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Abstract

As for individual differences, spatial ability has been considered as an important component of intelligence. Nevertheless, neural correlates across a wide range of psychometric tests have not been elucidated with respect to individual differences in spatial ability. In this study, we compared individuals with high- and low-spatial ability through functional magnetic resonance imaging during psychometric tests of five problem types that are developed to assess spatial ability. Neural substrates underlying the psychometric tests corresponded to the cognitive network, including the dorsal attention system and the default-mode network, responsible for general cognitive functions. As regards adaptive modulation of activations depending on the difficulty level of the psychometric tests, only the high-spatial group exhibited an increase in activation in the fronto-parietal network. These results indicate that neural adaptability to changing cognitive load across the psychometric tests is a neural correlate that accounts for individual differences in spatial ability.

Keywords: cognitive load, difficulty level, fronto-parietal network, functional magnetic resonance imaging, neural adaptability, psychometric test, spatial ability.

INTRODUCTION

It is well known in literature that spatial ability is one of the core components of human intelligence (Cattell, 1963; Lohman, 1988; Thurstone, 1938). Spatial ability is defined as the ability to generate, retain, retrieve, and transform well-structured visual images (Lohman, 1994). Based on the claim that spatial ability is not a unitary construct, it involves different aspects of generation, storage, retrieval, and transformation of visuo-spatial information. A broad array of spatial factors that included spatial visualization and spatial relations was identified as most prominent (Carroll, 1993; French, 1951; Lohman, 1988, 2000). The factor of spatial visualization is regarded as linked to the ability to comprehend imaginary movements in a three-dimensional space or the ability to manipulate objects in imagination; and the factor of spatial relations as the ability to perceive spatial patterns or the ability to maintain the orientation of objects in space (French, 1951).

Several psychometric tests were suggested as the markers to distinguish the factors. The factor of spatial visualization was suggested to be measured through the tests such as a form board test, a hole punching test, and a surface development test (Ekstrom, French, & Harman, 1976; French, Ekstrom, & Price, 1963); and the factor of spatial relations through the tests on card rotations and cube comparisons (Ekstrom et al., 1976; French et al., 1963).

Recent advances in neuroimaging techniques elucidated neural correlates of spatial ability by using combined applications of neuroimaging and psychometric tests. Although functional and anatomical neural correlates of spatial ability were elucidated with respect to individual differences (Wanzel et al., 2007; Wolbers, Schoell, & Buchel, 2006) and were contrasted between sexes (Koscik, O'Leary, Moser, Andreasen, & Nopoulos, 2009), those studies used only a mental rotation test for the assessment of spatial ability. In this respect, use of a set of psychometric tests is in need for further exploration into the nonunitariness of spatial ability.

With regard to neural function, individual differences in neural adaptability could be related to individual differences in intelligence. Neural adaptability was demonstrated as adaptive modulation of neural resources in response to cognitive variables such as temporal expectancy, habituation, and information processing load. To be more specific, in event-related potentials (ERP) investigations of auditory stimuli, the difference in overall ERP amplitudes in response to the stimuli between unexpected and expected stimuli was shown to be correlated with intelligence in normal individuals (Schafer, 1982). The difference was also contrasted between normal individuals and mentally retarded individuals (Jensen, Schafer, & Crinella, 1981). Habituation of ERP amplitudes to repetitive stimuli was shown in normal individuals, but not in Down syndrome individuals (Schafer & Peeke, 1982). In a PET (positron emission tomography) investigation of problem solving, differential glucose metabolic rates for difficult and easy problems were exhibited only in individuals with high reasoning ability (Larson, Haier, LaCasse, & Hazen, 1995). In an fMRI (functional magnetic resonance imaging) investigation of sentence comprehension, differential activations of the left hemisphere language regions for low- and high-frequency words were shown only in individuals skilled in reading (Prat, Keller, & Just, 2007).

When psychometric tests are different in the difficulty level, individual differences in spatial ability are expected to be understood in terms of neural adaptability to cognitive load which may vary according to the difficulty level of psychometric tests. In the current fMRI investigation of spatial ability, we addressed two questions: (1) Which regions compose the cognitive network that commonly subserves a set of psychometric tests of spatial ability? (2) Are there individual differences in spatial ability in terms of neural adaptability across psychometric tests?

METHODS

Subjects

Thirty young healthy male college students (ranged between 20-23 years old) participated in the study. They were recruited by announcements on the bulletin boards of the local university. All participants reported no history of psychiatric or neurological abnormality and submitted the signed informed consent forms.

Pretest

All participants underwent psychometric paper-and-pencil tests (pretest) before the fMRI scanning. The tests consisted of five problem types that include mental rotation, surface development, aperture passing, orthographic projection, and hole punching. In the aperture passing test, the test taker is requested to find an object which fits the given view on a projection plane, while in the orthographic projection test, the test taker is given two views of an object, e.g., the front and the side views, and then asked to find a corresponding third view, e.g., the plan view. Those psychometric tests are known to draw on spatial visualization and spatial relations according as their relevant problem types require. It is reported in literature that surface development and hole punching draw on spatial visualization, mental rotation on spatial relations (Pellegrino and Kail, 1982).

The pretest consisted of 30 problems, with 6 problems of each problem type. To obtain the test score, we counted the number of the correct answers and that of the incorrect answers, subtracted the latter from the former value, and scaled this difference linearly into a score which lies between 0 and 100.

fMRI data acquisition and field test

Our fMRI data were acquired from a 3.0T ISOL FORTE scanner (ISOL Technology, Gyeonggi, Korea). A total of 177 whole-brain images were collected using a T2*-weighted single-shot echo-planar imaging (EPI) sequence (repetition time (TR) = 3,000 msec, echo time (TE) = 35 msec, number of slices = 36, slice thickness = 3 mm, matrix size = 64 × 64, field of view = 220 mm × 220 mm).

We used different problems for tests during scanning (field test) with the same five problem types as considered for the pretest except that the orthographic projection test is replaced with the picture completion test. The orthographic projection test did not seem appropriate for the fMRI scanning due to its difficulty level and test time. Participants were carefully informed of the procedure of the field test prior to the scanning.

The field test consisted of 42 problems: 12 for picture completion, 12 for mental rotation, 6 for surface development, 6 for aperture passing, and 6 for hole punching. The problems of each problem type were partitioned into three sets and the total of 15 sets was presented in random order for each participant. Each set of problems for which 21 seconds were allotted was preceded by a 6-second display of instruction on how to solve the problems in the set.

Each problem was displayed with two figure frames, one of which forms a stimulus figure and the other a test probe as shown in Figure 1. If the test probe well corresponds to the stimulus figure, the participant is supposed to answer ‘Yes’ by pressing the left mouse button; otherwise ‘No’ by pressing the right mouse button. The participant may not respond at all if s/he is not sure of the answer of a problem. The score of the field test was obtained in the same way as for the pretest.

Classification into high- and low-spatial groups

The participants who showed a large discrepancy between the two scores, one from the pretest and the other from the field test, were excluded because their attitudes towards the tests did not seem sincere. Three algorithms of clustering methods, single, complete, and average linkage algorithms, were applied to the other participants' scores and two groups were determined based on the clustering results of the three methods.

We will call the group corresponding to higher scores of the tests a *high-spatial* group and the other group a *low-spatial* group. The participants in the high-spatial (or low-spatial) group will be called high-spatial (or low-spatial) participants.

After classifying the participants into two groups, group differences in the performance were confirmed for each problem type via two-sample t-tests of the field test scores. A p-value less than 0.05 was considered statistically significant. Moreover, the order of difficulty level of the five problem types was assessed for each group based on the field test scores.

fMRI data analysis

Preprocessing and statistical analysis of the fMRI data were carried out using an SPM8 software (Wellcome Institute of Cognitive Neurology, London, UK). Each participant's fMRI data were preprocessed and statistically analyzed on an individual level, and then parameter estimates from contrasts in individual participant models were entered into random-effects analysis.

The preprocessing steps included spatial realignment to the mean volume of a series of images, normalization into the same coordinate frame as the MNI-template brain, and smoothing using a Gaussian filter of 8 mm FWHM.

In random-effects analysis we used factorial designs for analysis of variance (ANOVA) for repeated measures. With a factorial design that included group (high- and low-spatial groups) as a between-group factor and problem type (picture completion, mental rotation, surface development, aperture passing, and hole punching) as a within-group factor, the main and the interaction effects of group and problem type were assessed.

Common activations and deactivations across five problem types were searched for by cognitive conjunction (Price & Friston, 1997). Under the conjunction null hypothesis of lack of effects in any problem types, the regions subserving common cognitive operations underlying five problem types were expected to be disclosed.

For inspecting differences in neural adaptability between high- and low-spatial groups, a linear relationship of activations with the difficulty level of five problem types was assessed. With a factorial design that included test type as a within-group factor for each group, linear contrasts based on the order of difficulty level between five problem types were applied.

In all statistical inferences, the statistical significance was determined at the height threshold of a family-wise error-corrected *p*-value less than 0.05 and the cluster extent threshold of an uncorrected *p*-value less than 0.05.

RESULTS

Grouping into high- and low-spatial groups

As displayed in Figure 2, three participants were excluded before grouping due to abnormality in scores between the pretest and the field test and the other twenty-seven participants were partitioned into two groups. The complete and average linkage algorithms yielded the same sets of clusters consisting of fifteen high-spatial participants and twelve low-spatial participants.

Figure 3 exhibits the performance of the two groups based on the field test scores. The two groups showed significant differences in the performance for all problem types. According to the field test scores, the difficulty level of five problem types is in the order of hole punching, aperture passing, surface development, mental rotation, and picture completion from high to low in the high-spatial group, whereas it is in the order of hole punching, surface development, aperture passing, mental rotation, and picture completion in the low-spatial group.

Main and interaction effects on activation

In ANOVA for repeated measures with group and problem type as between-groups and within-group factors respectively, the main and the interaction effects of group and problem type were assessed. Figure 5 displays the main effects of group and problem type. There were no group-by-problem type interactions at the given threshold.

The main effects of group were shown over multiple cortical regions that covered the frontal lobe, the posterior parietal cortex, the temporal cortex, and the occipital cortex. The main effects of problem type were exhibited in the prefrontal cortex, the posterior parietal cortex, and the occipital cortex.

Common brain activations and deactivations by conjunction analysis of five problem types

The conjunction null hypothesis about the lack of effects in any problem types is considered in search of the regions commonly subserving activations and deactivations in response to five problem types. Figure 4 exhibits common activations and deactivations across five problem types and Table 1 lists the regions of statistical significance.

The lateral premotor area (frontal eye fields (FEF)), the dorsomedial frontal lobe (supplementary motor area (SMA)), the posterior parietal cortex (predominantly along the intraparietal sulcus (IPS)), the occipital cortex, and the insula were commonly bilaterally activated. The posterior medial regions, including the posterior cingulate gyrus (PCG), the precuneus, and the cuneus, the medial prefrontal cortex, and the lateral regions in the temporo-parietal cortex were commonly deactivated.

Linear relationship of activations with the difficulty level of psychometric tests

A linear relationship of activations with the rank order of the difficulty levels of the five problem types was proposed to exhibit modulation of activations depending on the changing difficulty levels of psychometric tests. Figure 6 exhibits the linear relationship of activations for each group and Table 2 lists the regions of statistical significance.

The positive linear relationship, that is, higher activations with more difficult problem types, was observed in the lateral prefrontal cortex and the posterior parietal cortex for the high-spatial group, but no positive relationship for the low-spatial group. Negative linear relationship, that is, lower activations with more difficult problem types, was shown in the occipital cortex for both groups and in the cerebellum only for the low-spatial group.

In Figure 7, the regions of the positive linear relationship were displayed together with the regions of higher activations for the high-spatial group. The selected eight regions of interest, the bilateral dorsolateral prefrontal cortex, the bilateral left inferior parietal gyrus, the bilateral left superior parietal gyrus, and the bilateral precuneus, display the positive linear relationship of activations with the difficulty level of problem types. The posterior parietal cortex demonstrated both the positive linear relationship and higher activations, while it was only the positive linear relationship as for the dorsolateral prefrontal cortex. Moreover, the regions of the positive linear relationship displayed a pronounced leftward asymmetry in strength and extent.

DISCUSSION

In this study, we performed fMRI experiments with a set of psychometric tests of five problem types that were developed for assessment of spatial ability. We searched for the cognitive network underlying the psychometric tests and found individual differences in spatial ability in terms of neural adaptability to changing cognitive loads which are required for a set of psychometric tests.

Common neural substrates for spatial ability

A conjunction analysis disclosed activations and deactivations caused by cognitive components common to the five problem types (Figure 4 and Table 1). The psychometric tests commonly activated a previously characterized attention network, including the FEF, the SMA, the IPS, and the insula. The bilateral FEF and the IPS compose the regions called the "dorsal attention system", which is involved in top-down orienting of attention (Corbetta & Shulman, 2002). Also, the SMA and the insula are activated by diverse cognitively demanding tasks (Cabeza & Nyberg, 2000; Duncan & Owen, 2000).

Common deactivations were demonstrated in the regions of the so called "default-mode network" which includes the PCG and the medial prefrontal cortex as main nodes (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Greicius, Krasnow, Reiss, & Menon, 2003; Raichle et al., 2001). The default-mode network is the regions that routinely exhibit deactivations during the performance of cognitively demanding tasks (Mazoyer et al., 2001; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003; Shulman et al., 1997).

We could see correspondence of the regions of common activations and deactivations in response to the psychometric tests to the previously known cognitive networks involved in a variety of cognitively demanding tasks. The common involvement of those identified cognitive networks indicates the contribution of general cognitive operations that are required for the psychometric tests. A high correlation between spatial ability and general intelligence, especially fluid ability (Colom et al., 2002), may be due to the overlap of general cognitive operations responsible for spatial ability tests and general intelligence tests.

Neural adaptability associated with individual differences in spatial ability

In ANOVA for repeated measures with group and problem type as between-group and within-group factors respectively, we could see significant main effects in group and problem type but no significant interaction effect of them (Figure 5). It implies that there were no differential effects of problem types on activations between high- and low-spatial groups.

We compared modulation of activations in response to the changing difficulty levels of the five problem types between high- and low-spatial groups (Figure 6 and Table 2). The high-spatial group exhibited the positive linear relationship in the prefrontal cortex and the posterior parietal cortex, while the low-spatial group showed no such relationship. Regarding information processing load, difficult problem types are supposed to require a high cognitive engagement. Stronger recruitment of the fronto-parietal cortex is shown in the high-spatial group only in response to higher difficulty levels of problem types, and it demonstrates individual differences in spatial ability in terms of neural adaptability to changing cognitive demands imposed by the psychometric tests we used for this study.

Involvement of the fronto-parietal cortex with changing cognitive loads only in the high-spatial group indicates that the fronto-parietal cortex plays a key role in accounting for individual differences in spatial ability or intelligence. Increased activations in the fronto-parietal cortex, specifically in the posterior parietal cortex, in response to the difficulty levels of problems, were related to superior intelligence (Lee et al., 2006). Indeed the fronto-parietal cortex was suggested to be responsible for individual differences in intelligence according to the parieto-frontal integration theory (P-FIT) as derived from a review of neuroanatomic aspects of intelligence (Jung & Haier, 2007) and verified by subsequent studies (Colom et al., 2009; Prabhakaran & Rypma, 2007).

In a functional connectivity study, the fronto-parietal network was proposed as a control system to integrate information from the dorsal attention system and the default-mode network (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). With common activations on the dorsal attention system and common deactivations on the default-mode network, the involvement of the fronto-parietal cortex in neural adaptability may reflect the roles of the fronto-parietal network for adaptive integration of the outcomes of multiple cognitive operations associated with the two systems.

As shown in Figure 7, the posterior parietal cortex showed adaptive modulation of activations in response to changing problem types as well as higher average activations across various problem types. The dorsolateral prefrontal cortex however exhibited only adaptive modulation of activations. The dorsolateral prefrontal cortex is responsible for executive functions and working memory (Robertson, Tormos, Maeda, & Pascual-Leone, 2001) and moreover activations in the prefrontal cortex are shown to increase along with working memory load only but not with visual attention load (Tomasi, Chang, Caparelli, & Ernst, 2007). The dorsolateral prefrontal cortex is considered to be recruited only for cognitively demanding tasks that require increased cognitive load specifically in the working memory, which is employed for maintaining visuo-spatial information in an active state of spatial ability.

The psychometric tests used in this study were designed for spatial tasks. Although the performance of spatial tasks is hypothesized to be primarily the responsibility of the right hemisphere, the leftward asymmetry of the regions of the positive linear relationship is likely to present a different mechanism of hemispheric specialization for individual differences in spatial ability. Further investigation is in need to explore the underlying mechanisms involved in solving different types of spatial tasks.

Activations in the occipital cortex, which are considered to be due to perceptual load in the visual search for finding features in visual images, showed a negative linear relationship with cognitive load in both high- and low-spatial groups. This result can be explained in light of Hay et al.'s (2006) contention that there is a distinction between tasks of high perceptual load and high cognitive load depending on whether attention is focused on the target or distributed over more than one task. Easy problem type such as picture completion may be regarded as tasks of high perceptual load rather than tasks of high cognitive load. In the same context, decreased activations in the occipital cortex could be induced by the shift from tasks of high perceptual load to tasks of high cognitive load.

In summary, the shift from easy problem types to difficult problem types requires additional cognitive processes. An increase in cognitive load, specifically in working memory, leads to increment of activation in the fronto-parietal cortex, and stress on cognitive load rather than on perceptual load induces decrement of activation in the occipital cortex. Stronger recruitment of the fronto-parietal cortex with an increase in cognitive load is suggested to play a key role for a successful performance in spatial ability tests.

In this study of spatial ability using a set of psychometric tests, cognitive load refers to the amount of visuo-spatial information the brain has to manage during problem-solving. According to the demonstrated neural adaptability to changing cognitive load in the high-spatial group, it is suggestible that the dynamic shifting of cognitive resources in response to various amounts of visuo-spatial information is crucial for high-spatial ability.

Conclusions

Several psychometric tests for spatial ability were subserved by the previously known cognitive network involved in a variety of cognitively demanding tasks. It indicates that the spatial ability tests commonly require general cognitive functions, supporting the overlap of spatial ability with general intelligence.

High-spatial ability was demonstrated in adaptive modulation of activations in response to psychometric tests of varying difficulty levels as well as in average activations across the psychometric tests. Only the high-spatial group recruited the fronto-parietal network with an increase in cognitive demand which is brought about by difficult psychometric tests. Neural adaptability is considered to be an attribute underlying individual differences in spatial ability and also in intelligence in general.

Adaptive modulation of functional connectivity as well as activations in response to changing cognitive demand is worth investigation in future studies. The studies on neural adaptability for spatial ability might help us gain insight into individual differences in spatial ability with respect to neural function and moreover into the neuroscientific nature of the psychometric notion of “difficulty” in spatial ability tests.

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Table 1. Brain regions that showed common brain activations and deactivations across five problem types.

(a) Common activations

Brain region	Side	Peak MNI coordinates (mm)			Volume (mm^3)	T-score
		x	y	z		
Superior parietal gyrus	R	24	-68	50	10568	26.7561
	L	-24	-64	54	11776	22.0345
Superior occipital gyrus	R	24	-68	48	4728	26.4414
	L	-26	-70	34	4536	14.4798
Angular gyrus	R	26	-64	50	4048	25.0773
	L	-30	-52	38	208	10.9123
Middle occipital gyrus	R	28	-72	40	12840	20.6704
	L	-28	-28	-94	9808	14.3749
Cuneus	R	20	-76	48	608	19.7261
	L	-20	-74	38	240	9.8630
Inferior frontal gyrus	L	-50	10	28	7328	19.3064
	R	50	48	50	7000	17.6276
Precuneus	R	16	-72	50	1872	19.3064
	L	-14	-74	56	4424	19.0965
Inferior parietal gyrus	L	-28	-54	54	11296	18.4670
	R	30	-56	54	7536	18.0473
Inferior occipital gyrus	R	32	-92	-4	3264	17.5227
	L	-26	-90	-2	3688	12.1714
Middle frontal gyrus	R	28	6	54	4656	17.2079
	L	-24	4	50	3640	14.3749
Precentral gyrus	L	-52	8	28	6520	17.2079
	R	50	6	22	5104	16.0537
Superior frontal gyrus	R	26	4	54	3120	16.1586
	L	-24	0	48	4680	15.0044
Postcentral gyrus	L	-42	-34	44	7528	15.9488
	R	48	-30	50	3832	12.0665
Supramarginal gyrus	L	-48	-30	36	2856	14.8995
	R	44	-40	46	6080	14.8995
Rolandic operculum	R	50	6	18	1080	13.4305
	L	-46	6	18	680	9.3384
Supplementary motor area	L	-4	12	50	3688	12.4862
	R	2	12	50	1488	9.7581
Inferior temporal gyrus	R	46	-60	-16	1640	11.0172
	L	-50	-56	-22	120	5.9808
Fusiform gyrus	R	44	-60	-16	392	10.5975
	L	-40	-82	-12	496	8.0793
Calcarine fissure	R	24	-90	2	736	9.5483
	L	-20	-98	-2	576	8.9187
Median cingulate gyrus	L	-6	14	44	904	9.3384
	R	2	2	16	1520	7.9744
Insula	R	34	22	-2	1536	9.1286
	L	-40	2	20	944	7.3448
Lingual gyrus	R	24	-90	-6	176	7.5547
	L	-18	-90	0	16	6.9251
Cerebellar hemisphere	L	-48	-68	-18	176	6.9251
Putamen	R	30	16	-2	32	5.6660
Middle temporal gyrus	R	38	-68	24	24	5.6660
Anterior cingulate gyrus	R	10	28	30	8	4.8266

(b) Common deactivations

Brain region	Side	Peak MNI coordinates (mm)			Volume (mm^3)	T-score
		x	y	z		
Precuneus	R	6	-62	26	7216	13.3660
	L	0	-60	30	5464	12.1080
Cuneus	R	8	-60	22	1584	12.0032
	L	0	0	-72	2576	11.5839

Posterior Cingulate gyrus	R	2	-56	32	1616	11.8984
	L	-2	-2	-48	2256	11.6887
Median cingulate gyrus	R	0	-52	34	3520	11.6887
	L	-2	-4	-46	2200	11.0073
Calcarine fissure	R	8	-60	20	1216	11.0073
	L	0	-66	22	816	8.3865
Angular gyrus	L	-52	-70	34	3880	10.7976
	R	56	-62	30	2528	9.8017
Middle occipital gyrus	L	-50	-70	38	1136	10.2735
	R	56	-64	26	192	9.2252
Middle temporal gyrus	L	-48	-48	-64	6360	9.3300
	R	56	56	-66	2920	8.3865
Inferior parietal gyrus	L	-54	-62	42	384	8.4913
	R	56	-60	40	208	8.0196
Paracentral lobule	R	2	-34	54	576	8.2293
	L	-2	-34	54	80	6.9189
Supramarginal gyrus	L	-62	-50	36	760	8.0196
	R	64	62	-48	96	5.5036
Superior temporal gyrus	R	58	-58	24	904	7.2858
	L	-64	-50	24	128	6.0278
Superior frontal gyrus	R	2	54	2	1128	6.4995
	L	-2	54	6	48	5.5036
Inferior temporal gyrus	R	54	-6	-26	560	6.2899
	L	-52	-2	-32	344	5.6085
Supplementary motor area	R	4	-26	54	288	6.1851
Anterior cingulate gyrus	L	-2	52	4	160	6.0278
	R	2	48	6	24	4.9795
Lingual gyrus	R	10	10	-58	64	5.8706
	L	-4	-56	8	24	5.2416
Heschl gyrus	R	42	-16	14	328	5.8181
Insula	R	42	-14	14	40	5.7133
Rolandic operculum	R	44	-16	14	80	5.6085

Table 2. Brain regions where activations were correlated with the difficulty level of five problem types.

(a) Positive linear relationship

Brain region	Side	Peak MNI coordinates (mm)			Volume (mm^3)	T-score
		x	y	z		
High-spatial group						
Middle frontal gyrus	L	-32	12	54	7592	8.8011
	R	24	22	56	1408	6.3912
Superior parietal gyrus	L	-38	-64	56	1184	7.9725
	R	10	-70	54	408	6.8609
Precuneus	L	-6	-68	50	3688	7.9707
	R	10	-70	56	2048	6.6298
Inferior parietal gyrus	L	-38	-62	54	5120	7.7846
	R	56	-38	54	440	5.6951
Angular gyrus	L	-40	-62	50	1752	7.1825
Superior frontal gyrus	L	-22	22	58	1592	7.1085
	R	24	26	52	1152	6.6504
Inferior frontal gyrus	L	-42	36	28	2920	6.5704
Precentral gyrus	L	-38	10	48	224	6.1756
Supramarginal gyrus	L	-52	-42	36	416	5.7492

(b) Negative linear relationship

Brain region	Side	Peak MNI coordinates (mm)			Volume (mm^3)	T-score
		x	y	z		
High-spatial group						
Cuneus	R	14	-100	12	368	6.5090
	L	-10	-100	16	24	5.6272
Superior occipital gyrus	L	-14	-100	16	280	6.2514
	R	14	-98	18	136	6.0857
Middle occipital gyrus	L	-18	-100	12	24	5.3547
Low-spatial group						
Superior occipital gyrus	R	24	-92	24	624	8.2949
	L	-10	-102	10	376	6.8960
Middle occipital gyrus	R	26	-90	22	152	6.9404
	L	-18	-100	12	16	5.3707
Cuneus	L	18	-100	12	96	6.2529
		-8	-98	12	16	5.5006
Cerebellar hemisphere	R	20	-76	-18	296	6.1322
Fusiform gyrus	R	20	-76	-14	112	5.8360

Figure 1. Five problem types used in the field test during the fMRI scanning. Each problem consists of two figure frames, one for stimulus and the other for test probe.

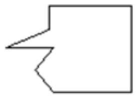
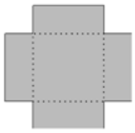
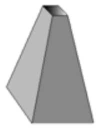
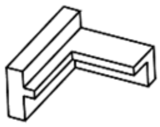
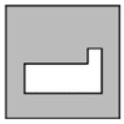
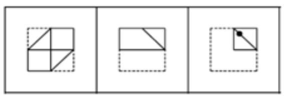
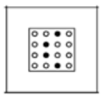
Problem type	Stimulus	Test probe	Answer
Picture completion			No
Mental rotation			No
Surface development			No
Orthographic projection			Yes
Hole punching			No

Figure 2. Grouping of twenty-seven participants into high- and low-spatial groups. The grouping was resulted from three algorithms of clustering methods, complete (A), average linkage (B), and single (C), using the scores from the pretest and the field test. The complete and average linkage algorithms yielded the same grouping of fifteen high-spatial participants and twelve low-spatial participants. Circles and triangles indicate the participants in two groups.

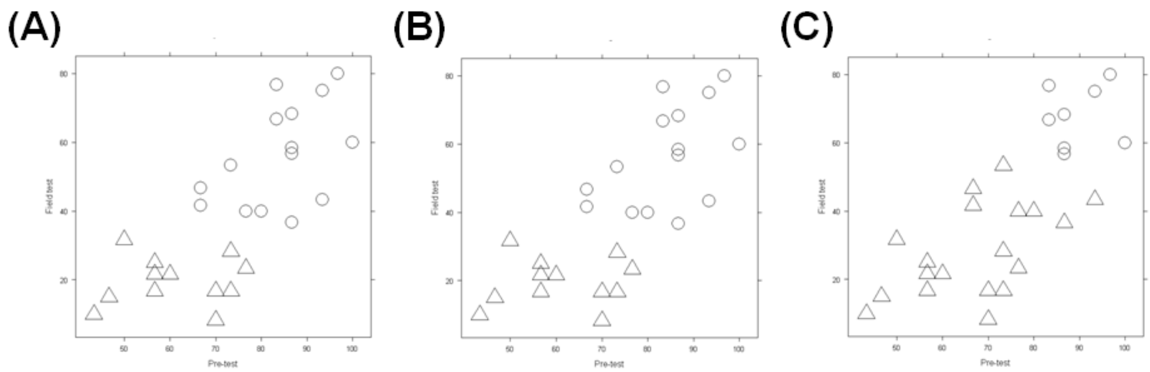


Figure 3. Comparison of the field test scores between high- and low-spatial groups. The two groups are different with the p-values less than 0.05 for all the test types. The two groups showed significant differences in the scores for all problem types. Stars indicate the statistical significance determined at a p-value less than 0.05.

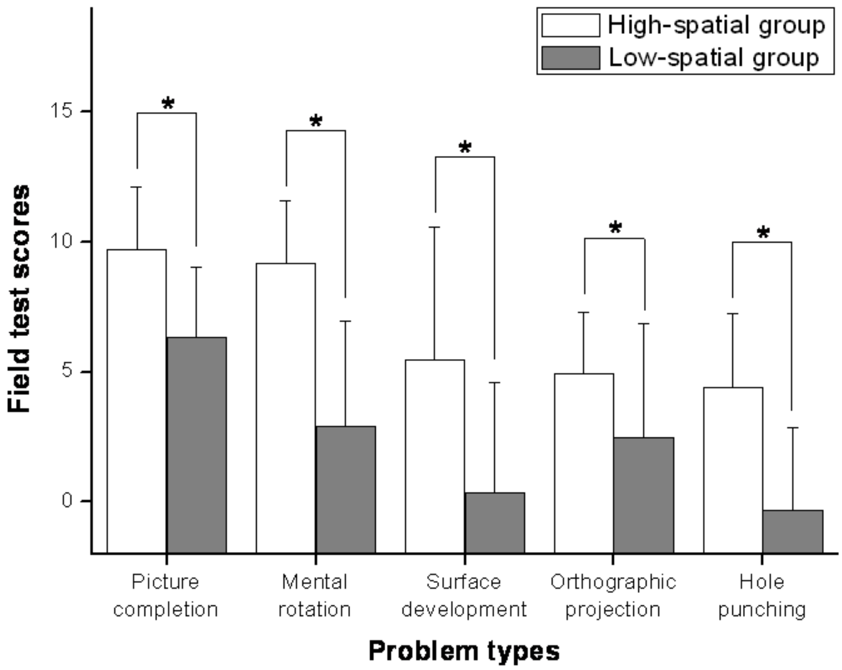


Figure 4. Common brain activations and deactivations across five problem types. The height threshold was determined at a family-wise error-corrected p-value less than 0.05 and the cluster extent threshold at an uncorrected p-value less than 0.05. Red-yellow indicates the common brain activations and blue-green indicates the common brain deactivations. Slices are arranged in neurological orientation.

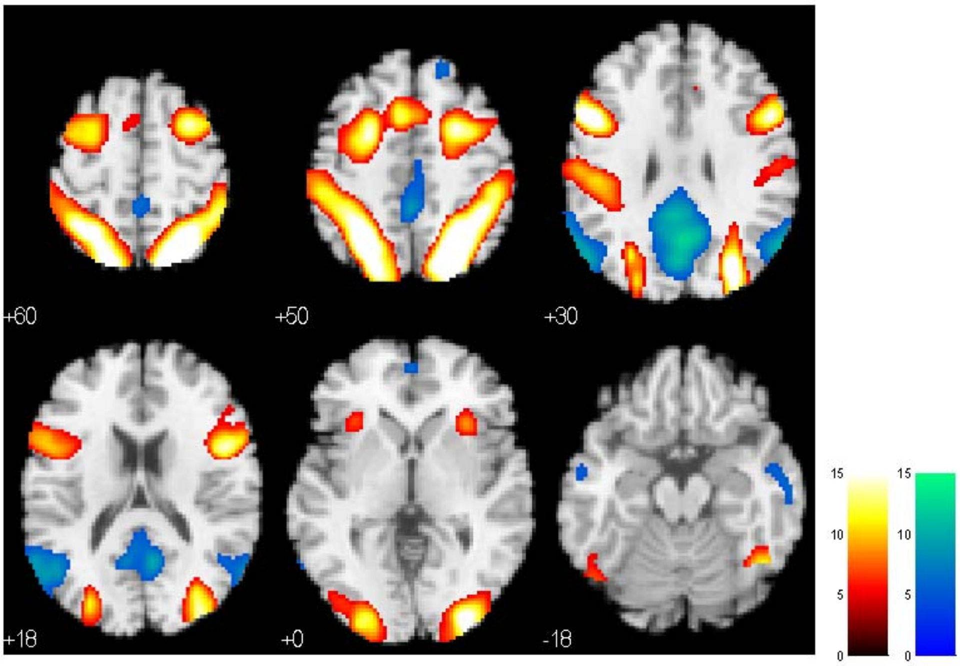


Figure 5. Main effects of group (A) and problem type (B) in ANOVA for repeated measures with group and problem type as between-group and within-group factors respectively. The height threshold was determined at a family-wise error-corrected p-value less than 0.05 and the cluster extent threshold at an uncorrected p-value less than 0.05.

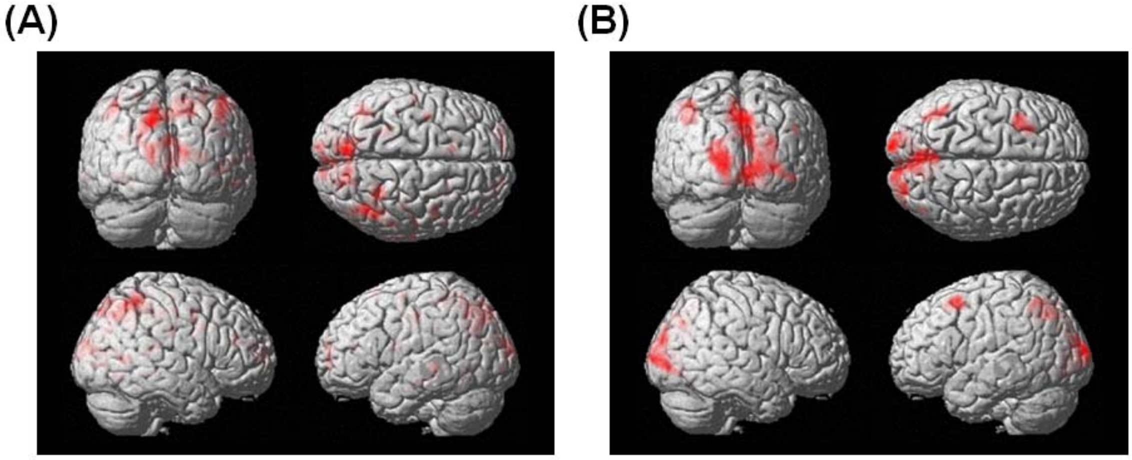


Figure 6. Main effects of problem type for the high-spatial group (A) and the low-spatial group (C), and the regions of the linear relationship of activations with the rank order of the difficulty level of five problem types for the high-spatial group (B) and the low-spatial group (D). The height threshold was determined at a family-wise error-corrected p-value less than 0.05 and the cluster extent threshold at an uncorrected p-value less than 0.05. Red-yellow indicates the positive linear relationship and blue-green indicates the negative linear relationship. Slices are arranged in the neurological orientation.

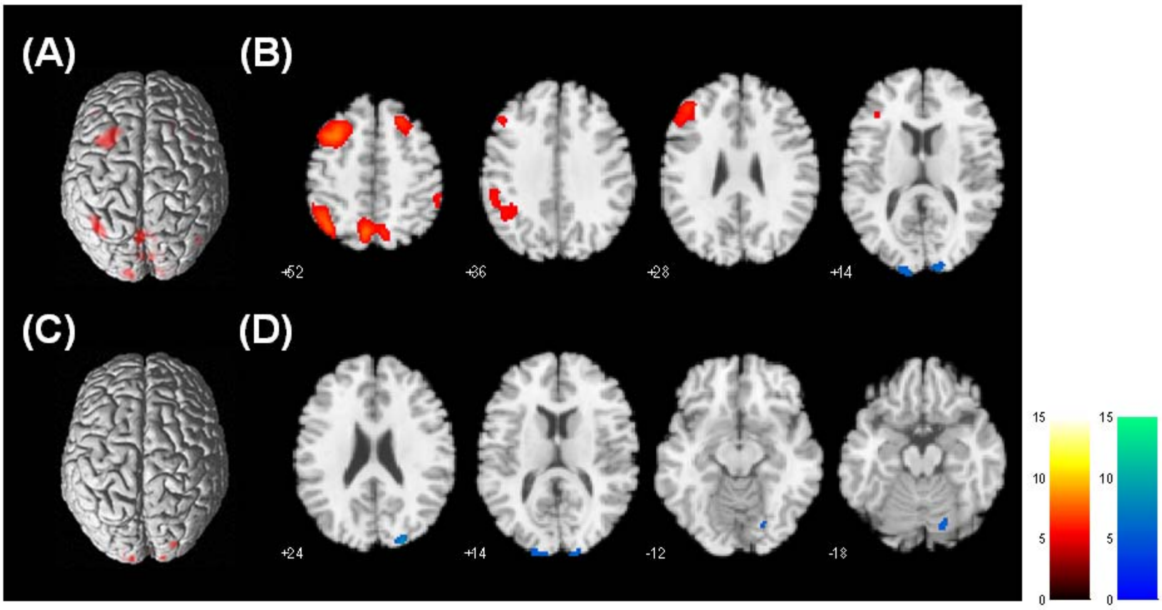


Figure 7. Superposition of two sets of brain regions, one set (red) displaying higher average activation averaged over five problem types for the high-spatial group and the other set (green) displaying the positive relationship of activations with the difficulty levels of problem types for the high-spatial group. The height threshold was determined at a family-wise error-corrected p-value less than 0.05 and the cluster extent threshold at an uncorrected p-value less than 0.05. The bar graphs show variation in activation in response to the difficulty levels of the five problem types at the eight regions of interest, the bilateral dorsolateral prefrontal cortex, the bilateral left inferior parietal gyrus, the bilateral left superior parietal gyrus, and the bilateral precuneus. The five problem types from left to right in the bar graphs is in the order of picture completion, mental rotation, surface development, aperture passing, and hole punching from low to high in the difficulty level (DLPFC: dorsolateral prefrontal cortex; IPG: inferior parietal gyrus; SPG: superior parietal gyrus).