with high gf showed stronger activation of some frontal and parietal regions when the activity related to complex reasoning items was compared with the one associated with problems of moderate difficulty. These differences were significant for DLPFC and Pre-SMA. Low-ability subjects presented an opposite pattern with a decrement of the signal which was mostly evident in DLPFC and in the posterior parietal regions. We suggest that the reported patterns reflect substantial differences in problem-solving strategies in response to increasing demands. Consistent with the neural efficiency hypothesis [Haier et al., 1988; Naubauer et al., 2004] greater intellectual abilities induced high gf participants to spend less overall cognitive resources on moderate fluid problems and more when reasoning on complex task. This probably yielded to an overall increment of BOLD signal among the fronto-parietal network when the stimuli complexity increases. On the other hand, volunteers with lower intellectual abilities (that is the low-gf sample) needed to spend

considerable mental effort even when solving moderate-level problems. Then, when asked to reason on complex matrices, they might have experienced a sort of “overload” of their partly limited resources. The corresponding neural expression of this cognitive phenomenon could be identified with the decrement of signal intensity when comparing complex to moderate items.

Our results partially converge with the findings reported in a early PET study in which the impact of individual fluid ability was investigated during the execution of easy and hard working memory tasks adapted to participants ability [Larson et al., 1995]. One main result was a different pattern of changes in neural activity between low and high ability samples when comparing hard versus easy problems. Higher gf subjects had an enhancement of cortical glucose use while lower gf subjects showed a significant decrement of brain activity. In that study however the different pattern of signal variation, when analyzed as the ratio between ROI and overall glucose metabolic rate, amplified inter-group variability in cortical activation with the high-ability subjects showing greater activity than the low-ability subjects. Our findings are consistent with the data reported in a recent EEG investigation which analyzed the relationship between event-related desynchronization/synchronization (ERD/ERS) in the alpha band and individual differences in gf [Doppelmayr et al., 2005]. The authors obtained a significant interaction between task difficulty (a modified version of the Raven Standard Matrices) and the subjects' IQs, with the higher gf participants showing weaker activation during the easy problem and a significant increase from easy to difficult tasks that did not occur in the low ability subjects. By contrast lower gf presented a decreased activity in the alpha band (interpreted in terms of smaller cortical activation) as stimuli complexity increased.

Our hypothesis is also supported by a class of evidence which documented differential patterns of response in some areas of the frontal region (the one involved in executive attention mainly) following increasing cognitive demand. In the neuroscience of intelligence, Kroger et al. [2002] reported a greater activation of DLPFC as a function of task complexity, with involvement of the most anterior part following the highest level of fluid reasoning. Similarly, some fMRI investigations showed a linear activity increase in those region (especially DLPFC) anatomically networked to WM in response to an enhancement of cognitive load [Braver et al., 1997; Jonides et al., 1997]. But these same regions mediating attentional control (especially DLPFC but also the parietal cortex) were the ones showing unchanged or even decreased brain activity when cognitive demands were excessive probably reflecting an attentional resources limitation [Kane and Engle, 2002].

Besides, when the cortical activities of the two groups were directly compared, we observed that the low-ability participants showed a greater activation in DLPFC and Pre-SMA regions specifically when solving matrices of moderate difficulty. This phenomenon can be related to the stronger recruitment of prefrontal regions by

low-ability subjects which may require more executive control than higher ability individuals to perform successfully even when dealing with simple task [Rypma et al., 2006]. Our findings seem to bring up again the relevance of frontal activities in supporting fluid intelligence [Duncan et al., 2000]. Even if the current study does not distinguish among those cognitive functions that contribute, previous data about the strong involvement of executive process and goal management in fluid reasoning suggest the hypothesis that the greater activation observed in the frontal regions might be related to a different modulation of attention. That is low-ability subjects probably loaded more on the executive during moderate reasoning respect to high-IQ subjects, hence experiencing higher rate of prefrontal activations. In a recent fMRI investigation, Gray et al. [2003] showed that DLPFC activity during interference trials in a 3-back WM task was the one that best predicted subjects' fluid abilities. Accordingly, others studies emphasized the importance of storing information and actively maintaining access to stimulus representations and goals—especially in high interference contexts—which are mainly mediated by prefrontal cortex activity [Duncan et al., 1995, 1996; Waltz et al., 1999]. Moreover, Kane and Engle [2002] strongly indicated this feature as the linking bridge between WM and fluid intelligence, finding evidence for a unique executive-attention role played by lateral and medial prefrontal cortices. Certainly, further studies exploring the characteristic features of prefrontal contributions and their relation with fluid intelligence are needed especially in light of the different patterns of activation reported in the current study.

However, we must acknowledge that the unbalanced gender ratio between low- (all females) and high-IQ samples (4 males and 6 females) might have partially affected our results. Specifically, recent fMRI investigations have shown that males and females may possibly present different patterns of activation conditioned by task nature and somewhat independent from behavioral performance [Bell et al., 2006; Ragland et al., 2000]. To exclude this possible bias we compared the neural activities of the two groups not including the male participants. From a comparison of part A and B of Figure 5, we observe a similar trend between the two sets of analysis where the low-IQ sample shows apparent greater activities in pre-SMA and DLPFC areas during figural reasoning. Even if the sample size was relatively small we obtained an observed power of 0.88 which indicates that these interactions might be statistically significant and 88% of similar studies performed on samples consisting of the same number of subjects.

Nonetheless when directly tested (one-way ANOVA) the revealed differences were significant only for the right DLPFC. Therefore when considering the female subjects only, the gap between pre-SMA activations in low- and high-IQ samples resulted reduced. This might be probably due to the relative smaller number of cases used in the second set of analysis but it could also be ascribed to differences in activation associated with gender. This hypothesis was verified

and the comparison between the ROIs neural activities of males and females of the high-IQ sample did not reveal any significant difference. Taken together, these results seem to exclude the possibility that the differential patterns of neural responses to reasoning complexity observed in low- and high-IQ subjects may be a consequence of gender or may be influenced by it. Anyway the small number of cases used in the analysis (especially in the comparison between male and female participants performed on the high-IQ group) drives us to be cautious in completely excluding the influence of gender and further explorations taking into account this possible bias are needed.

Gur et al. [2000] explored sex differences during the execution of easy and hard versions of a verbal-reasoning (analogies) task (a design similar to the one used in the current study). In particular, both male and female participants revealed an enhancement of activity in response to increasing difficulty. This enhancement was higher for the male volunteers which also showed stronger activation during the easy version of the verbal analogies. These findings are inconsistent with our results which revealed differential patterns of activations between the groups and stronger activity for the low-IQ sample (all females) during reasoning on moderate difficulty problems. Finally, it is worth of note that not all studies have found a significant gender effect [Schlosser et al., 1998; Shaw et al., 2006].

In conclusion, the current investigation supports the notion of a widely distributed network underpinning fluid intelligence whose activity is strongly modulated by a cognitive effort investment. This can be neurally expressed by differential patterns of BOLD variation following increasing difficulty among participants with different intellectual ability. Furthermore, the involvement of prefrontal cortex in differencing activation between groups suggests variability in modulating attentional resources among subjects with diverse gf and brings up again the relevance of this region in supporting fluid intelligence.

ACKNOWLEDGMENTS

We would like to thank Fiscellus Mons for the kind support to this study. We also thank Prof. Maurizio Corbetta for valuable comments on the manuscript. A special thank goes to Dr. Erika Pilar Pancella for revising the English style of the manuscript.

REFERENCES

- Bell EC, Willson MC, Wilman AH, Dave S, Silverstone PH (2006): Males and females differ in brain activation during cognitive tasks. *Neuroimage* 30:529–538.
- Blair C (2006): How similar are fluid cognition and general intelligence? A developmental neuroscience perspective on fluid cognition as an aspect of human cognitive ability. *Behav Brain Sci* 29:109–125.
- Boynton GM, Egel SA, Glover JH, Heeger DJ (1996): Linear system analysis of functional magnetic imaging in human V1. *J Neurosci* 16:4207–4221.

- Braver TS, Cohen JD, Nyström LE, Jonides J, Smith EE, Noll DC (1997): A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage* 5:49–62.
- Bullmore E, Brammer M, Williams S, Rabe-Hesketh S, Janot N, David A, Mellers J, Howard R, Sham P (1996): Statistical methods of estimation and inference for functional MR image analysis. *Magn Reson Med* 35:261–277.
- Carpenter PA, Just MA, 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.
- Carpenter PA, Just MA, Reichle ED (2000): Working memory and executive function: evidence from neuroimaging. *Curr Opin Neurobiol* 10:195–199.
- Carroll JB (1993): *Human Cognitive Abilities: A Survey of Factor Analytic Studies*. New York: Cambridge University Press. 828 p.
- Carroll JB (2003): The higher-stratum structure of cognitive abilities: Current evidence supports g and about ten broad factors. In: Nyborg H, editor. *The Scientific Study of General Intelligence. Tribute to Arthur R. Jensen*. Oxford: Elsevier Science. pp 5–21.
- Cattell RB (1987): *Intelligence: Its Structure, Growth and Action*. New York: Elsevier. 694 p.
- Cattell RB, Cattell AKS (1973): *The Culture—Fair Test*. Champaign: IPAT.
- Cattell RB, Cattell AKS (1981): *The Culture—Fair Test*. Firenze: O.S.
- Christoff K, Prabhakaran V, Dorfman J, Zhao Z, Kroger JK, Holyoak KJ, Gabrieli JD (2001): Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage* 14:1136–1149.
- Conway ARA, Kane MJ, Bunting MF, Hambrick DZ, Wilhelm O, Engle R (2005): Working memory span tasks: A methodological review and user's guide. *Psychon Bull Rev* 12:769–786.
- Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL (2000): Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci* 3:292–297.
- Deary IJ (2000): *Looking down on human intelligence*. New York: Oxford University Press. 379 p.
- Doppelmayr M, Klimesch W, Sauseng P, Hodlmoser K, Stadler W, Hanslmayr S (2005): Intelligence related differences in EEG-bandpower. *Neurosci Lett* 381:309–313.
- Duncan J (2001): An adapting coding model of neural function in prefrontal cortex. *Nat Rev Neurosci* 2:820–829.
- Duncan J (2005). Prefrontal cortex and Spearman's g. In: Duncan J, Phillips L, McLeod P, editors. *Measuring the Mind: Speed, Control and Age*. New York: Oxford University Press. pp 249–272.
- Duncan J, Owen AM (2000): Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci* 23:475–483.
- 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. *Cognit Psychol* 30:257–303.
- Duncan J, Seitz RJ, Kolodny J, Bor D, Herzog H, Ahmed A, Newell FN, Emslie H (2000): A neural basis for general intelligence. *Science* 289:457–460.
- Fletcher PC, Shallice T, Dolan RJ (1998): The functional roles of prefrontal cortex in episodic memory. *Brain* 121:1239–1248.
- Forbes AR (1964): An item analyses of the advanced matrices. *Br J Educ Psychol* 34:1–14.
- Friston KJ, Holmes AP, Worsley KG, Poline JB, Frith CD, Frackowiak RS (1995): Statistical parametric maps in functional imaging: A general linear approach. *Hum Brain Mapp* 2:189–210.
- Friston KJ, Williams S, Howard R, Frackowiak RSJ, Turner R (1996): Movement related effects in fMRI time series. *Magn Reson Med* 35:346–355.
- Geake JG, Hansen PC (2005): Neural correlates of intelligence as revealed by fMRI of fluid analogies. *Neuroimage* 26:555–564.
- Gray JR, Thompson PM (2004): Neurobiology of intelligence: Science and ethics. *Nat Rev Neurosci* 5:471–482.
- Gray JR, Chabris CF, Braver TS (2003): Neural mechanisms of general fluid intelligence. *Nat Neurosci* 6:316–322.
- Gur RC, Alsop D, Glahn D, Petty R, Swanson CL, Maldjian JA, Tureusky BI, Detre JA, Gee J, Gur RE (2000): An fMRI study of sex differences in regional activation to a verbal and a spatial task. *Brain Lang* 74:157–170.
- Haier RJ, Siegel BV, Nuechterlein KH, Hazlett E, Wu J, Paek J, Browning H, Buchsbaum MS (1988): orbital glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. *Intelligence* 12:199–217.
- Hajnal JV, Myers R, Oatridge A, Schwieso JE, Young IR, Bydder GM (1994): Artifacts due to stimulus correlated motion in functional imaging of the brain. *Magn Reson Med* 31:283–291.
- Hon N, Epstein RA, Owen AM, Duncan J (2006): Frontoparietal activity with minimal decision and control. *J Neurosci* 26:9805–9809.
- Horn JL (1998): A basis for research on age differences in cognitive capabilities. In: McArdle JJ, Woodcock R, editors. *Human Cognitive Abilities in Theory and Practice*. Chicago: Riverside. pp 57–91.
- Hunt E (1974): Quote the raven? Nevermore! In: Gregg LW, editor. *Knowledge and Cognition*. Hillsdale: Erlbaum. pp 129–158.
- Jensen A (1998): *The g Factor*. Westport: Praeger. 648 p.
- Jonides J, Schumacher EH, Smith EE, Lauber EJ, Awh E, Minoshima S, Koeppel RA (1997): Verbal working memory load affects regional brain activation as measured by PET. *J Cogn Neurosci* 9:462–475.
- Jung RE, Haier RJ (2007): The parieto-frontal integration theory (P-FIT) of intelligence: Converging neuroimaging evidence. *Behav Brain Sci* 30:135–187.
- Kane MJ, Engle RW (2002): The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psych Bull* 128:637–671.
- Kane MJ, Hambrick DZ, Conway ARA (2005): Working memory capacity and fluid intelligence are strongly related constructs: Comment on Ackerman, Beier, and Boyle. *Psychol Bull* 131: 66–71.
- Kaufman JC, Kaufman AS (2006): Some considerations concerning neurological development and psychometric assessment. *Behav Brain Sci* 29:137–138.
- Kroger JK, Sabb FW, Fales CL, Bookheimer SY, Cohen MS, Holyoak KJ (2002): Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: A parametric study of relational complexity. *Cereb Cortex* 12:477–485.
- Larson GE, Haier RJ, Casse LL, Hazen K (1995): valuation of a "Mental Effort" hypothesis for correlations between cortical metabolism and intelligence. *Intelligence* 21:267–278.
- Lee KH, Choi YY, Gray JR, Cho SH, Chae J, Lee S, Kim K (2006): Neural correlates of superior intelligence: Stronger recruitment of posterior parietal cortex. *Neuroimage* 29:578–586.
- Miller EK, Cohen JD (2001): An integrative theory of prefrontal cortex function. *Annu Rev Neurosci* 24:167–202.

-
- Neubauer AC, Grabner RH, Freudenthaler HH, Beckmann JF, Guthke J (2004): Intelligence and individual differences in becoming neurally efficient. *Acta Psychol* 116:55–74.
- Prabhakaran V, Smith JA, Desmond JE, Glover GH, Gabrieli JD (1997): Neural substrates of fluid reasoning: An fMRI study of neocortical activation during performances of the raven's progressive matrices test. *Cogn Psychol* 33:43–63.
- Ragland JD, Coleman AR, Gur RC, Glahn DC, Gur RE (2000): Sex differences in brain-behavior relationships between verbal episodic memory and resting regional cerebral blood flow. *Neuropsychologia* 38:451–461.
- Raven JC (1965): *Advanced Progressive Matrices: Sets I and II*. London: Lewis.
- Raven JC (1976): *Standard Progressive Matrices: Sets A, B, C, D and E*. Oxford: Oxford Psychologists Press.
- Rypma B, Berger JS, Prabhakaran V, Bly BM, Kimberg DY, Biswal BB, D'Esposito M (2006): Neural correlates of cognitive efficiency. *NeuroImage* 33:969–979.
- Schlösser R, Hutchinson M, Joseffer S, Rusinek H, Saarimaki A, Stevenson J, Dewey SL, Brodie JD (1998): Functional magnetic resonance imaging of human brain activity in a verbal fluency task. *J Neurol Neurosurg Psychiatry* 64:492–498.
- Shomstein S, Yantis S (2004): Control of attention shifts between vision and audition in human cortex. *J Neurosci* 24:10702–10706.
- Shaw P, Greenstein D, Lerch J, Clasen L, Lenroot R, Gogtay N, Evans A, Rapoport J, Giedd J (2006): Intellectual ability and cortical development in children and adolescents. *Nature* 440:676–679.
- Spearman C (1904): "General intelligence": Objectively determined and measured. *Am J Psychol* 15:201–292.
- Sternberg RJ (2000): Cognition. The holy grail of general intelligence. *Science* 289:399–401.
- Sternberg RJ (2005): The importance of converging operations in the study of human intelligence. *Cortex* 41:243–244.
- Talairach J, Tournoux P (1988): *Coplanar Stereotaxic Atlas of the Human Brain*. New York: Thieme. 132 p.
- Waltz JA, Knowlton BJ, Holyoak KJ, Boone KB, Mishkin FS, De Menezes Santos M, Thomas CR, Miller BL (1999): A system for relational reasoning in human prefrontal cortex. *Psychol Sci* 10:119–125.
- Weinberger DR, Berman KF, Zec RF (1986): Physiologic dysfunction of dorsolateral prefrontal cortex in schizophrenia. *Arch Gen Psychiatry* 43:114–124.
- Woolrich MW, Ripley BD, Brady M, Smith SM (2001): Temporal autocorrelation in univariate linear modeling of fMRI data. *Neuroimage* 14:1370–1386.
- World Medical Organization (1996): Declaration of Helsinki. *Br Med J* 313:1448–1449.
-