

The predictive value of white matter organization in posterior parietal cortex for spatial visualization ability

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Received 20 February 2006; revised 21 April 2006; accepted 9 May 2006
Available online 21 June 2006

Humans differ substantially in their ability to imagine spatial transformations of novel stimuli (i.e., mental rotation). Whereas “high-spatial” individuals are able to maintain high-quality representations even after complex mental transformations, “low-spatial” individuals often experience substantial degradation of the initial representation. Even though subdivisions of the posterior parietal cortex are known to instantiate the necessary spatial transformations, a direct demonstration of neuroanatomical differences predicting this behavioral variability is currently missing. Because recent evidence suggests that interindividual differences on the behavioral level might be related to regionally specific white matter organization, we addressed this question using diffusion tensor imaging in combination with well-established psychometric tests. As expected, behavioral results revealed a substantial disparity in mental rotation performance. Most importantly, despite controlling for differences in spatial short-term memory capacity, we observed a tight relationship between mental rotation proficiency and white matter organization near the anterior part of the intraparietal sulcus. Whereas high-level proficiency was paralleled by high fractional anisotropy (FA) values, the opposite pattern was observed in “low spatials”. The present results strongly indicate that the efficiency of information transfer between posterior parietal regions involved in the mental transformation process could be one decisive factor in individual spatial visualization proficiency.

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Introduction

Spatial visualization, the ability to imagine transformations of objects (e.g., mental rotation), is a fundamental aspect of many everyday tasks like mechanical reasoning (Hegarty and Waller, 2005). In the human brain, these transformations are subserved primarily by subdivisions of the posterior parietal cortex (Cohen et

al., 1996; Carpenter et al., 1999; Harris and Miniussi, 2003; Harris et al., 2000; Zacks et al., 2003a). For example, the intraparietal sulcus processes spatial information about position, orientation, size, etc., in various egocentric reference frames (Andersen et al., 1997). In addition, direct intracortical stimulation of the superior parietal cortex severely affects mental rotation performance (Zacks et al., 2003a), and transcranial magnetic stimulation over adjacent regions evokes similar effects when applied 400–600 ms after stimulus onset (Harris and Miniussi, 2003). This clearly shows that the activity in posterior parietal cortex as observed in functional neuroimaging studies on mental rotation (Cohen et al., 1996; Carpenter et al., 1999; Barnes et al., 2000; Harris et al., 2000; Jordan et al., 2001; Wolbers et al., 2003) does not reflect early perceptual processing but rather the subsequent spatial transformation of the imagined object.

Despite a common cognitive architecture, humans differ substantially in their ability to perform spatial visualization tasks (Hegarty and Waller, 2005). Whereas items on simple mental rotation tests (i.e., rotation of alphanumeric characters) can easily be solved by most people, there appears to be a maximum level of accuracy an individual can achieve for complex spatial visualization tasks (i.e., rotation of Shepard–Metzler figures or paper-folding tests). In these tests, performance does not improve with more time on the task (Lohmann, 1986). The individual proficiency level is not only determined by the ability to construct and store a high-level representation of a novel stimulus, but also to maintain the quality of that representation after mental transformations (Just and Carpenter, 1985; Hegarty and Waller, 2005). Individuals with low-spatial visualization abilities often “lose” some information about the stimulus after mental transformations (Just and Carpenter, 1985). This might be caused by an inferior information exchange between the participating brain structures, which could entail a gradual degradation of the initial representation.

Apart from possible strategic differences, it is reasonable to speculate that such interindividual variability might have an underlying neuroanatomical substrate. Efficient communication in the human brain relies on the integrity of white matter tracts. Subtle abnormalities in white matter organization have been linked

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Available online on ScienceDirect (www.sciencedirect.com).

to disabilities like dyslexia and developmental stuttering (Klingberg et al., 2000; Sommer et al., 2002). Most importantly, even in healthy populations, preliminary evidence suggests that interindividual differences on the behavioral level might be related to neuroanatomical factors like regionally specific white matter organization (Bengtsson et al., 2005; Tuch et al., 2005). As a consequence, the question arises if individual spatial visualization ability could be influenced by the efficiency of information transfer between the participating posterior parietal areas. The present study addressed this question using diffusion tensor imaging and well-established psychometric tests. We specifically chose a complex cubes rotation paradigm to measure individual spatial visualization ability, and fractional anisotropy (FA) served to characterize the coherence of the orientation of white matter tracts. Given the well-established importance of the posterior parietal cortex for implementing the necessary mental spatial transformations, we hypothesized a correspondence between mental rotation proficiency and FA values within this region.

Materials and methods

Participants

Sixteen healthy male volunteers (19–29 years) with normal or corrected-to-normal vision gave written informed consent to participate in this study that was approved by the local ethics committee. All subjects understood the instructions without difficulty, and none was aware of the hypotheses at the time of testing.

Behavioral testing

With regard to mental rotation, high- and low-spatial individuals differ in the complexity of items they can rotate and not merely in the speed of rotation (Lohmann, 1986). Tasks like three-dimensional rotation or paper-folding measure the ability to construct a high-quality representation of a stimulus and to maintain that quality after mental transformations. Most importantly, test items can often not be solved by all individuals, even when no time limit is imposed (Hegarty and Waller, 2005). To uncover such stable interindividual differences in spatial visuali-

zation ability, we employed a well-established cube rotation paradigm, requiring subjects to compare drawings of three-dimensional cubes (Gittler, 1990, Fig. 1a). No time limit was set and scores reflected the absolute number of correct responses (maximum: 17).

Performance in mental rotation tests not only depends on efficient mental transformation processes, but it is also influenced by individual spatial working memory capacity. In addition to the executive component of spatial working memory, efficient short-term storage is an integral part of successful performance in spatial visualization tests (Shah and Miyake, 1996; Miyake et al., 2001). However, given that the present study aimed at identifying neuroanatomical foundations of differences in spatial transformation processes, we regressed out the contribution of spatial short-term memory. Specifically, we measured immediate recall performance of the Rey–Osterrieth complex figure (Osterrieth, 1944) to control for differences in spatial short-term memory. Shortly after copying the complex figure, participants were asked to redraw it based on their memory representation. The quality of the individual drawings was assessed according to a standard scoring scheme (Lezak, 1995), yielding a single spatial short-term memory score (maximum: 34).

DTI scanning

Diffusion tensor imaging was performed with an echo planar imaging sequence (54 slices, voxel size: $2 \times 2 \times 2$ mm, b value: 1000, TE = 113 ms, TR = 8500 ms) at 3 Tesla (Siemens Trio). Diffusion-weighted images were sensitized for diffusion along 60 different directions, and four measurement replications served to improve signal-to-noise ratio in the tensor maps. In addition, we acquired a high-resolution T_1 -weighted image of each participant using a fast-low-angle-shot sequence (flip angle = 25° , TR = 15 ms, TE = 4.92 ms, voxel size: $1 \times 1 \times 1$ mm).

Image processing and statistical analysis

All analyses were carried out using the diffusion toolbox as implemented in SPM2 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm2>). For preprocessing, diffusion-weighted images were motion-corrected and coregistered to the high-resolution T_1 -weighted

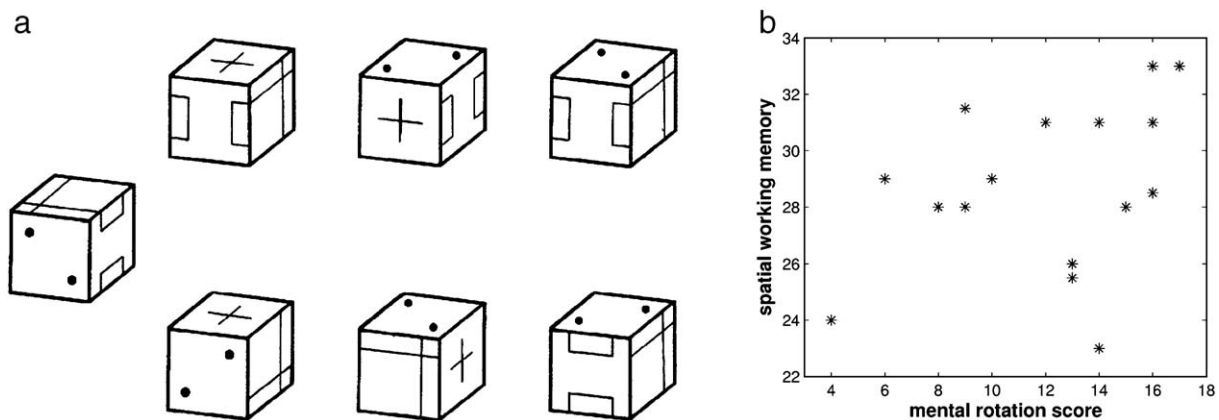


Fig. 1. (a) Mental rotation paradigm. Participants had to determine whether the reference cube on the left side could be identical to any of the six cubes. No time limit was set. In the example shown here, the middle cube in the lower row would be the correct answer. (b) Behavioral results. Mental rotation scores indicate the absolute number of correct responses (maximum: 17); spatial short-term memory scores were calculated according to a standard scoring scheme (maximum: 34). As expected, mental rotation and spatial short-term memory scores were moderately correlated ($r = 0.36$).

image, which we spatially normalized to the MNI template brain (Evans et al., 1993). The resulting normalization parameters were subsequently applied to the diffusion-weighted images, reorienting the gradient directions accordingly.

Following preprocessing, second-order diffusion tensors and fractional anisotropy (FA) values were established using the standard multiple regression approach. Individual FA images – reflecting the coherence of the orientation of fibers on a voxel-by-voxel basis – were smoothed using an 8-mm full-width at half-maximum isotropic Gaussian kernel. Subsequently, these images were entered into a multiple regression analysis with mental rotation and spatial short-term memory scores as predictor variables. Appropriate linear contrasts on the parameter estimates allowed us to study the relationship between FA and mental rotation ability while controlling for the contribution of spatial short-term memory. For all analyses, the threshold was set to $P < 0.05$ corrected for multiple comparisons. Given our a priori hypotheses about the importance of posterior parietal cortex and a recent study that identified areas specific to mental rotation as opposed to object recognition (Gauthier et al., 2002), we defined several regions of interest (ROI), and correction for multiple comparisons was based on these regions. Specifically, we used the WFU pickatlas (Maldjian et al., 2003) to create anatomical ROIs for the angular gyrus, the precuneus and superior parietal cortex. In addition, we defined intraparietal areas AIP and CIP as spherical volumes with a 10-mm radius surrounding previously reported coordinates: AIP: $\pm 40, -42, 36$ (Grefkes et al., 2002); CIP: $-9, -75, 54/24, -66, 60$ (Shikata et al., 2003). Elsewhere in the brain, correction was based on the entire search volume.

FA is higher in white than in grey matter due to the densely packed fibers. The multiple regression analysis revealed significant effects in regions close to the border between white and grey matter (see Results). Therefore, we were concerned that the correlation between FA and mental rotation performance could be artificially high if voxels showing a significant effect lay predominantly in grey matter in “low spatial” and predominantly in white matter in “high spatial.” To keep this source of error to a minimum, we performed post hoc analyses in which we investigated the unsmoothed FA maps. Specifically, we determined FA in regions of interest ($12 \times 12 \times 12$ mm) surrounding the posterior parietal peak voxels as obtained from the multiple regression analysis ($[-36, -40, 46$ mm], $[-42, -56, 30$ mm], $[50, -58, 36$ mm]; see Results). For each participant, we then established all voxels within these regions of interest that contained white matter by using segmented high-resolution T_1 -weighted scans. Coregistration between diffusion-weighted and T_1 -weighted images ensured a match of structures between modalities. Finally, we determined partial correlation coefficients between mental rotation scores and average FA over white matter voxels for each region of interest while controlling for the influence of spatial short-term memory.

Results

Behavioral data

Behavioral results revealed substantial disparity in mental rotation proficiency (mean: 12, SD: 3.9, range: 4–17; see Fig. 1b). Despite the lack of a time limit, some participants could not even achieve 25% correct responses. In sharp contrast, one subject was

able to provide correct answers for all 17 items. Furthermore, mental rotation scores were moderately correlated with spatial short-term memory performance ($r = 0.36$, Fig. 1b). This result confirms previous findings highlighting the importance of spatial short-term memory for spatial visualization ability (Shah and Miyake, 1996).

Diffusion tensor imaging

Using a multiple regression approach, we were able to study the specific relationship between fiber orientation coherence and mental rotation proficiency. While controlling for the contribution of spatial short-term memory, we observed a significant positive correlation between mental rotation scores and FA values in a left posterior parietal region (Fig. 2; Table 1). The local maximum of this significant cluster $[-36, -40, 46]$ was located in the vicinity of previously reported coordinates for anterior intraparietal area AIP: $[-37.3, -39.6, 47]$ (Shikata et al., 2001); $[40, -42, 36]$ (Grefkes et al., 2002); and $[-36, -39, 39]$ (Shikata et al., 2003). In the corresponding region of the right hemisphere, we observed a trend towards significance (Table 1). In addition, significant effects emerged in the angular gyrus bilaterally (Table 1). In all these regions, better mental rotation performance was paralleled by higher orientation coherence of white matter tracts. Elsewhere in the brain, no further significant results were obtained.

Post hoc analyses (see Materials and methods) served to verify that the interindividual differences in FA values were driven by differences in white matter only. We correlated mental rotation scores with average FA in regions of interest centered on the local maxima in posterior parietal cortex. However, the signal from all non-white matter voxels – as determined by the segmented high-resolution T_1 -weighted scans – was excluded when computing average FA. As can be seen in Fig. 3, we observed a tight correspondence between mental rotation performance and FA values in the vicinity of the anterior intraparietal sulcus (partial correlation coefficient: $r = 0.53$, $P < 0.05$). Whereas participants with high mental rotation scores were characterized by high FA values, low-spatial individuals showed the opposite pattern. In contrast, we did not obtain significant partial correlation coefficients in both ROIs in the angular gyrus (both $P > 0.05$). These results indicate that in these regions, the significant z scores observed in the initial multiple regression analysis were predominantly driven by signal originating from grey matter.

Discussion

The present study revealed a striking correspondence between white matter organization in posterior parietal cortex and spatial visualization ability. Despite controlling for the contribution of spatial short-term memory, mental rotation scores were strongly correlated with fractional anisotropy values in the vicinity of the anterior part of the intraparietal sulcus and in the angular gyrus. Post hoc analyses revealed that this correspondence was driven by FA values originating from white matter in anterior intraparietal cortex only. In accordance with previous studies on different cognitive operations (Johansen-Berg et al., 2004; Bengtsson et al., 2005; Tuch et al., 2005), our results support the notion that structure and function are tightly related in the human brain.

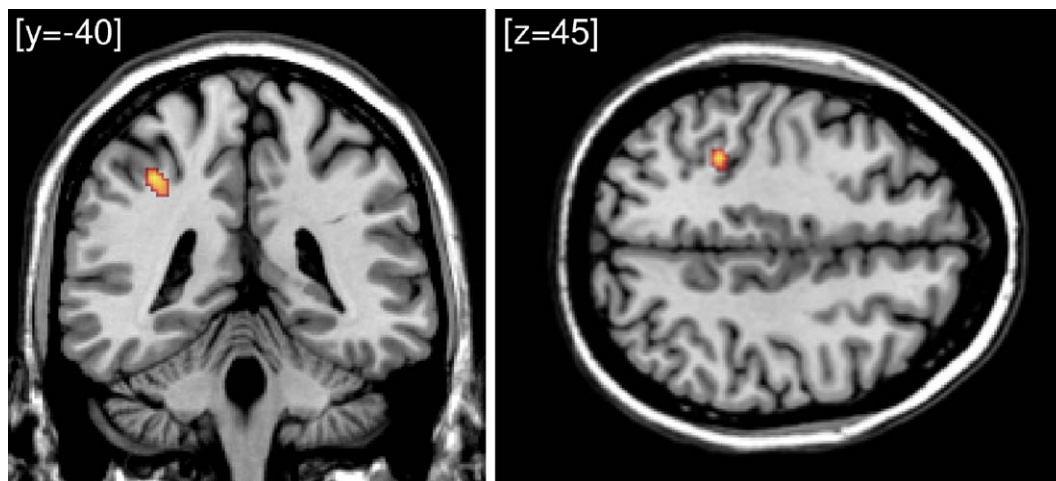


Fig. 2. Correspondence between fractional anisotropy and mental rotation scores. Regions in the vicinity of anterior intraparietal area AIP showing a significant correlation between fractional anisotropy and mental rotation ability (cluster size: $n = 31$ voxels). Note that the effect of spatial short-term memory was regressed out. To show the subthreshold extent of the cluster, results of the random effects analysis are displayed with a threshold of $P < .001$ (uncorrected) on the MNI template brain.

Mental rotation is a complex cognitive operation that requires a dynamic interplay between cortical structures processing (i) representations of external objects, (ii) imagined motion in two- or three-dimensional space, and (iii) spatial attributes like stimulus orientation, position of object parts, etc. Posterior parietal subdivisions are known to be of major importance for many of these processes in both monkeys and humans (Andersen et al., 1997; Grefkes and Fink, 2005). The caudal part of the intraparietal sulcus – often referred to as area CIP – represents spatial orientation of visual stimuli based on various cues like texture gradients (Shikata et al., 1996, 2001; Grefkes and Fink, 2005). It also possesses short-term memory capacity, as it is recruited when we compare spatial orientation between perceived and memorized stimuli (Shikata et al., 2001). In contrast, area VIP – located in the ventral part of the intraparietal sulcus – is involved in polymodal motion processing (Bremmer et al., 2001). With regard to visual motion, this function presumably depends on input from the motion sensitive areas MT/MST, which are known to project to VIP and to area LIP in the lateral compartment of the intraparietal sulcus (Baizer et al., 1991). During mental rotation, participants are required to imagine one stimulus moving in order to match the orientation between the imagined and the reference stimulus. Presumably, it is this combination of constant motion imagery and orientation monitoring that is reflected in increasing posterior

parietal activation with increasing rotation magnitude in parametric neuroimaging studies (Carpenter et al., 1999; Harris et al., 2000; Podzebenko et al., 2002; Zacks et al., 2003b).

Once imagined and reference stimuli are matched with respect to spatial orientation, deciding on whether or not they are identical constitutes the final step in a mental rotation task. This again requires a comparison between a stimulus actively held in working memory and a perceived one. In non-human primates, the anterior part of the intraparietal sulcus (area AIP) is predominantly involved in transforming spatial attributes of external stimuli into appropriate hand actions (Jeannerod et al., 1995; Andersen et al., 1997). Some AIP neurons are sensitive to the axis of orientation, shape and size (Murata et al., 2000), and they even have a short-term memory function for three-dimensional objects (Murata et al., 1996). The human equivalent of area AIP not only supports cross-

Table 1
Spatial coordinates of the local maxima in the group analysis ($P < 0.05$ corrected)

Region	Coordinate (x, y, z, in mm)		Voxel level (z score)
	LH	RH	
Intraparietal sulcus	-36, -40, 46		4.02
	-38, -42, 48		3.81
		32, -36, 40	2.10 (n.s.)
Angular gyrus	-42, -56, 30		3.26
		50, -58, 36	4.06
		46, -56, 32	3.91

RH—right hemisphere, LH—left hemisphere, n.s.—non-significant.

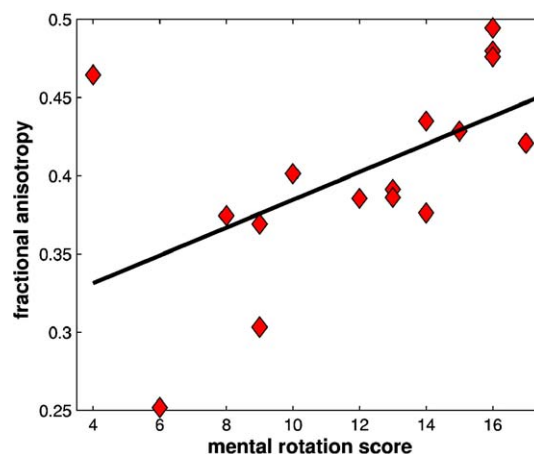


Fig. 3. Post hoc analysis based on unsmoothed FA maps. Average FA values from the region of interest centered on the local maximum in anterior IPS ([-36, -40, 46 mm]) and mental rotation scores for all 16 participants. To exclude confounding effects arising from non-white matter voxels, we computed average FA on the unsmoothed FA maps only over white matter voxels (as determined by the segmented high-resolution T₁-weighted scans). Participants with superior performance were characterized by high FA values, whereas low-spatial individuals showed the opposite pattern.

modal transfer between visual and tactile modalities, but most importantly it is also recruited when we compare the appearance of perceived and memorized objects that are presented in the same modality (Grefkes et al., 2002). Taken together, these findings strongly suggest that AIP is able to create a description of a stimulus that can be used to guide hand movements (Jeannerod et al., 1995) or to compare it against other stimuli.

How does area AIP assemble comprehensive stimulus descriptions? In the monkey brain, AIP is known to share dense connections with several posterior parietal areas and with infero-temporal cortex (Webster et al., 1994; Lewis and Van Essen, 2000; Nakamura et al., 2001; Padberg et al., 2005). Consequently, it has been suggested that AIP fulfills an integrator function: it combines information about orientation and size originating from more posterior areas in the IPS (i.e., CIP), along with information about object shape from infero-temporal cortex (Murata et al., 2000). Because efficient information transfer between these regions is crucial for mental rotation tasks, it comes as no surprise that virtual lesions over posterior parietal cortex as induced by electrical or magnetic stimulation severely impair behavioral performance (Harris and Miniussi, 2003; Zacks et al., 2003a).

In light of the described functions of the human posterior parietal cortex, we believe that the strong correlation between mental rotation proficiency and FA values in the present study indicates that the efficiency of information transfer between AIP and other posterior areas could be one decisive factor in individual spatial visualization ability. To maintain a high-quality representation of a stimulus even after successive steps of imagined motion, AIP depends on high-quality information transfer from posterior subdivisions of IPS and from infero-temporal cortex. Low-spatial visualization abilities have been described as a partial loss of details in a stimulus representation after mental transformations (Just and Carpenter, 1985). In the present study, such participants were characterized by relatively low FA values near the anterior intraparietal sulcus. This reduced coherence of white matter organization could result in an inferior information transfer to and from AIP during the imagined rotation, which ultimately entails a gradual degradation of the stimulus description. As a consequence, comparing the imagined stimulus to a reference stimulus becomes a difficult task, and the overall performance in spatial visualization paradigms is adversely affected.

The complexity of the rotation process also influences the degradation of an imagined stimulus representation. Higher rotation angles are not only paralleled by increasing reaction times, but also by decreasing accuracy (Gauthier et al., 2002). Therefore, the difference between high- and low-spatial individuals needs to be conceptualized as a continuum: mental transformations of imagined stimuli always entail some kind of degradation, but its magnitude differs across individuals. This magnitude might in turn be determined by the efficiency of information transfer between posterior parietal structures.

Finally, interindividual differences in spatial working memory contribute to differences in spatial visualization ability (Shah and Miyake, 1996; Hegarty and Waller, 2005). Imagining spatial transformations relies on both the storage and executive control components of spatial working memory. However, we obtained significant correlations between fractional anisotropy values in posterior parietal cortex and behavioral performance, despite controlling for the influence of spatial short-term memory. These results strongly indicate that the observed variability in fractional

anisotropy values relates to the efficiency of the required spatial transformation processes. Conversely, recent evidence from children and adolescents demonstrates that the development of working memory capacity is predominantly linked to fractional anisotropy in frontal areas (Nagy et al., 2004), further upholding the established role of the dorsolateral prefrontal cortex for working memory tasks.

In closing, it is important to note that fractional anisotropy only provides an indirect measure of white matter integrity because it is sensitive to a variety of factors including myelination, axon diameter and density, and intra-voxel fiber crossing. Nevertheless, given the known functions of the posterior parietal cortex, we believe that our results provide neuroanatomical support for behavioral theories addressing interindividual differences in spatial abilities. To what extent this anatomical variability stems from genetic or epigenetic contributions remains to be determined in future studies.

Acknowledgments

We thank Stefan Klöppel for help with data analysis and the Physics Group at NeuroImage Nord in Hamburg. Mary Hegarty and Ferdinand Binkofski provided helpful comments on earlier drafts of the manuscript. This work was supported by the Volkswagenstiftung and the Bundesministerium für Bildung und Forschung (BMBF).

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