



## Women and men exhibit different cortical activation patterns during mental rotation tasks

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Received 19 November 2001; received in revised form 22 May 2002; accepted 5 June 2002

### Abstract

The strongest sex differences on any cognitive task, favoring men, are found for tasks that require the mental rotation of three-dimensional objects. A number of studies have explored functional brain activation during mental rotation tasks, and sex differences have been noted in some. However, in these studies there was a substantial confounding factor because male and female subjects differed in overall performance levels. In contrast, our functional brain activation study examined cortical activation patterns for males and females who did not differ in overall level of performance on three mental rotation tasks. This allowed us to eliminate any confounding influences of overall performance levels. Women exhibited significant bilateral activations in the intraparietal sulcus (IPS) and the superior and inferior parietal lobule, as well as in the inferior temporal gyrus (ITG) and the premotor areas. Men showed significant activation in the right parieto-occipital sulcus (POS), the left intraparietal sulcus and the left superior parietal lobule (SPL). Both men and women showed activation of the premotor areas but men also showed an additional significant activation of the left motor cortex. No significant activation was found in the inferior temporal gyrus. Our results suggest that there are genuine between-sex differences in cerebral activation patterns during mental rotation activities even when performances are similar. Such differences suggest that the sexes use different strategies in solving mental rotation tasks.

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**Keywords:** Mental rotation; Functional magnetic resonance imaging; FMRI; Sex differences; Spatial cognition; Intraparietal sulcus; Hemodynamic response

### 1. Introduction

Mental rotation is one of the few cognitive abilities for which men have been shown to consistently outscore women [37,43,63]. Environmental (experience-dependent, spatial activities, socialization) and biological (genetic, hormonal, evolutionary) factors are often discussed as possible causes for these sex differences [8,9,33]. Evidence for the role of environmental factors has been found in the frequently observed relation between participation in spatial activities and spatial ability, as well as in the fact that performance can be improved by training [2,29,42,46]. Environmental factors may interact with different strategies for the two sexes, such that males tend to use the generally more effective visual-spatial holistic strategies in which the object is pictured in the mind and then rotated. Women

tend to prefer less efficient verbal or analytical strategies that result in a more piecemeal mental rotation process [3,10,18,34,44,52]. Thus, a reasonable working hypothesis is that differences in strategies underlie differences in mental rotation performances of the sexes. However, it is unclear as to whether the different strategies in females and males depend on sex-specific brain development or on differential socialisation [32]. Explanations of sex differences in spatial performance in terms of biological factors are both indirect, as evidenced by evolutionary speculations about different selective pressures on males and females when navigating in the environment [55,56], and direct, in the demonstration that sex hormones play an important role in organizing a variety of sexually dimorphic behaviours [25]. For instance, sex hormones have been shown to be important in mental rotation performance, independently of differential experience [17]. Hausmann et al. have shown that testosterone and estradiol modulate spatial cognition during the menstrual cycle [27], and Maki and Resnik [38] recently pointed out that sex hormones like estrogen could influence

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cerebral blood flow and neuronal activation in women. Sex differences in functional cerebral organization, which may reflect organizational hormone effects, have also been implicated in differential mental rotation performance by the sexes [5], albeit without any direct evidence and without any suggestions as to the nature of “functional cerebral organization”.

A number of recent brain imaging papers have examined regional activation of the brain during mental rotation performance [7,11,17,26,31,35,47,58,59–62] but there are only four studies that have addressed sex differences [17,59–61] directly. Moreover, the results were inconsistent as far as sex differences are concerned. Unterrainer et al. [61] and Tagaier et al. [59] found different cortical activation patterns in dependence on the performance level rather on sex during visuospatial and mental rotation tasks [59,61]. Dietrich et al. [17] found no differences between women and men in the cortical activation patterns and in the performance during in a mental rotation task, but a much higher overall level of cerebral hemodynamic response during the high estrogen phase of the women [17]. In a mental rotation task with three-dimensional stimuli as used by Shepard and Metzler [53], Thomsen et al. [60] found significantly different activation patterns in women and men. Men showed predominantly parietal activation, while women showed inferior frontal activation [60]. The authors suggested that males and females may differ in the approach to three-dimensional mental rotation tasks, men using a “gestalt” strategy and women using a “serial” reasoning strategy, reminiscent of the earlier speculations about “holistic” and “analytic” strategies. Even in this case, it is not certain whether the sex differences are genuine or whether the differences are confounded with performance levels because men performed better than women on the mental rotation tasks. Thus, the observed differences could be due to differences between individuals of different performance levels rather than to differences specific to the sexes. This leads us to our present study, where cortical activation was studied in women and men who exhibited similar performance in mental rotation tasks, thus allowing us to evaluate the factor of sex independent of differences in performance levels.

## 2. Methods

### 2.1. Subjects

Twenty four healthy volunteers (14 women, mean age,  $21.3 \pm 3.2$  years; 10 men, mean age,  $25.8 \pm 5.8$  years) took part in the study. All Subjects were undergraduate psychology students enrolled at the University of Magdeburg. None of them had special experience in spatial cognition. All subjects (Ss) were also tested for their proficiency with respect to imagination and rotation of three-dimensional objects (paper-and-pencil versions of the mental rotation test, [43]). Subjects gave written informed consent according to institutional guidelines (Ethics Committee of the University of Magdeburg). All Ss except one man were consistent right handers according to the Annett Handedness Questionnaire [1]. We performed an additional analysis without the left-handed subject and obtained the same results as for the overall-analysis. We, therefore, report results based on all subjects.

### 2.2. Experimental design

Each subject took part in four experimental conditions: (1) mental rotation of the classical three-dimensional figures (3D), (2) mental rotation of abstract figures (ABSTRACT), (3) mental rotation of letters (LETTER), (4) same-different judgment of non-rotated figures of the mental rotation tasks (CONTROL). The 3D-objects were similar to those used by Shepard and Metzler [53]. The 2D abstract-objects corresponded to shapes first used by Hochberg and Gellman [28], and the letters represented “F” and “K”, as in the study by Corballis and Sergent [12] (representative samples of stimuli are depicted in Fig. 1). All stimuli were presented in pairs. Some of the paired mental rotation objects were identical except that they were rotated in picture plane for the 2D-objects and around one axis in space for the 3D-objects. Rotation was realised in steps of  $20^\circ$ , according to Hochberg and Gellman [28]. Pairs of stimuli were presented from a video-projector onto a screen, which was visible inside the scanner through a mirror. In the three rotation

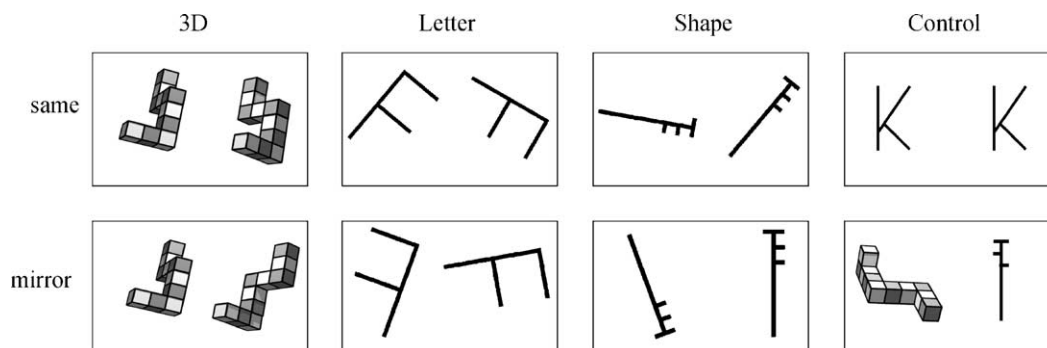


Fig. 1. Examples of pairs of stimuli used in the study.

conditions, subjects were told to turn the right figure clockwise to match the left, in order to decide whether it is the “same” or a “mirror” figure. We used this instruction according to Hochberg and Gellmann [28] in order to reduce the interindividual variance regarding the rotation strategies. The control condition (CONTROL) contains all three categories of “rotation” stimuli, in vertical orientation and in pairs of combinations of each with each other. Ss had to decide whether the stimuli belonged to the “same category” or not. This condition was designed to examine for the neural activation of merely perceiving the stimuli. Stimuli of all four conditions (three-dimensional, ABSTRACT, LETTER, CONTROL) were shown for 3.0 s, then the next stimulus pair was presented. Ss responded with a small keypad fixed on the thigh, indicating their choice by pressing one of two buttons with the index or the middle finger of their right hand. They were required to respond as quickly and accurately as possible. Only reaction times longer than 200 ms and shorter than 3000 ms were stored for later analysis. The mental rotation tests were given within a classical functional magnetic resonance imaging (fMRI) block design with alternating rest (60 s) and activation (60 s) conditions. One session consisted of 12 blocks alternating one resting block with two activation blocks (mental rotation, control). During the four resting blocks, subjects were required to fixate a spot (1 cm in diameter,  $1^\circ$  visual angle) displayed in the centre of the screen. The order of the two activation blocks was randomly chosen. Prior to each activation block a “warning figure” for about 4 s was given, containing examples of the stimuli of the following activation block. During the activation periods the mental rotation tasks (four blocks) or the control task (four blocks) were presented, comprised of 20 randomly chosen stimulus pairs. One session contained 80 stimulus pairs for the mental rotation condition (40 pairs in the condition “same”, 40 pairs in the condition “mirror”) and 80 stimulus pairs for the control condition (40 pairs in the condition “same category”, 40 pairs in the condition “different category”). Within each session, mental rotation tasks taken from one condition and control task were presented during the activation periods. The order of these three sessions was randomly chosen for each subject. Before each session, the subjects were given written instructions presented via a video-projector. Before scanning, and outside the scanner, subjects performed samples of tasks from all conditions in order to familiarise them with the tasks.

### 2.3. Scanning procedure

Functional magnetic resonance imaging was performed on a 1.5 T MRI system (General Electric, Waukesha, WI, USA), equipped with gradient echo planar imaging (repetition time,  $TR = 4.0$  s; echo time,  $TE = 40$  ms; field of view =  $200\text{ mm} \times 200\text{ mm}$ ; flip angle =  $90^\circ$ ; matrix size =  $64\text{ mm} \times 64\text{ mm} \times 26\text{ mm}$ ; voxel size =  $3.125\text{ mm} \times 3.125\text{ mm} \times 5.5\text{ mm}$ ). Three-dimensional anatomical images of the entire brain were obtained by using

a T1-weighted three-dimensional spoiled gradient echo pulse sequence ( $TR = 24\text{ ms}$ ,  $TE = 8\text{ ms}$ , flip angle =  $30^\circ$ ,  $FOV = 250\text{ mm} \times 250\text{ mm}$ , matrix size =  $256 \times 256 \times 124$ , voxel size =  $0.98\text{ mm} \times 0.98\text{ mm} \times 1.5\text{ mm}$ ).

### 2.4. Data analysis

Image analysis was performed on a PC using MATLAB 5.3 (Mathworks Inc., Natick, MA, USA) and SPM99 (<http://fil.ion.ucl.ac.uk/spm>). For the analysis, all images were realigned to the first volume, corrected for motion artefacts, normalised ( $4\text{ mm} \times 4\text{ mm} \times 4\text{ mm}$ ) into standard stereotaxic space (EPI-template provided by the Montreal Neurological Institute), and smoothed using an 8 mm full-width at half-maximum Gaussian kernel. Activated voxels were identified by the “General Linear Model” approach [20]. At the first level of analysis a statistical model for each S was computed, applying a box-car model, convolved with the modelled hemodynamic response and eliminating low-frequency noise. To test hypotheses about regionally specific condition effects, linear contrasts were employed for each S and condition, as suggested by Friston et al. [20]. The resulting set of voxel values for each contrast constitutes a statistical parametric map of the  $T$ -statistic ( $SPM(T)$ ). After this a second level analysis was performed, using the linear contrasts for each subject and condition. The statistical height threshold used in the analysis of main effects, for each subject as well as for the whole group, was set to  $P < 0.05$  ( $T > 4.7$ , corrected for multiple comparisons), for the LETTER- and ABSTRACT-conditions:  $P < 0.001$  ( $T > 3.4$ , uncorrected). The spatial extent threshold for all analyses was set at  $n = 10$  voxel ( $P < 0.001$ , corrected). The following main contrasts were defined: “3D versus CONTROL”, “LETTER versus CONTROL”, “ABSTRACT versus CONTROL”.

The  $SPM(T)$  for the contrasts for the comparisons between the three mental rotation conditions as well as for the comparison between women and men was thresholded at  $P < 0.001$  ( $T > 3.1$ , uncorrected), and a spatial extent threshold at  $n = 10$  voxel ( $P < 0.05$ , uncorrected). Because of our a priori defined hypotheses, based on results of our main effects, we used these uncorrected thresholds for the between group or between condition comparisons. A masking procedure as implemented in SPM99 was also used. With this masking procedure only those voxels were used for the statistical analysis that passed a height threshold of  $P = 0.001$  (uncorrected) for the appropriate baseline contrasts, e.g. 3D versus CONTROL as masking contrast for (3D versus CONTROL) versus (LETTER versus CONTROL) or women\_rotation versus CONTROL for the comparison (women\_rotation versus CONTROL) versus (men\_rotation versus CONTROL). The use of the masking procedure restricts the analyses to just those voxels in the mask created by the particular “task versus control” contrast, and thus voxels outside of the mask were excluded from the analysis. In order to avoid unnecessary comparisons, we

chose two orthogonal contrasts for the between-condition comparisons: (women and men: 3D versus CONTROL) versus (women and men: LETTER versus CONTROL and ABSTRACT versus CONTROL).

### 3. Results

#### 3.1. Behavioural data

Table 1 shows the mean reaction time for correct answers (RT) and errors with the corresponding standard deviations classified by the three mental rotation tasks for the women and the men. The performance data for the three combined mental rotation tasks are also shown. A two-way multivariate analysis of variance (MANOVA) with reaction time and errors as dependent variables, SEX as grouping factor, and mental rotation condition as repeated measure-

Table 1

Means and standard-deviations (S.D.) for women and men for the reaction times and errors for the three experimental conditions (3D, ABSTRACT, and LETTER) as well as the for the combined conditions (mental rotation)

Condition	3D	Letter	Abstract	Mental Rotation
Women ( <i>N</i> = 14)				
Reaction time (ms)				
Mean	1796.7	1556.3	1643.3	1665.4
S.D.	134.0	186.3	167.1	107.1
Errors (%)				
Mean	49.3	13.3	12.6	25.1
S.D.	14.3	10.7	9.6	10.5
Men ( <i>N</i> = 10)				
Reaction time (ms)				
Mean	1776.1	1463.1	1543.9	1594.4
S.D.	111.4	119.8	146.0	91.5
Errors (%)				
Mean	39.9	10.1	10.1	20.0
S.D.	16.5	9.7	5.3	9.2

ments factor (3D, LETTER, ABSTRACT) were computed. No significant sex difference in performance were found. This analysis revealed a significant effect for the mental rotation condition factor ( $F_{\text{Wilks-Lambda}}(4, 19) = 62.9$ ,  $P < 0.001$ ,  $\eta^2 = 0.93$ ). Subsequently performed univariate ANOVAs for each dependent variable demonstrated the same condition effect for each dependent variable (reaction time:  $F(1.5, 31.8) = 25.62$ ,  $P < 0.001$ ,  $\eta^2 = 0.54$ ; errors:  $F(1.5, 32.9) = 163.5$ ,  $P < 0.001$ ,  $\eta^2 = 0.88$ ; a Greenhouse–Geisser correction was used in case of heterogeneous variances). The influence of SEX and the interaction between SEX and CONDITION turned out to be weak or non-significant (MANOVA: SEX:  $F(2, 21) = 1.38$ ,  $P = 0.27$ ,  $\eta^2 = 0.12$ ; SEX  $\times$  CONDITION:  $F(4, 19) = 0.61$ ,  $P = 0.66$ ,  $\eta^2 = 0.11$ ). In order to “unpack” the CONDITION effect, subsequent Bonferroni-corrected *t*-tests for dependent samples were computed revealing longer reaction times for the 3D-condition than for the LETTER- ( $t = 6.0$ , d.f. = 23,  $P < 0.001$ ) and ABSTRACT-conditions ( $t = 4.3$ , d.f. = 23,  $P < 0.001$ ). The same picture emerged for the errors with more errors for the 3D-condition (3D versus LETTER:  $t = 13.5$ , d.f. = 23,  $P < 0.001$ ; 3D versus ABSTRACT:  $t = 14.8$ , d.f. = 23,  $P < 0.001$ ) (Table 1). In a further step the relation between angular disparity and RT was evaluated by applying two-way repeated measurement trend analysis with the nine angular disparities and the three mental rotation tasks as independent variables and SEX as between-subject factor. This analysis revealed a significant linear trend for the main effect of angular disparity ( $F(1, 22) = 60.6$ ,  $P < 0.001$ ,  $\eta^2 = 0.73$ ). There was also a moderate effect for a quadratic trend ( $F(1, 22) = 8.5$ ,  $P < 0.01$ ,  $\eta^2 = 0.28$ ). We did not find a significant interaction between the particular mental rotation task and angular disparity, thus demonstrating similar trends for the three tasks. No effect for SEX was seen (Fig. 2). Fig. 3 shows the reaction time as a function of the angular disparity as well as the percentage of correct responses separately for women and men for the three combined mental rotation conditions.

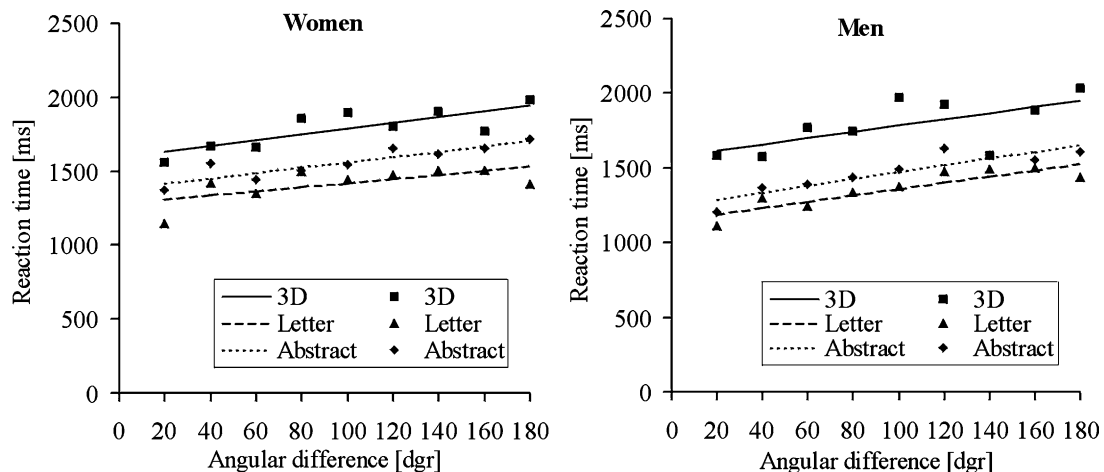


Fig. 2. Mean reaction time for the three mental rotation conditions for the “same” judgements as a function of angular difference for women and men. Also indicated are the regression lines.

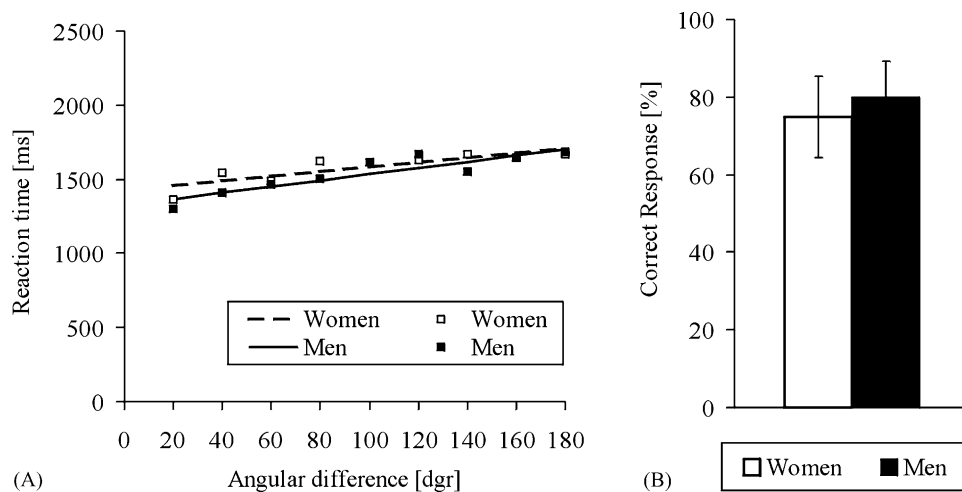


Fig. 3. (A) Mean reaction time for the combined mental rotation conditions for the “same” judgements as a function of angular difference for women and for men. Also indicated are the regression lines; (B) percentage of correct responses for the combined mental rotation tasks for both groups.

### 3.2. Neurophysiological data

The mental rotation tasks evoked different activation patterns in women and men. Women showed strongly significant bilateral activations during the 3D-condition in the superior parietal lobule (SPL), including the intraparietal sulcus (IPS). Significant activations were also found bilaterally in the caudal part of the dorsal premotor area (PMdc), the pre-supplementary motor area (pre-SMA), the inferior temporal gyrus (ITG) and the right inferior frontal gyrus (IFG). Similar activation patterns were found for the LETTER- and the ABSTRACT-conditions, but at a lower level of activation. In contrast, for men all three mental rotation tasks

evoked significant activation in the superior and middle occipital gyrus (SOG, MOG), including the parieto-occipital sulcus (POS). As in the women, the superior parietal lobule, premotor areas and the pre-supplementary motor area were activated. Additionally, a small activation was seen in the primary motor cortex for the 3D- and the LETTER-conditions.

Comparison between the three mental rotation conditions for each group demonstrated a generally significant higher activation for the mental rotation of the 3D-figures than for the mental rotation of the LETTERS or the ABSTRACT-figures in most of the above mentioned cortical regions (Table 2). No differences were seen for the comparison between the LETTER- and ABSTRACT-conditions.

Table 2

Brain areas and their stereotaxic coordinates for the whole group for the comparison of the 3D-condition vs. the ABSTRACT- and LETTER-conditions

Comparison	Anatomical region		x	y	z	T	P
3D vs. LETTER and ABSTRACT	Middle occipital gyrus	R	32	−84	8	7.1	**
	Posterior cerebellum	R	36	−76	−24	6.8	**
	Intraparietal sulcus	R	24	−64	52	5.0	**
	Superior parietal lobule	R	24	−72	48	4.8	*
	Inferior temporal gyrus	R	44	−64	−16	4.7	*
	Parieto-occipital sulcus	R	16	−84	40	4.1	*
	Posterior cerebellum	L	−32	−72	−32	6.1	**
	Cingulate gyrus	R	4	24	36	5.4	**
	Medial frontal gyrus, pre-SMA		0	12	48	4.9	**
	Inferior frontal gyrus	R	52	8	28	4.8	**
	Thalamus	R	8	−20	8	4.7	*
		L	−12	−24	8	4.3	*
	Middle occipital gyrus	L	−28	−88	12	4.6	*
	Superior parietal lobule	L	−24	−72	48	4.6	*
	Precentral sulcus, PMdc	R	32	−4	60	4.1	*
	Intraparietal sulcus	L	−36	−48	60	4.0	*
	Inferior frontal gyrus	L	−56	4	28	3.7	*

Note: *T*-values of the maxima from the comparisons are given. *x*, *y*, *z*: MNI coordinates in mm. L, R: left and right hemisphere. PMdc, caudal part of the premotor cortex; pre-SMA, pre-supplementary motor area.

\* *P* < 0.001 (uncorrected).

\*\* *P* < 0.05 (corrected).



In order to detect sex differences in the context of SPM, hemodynamic responses of men and women were compared by combining all three mental rotation tasks. We have chosen this strategy because it is basically difficult and sometimes impossible to calculate complex interaction effects in the context of a conventional SPM analysis. Complex interaction effects are explored in subsequent analyses employing volume of interest analysis (see below). Comparison of the combined three mental rotation conditions with the control conditions revealed the following regions of activation in men and women. Women exhibited a highly significant bilateral activation in the superior parietal lobule, including the intraparietal sulcus, the inferior parietal lobule (IPL), the middle occipital gyrus and the parieto-occipital sulcus. In addition, significant activations were found bilaterally in the caudal part of the dorsal premotor cortex, the presupplementary motor area (pre-SMA), the inferior temporal gyrus, and the right inferior frontal gyrus. In men, the mental rotation tasks showed significant activation in the right POS, the left pIPS and the left SPL. While both men and women showed PMdc and the pre-SMA activation, men showed an additional significant activation of the left motor cortex (M1). No significant activation was found in the ITG (Table 3, Fig. 4).

Comparing hemodynamic responses of women and men revealed stronger activations in women in the following areas: (1) bilaterally within the ITG on the right side extending into the MOG, (2) in the right SPL extending into the anterior and posterior IPS, (3) in the left IPL extending into the anterior IPS and (4) bilaterally in PMdc in the precentral gyrus. Men exhibited significant stronger activations in (1) the left pIPS and the right POS, and (2) bilaterally in the primary motor area (M1) (Table 4, Fig. 5).

### 3.2.1. Volume of interest analysis

In order to strengthen our analysis and to explore interaction effects in detail, we obtained hemodynamic responses from each subject and each condition from selected brain areas and subjected them to a multivariate ANOVA for repeated measurements with the three mental rotation conditions (3D, ABSTRACT, LETTER) as the independent variable and the SEX as the between-subject factor. For this, we selected 15 peak activation regions selected from the comparisons (women\_rotation versus CONTROL) and (men\_rotation versus CONTROL) (Table 3). From these peak activations, hemodynamic responses were obtained for each subject and each condition. Because each voxel constitutes a weighted mean of 20 surrounding voxels due to the used spatial smoothing procedure, the obtained measures can be understood as spherical volumes of interests (VOIs). The following VOIs were obtained for the comparison “women\_rotation versus CONTROL”: the right SPL (MNI-coordinates (mm): 20, –68, 52), right ITG (52, –60, –16), the right MOG (32, –88, 0), the left aIPS (–40, –48, 44), the left POS (–24, –76, 32), the left ITG (–48, –68, –12), the left pCB (–36, –76, –28), the left PMdc (–28, –4, 64), the right IFG (52, 8, 24). For the comparison (men\_rotation versus CONTROL) we defined: the right POS (12, –88, 40), the left pIPS (–36, –60, 56), and the left M1 (–28, –20, 56). Three regions showed significant activations in both women and men, and therefore the values of these regions were combined: the left SPL (women: –16, –76, 52, men: –28, –72, 56), the right PMdc (women: 28, –4, 56, men: 24, –8, 56), pre-SMA (women: left: –4, 16, 48, right: 4, 12, 52, men: 0, 12, 48). For each VOI, we obtained a *t*-value for each subject and each condition

Table 3

Brain areas and their stereotaxic coordinates for women and men for the combined three mental rotation conditions vs. all three CONTROL conditions

Comparison	Anatomical region		x	y	z	T	P
Women (rotation vs. CONTROL)	Superior parietal lobule	R	20	–68	52	13.7	**
	Inferior temporal gyrus	R	52	–60	–16	8.8	**
	Middle occipital gyrus	R	32	–88	0	8.5	**
	Superior parietal lobule	L	–16	–76	52	11.4	**
	Intraparietal sulcus	L	–40	–48	44	8.7	**
	Parieto-occipital sulcus	L	–24	–76	32	7.8	**
	Precentral sulcus, PMdc	R	28	–4	56	10.3	**
	Inferior temporal gyrus	L	–48	–68	–12	9.4	**
	Posterior cerebellum	L	–36	–76	–28	6.7	**
	Precentral sulcus, PMdc	L	–28	–4	64	9.3	**
	Medial frontal gyrus, pre-SMA	L	–4	16	48	7.8	**
	Medial frontal gyrus, pre-SMA	R	4	12	52	7.4	**
	Inferior frontal gyrus	R	52	8	24	6.9	**
Men (rotation vs. CONTROL)	Parieto-occipital sulcus	R	12	–88	40	10.5	**
	Posterior Intraparietal sulcus	L	–36	–60	56	8.6	**
	Superior parietal lobule	L	–28	–72	48	8.5	**
	Precentral sulcus, PMdc	R	24	–8	56	9.4	**
	Precentral gyrus, M1	L	–28	–20	56	6.9	**
	Medial frontal gyrus, pre-SMA		0	12	48	6.7	**

Note: *T*-values of the maxima from the comparisons against the control condition are given. *x*, *y*, *z*: MNI coordinates in mm. L, R: left and right hemisphere. M1, motor cortex; PMdc, caudal part of the premotor cortex; pre-SMA, pre-supplementary motor area.

\*\* *P* < 0.05 (corrected).

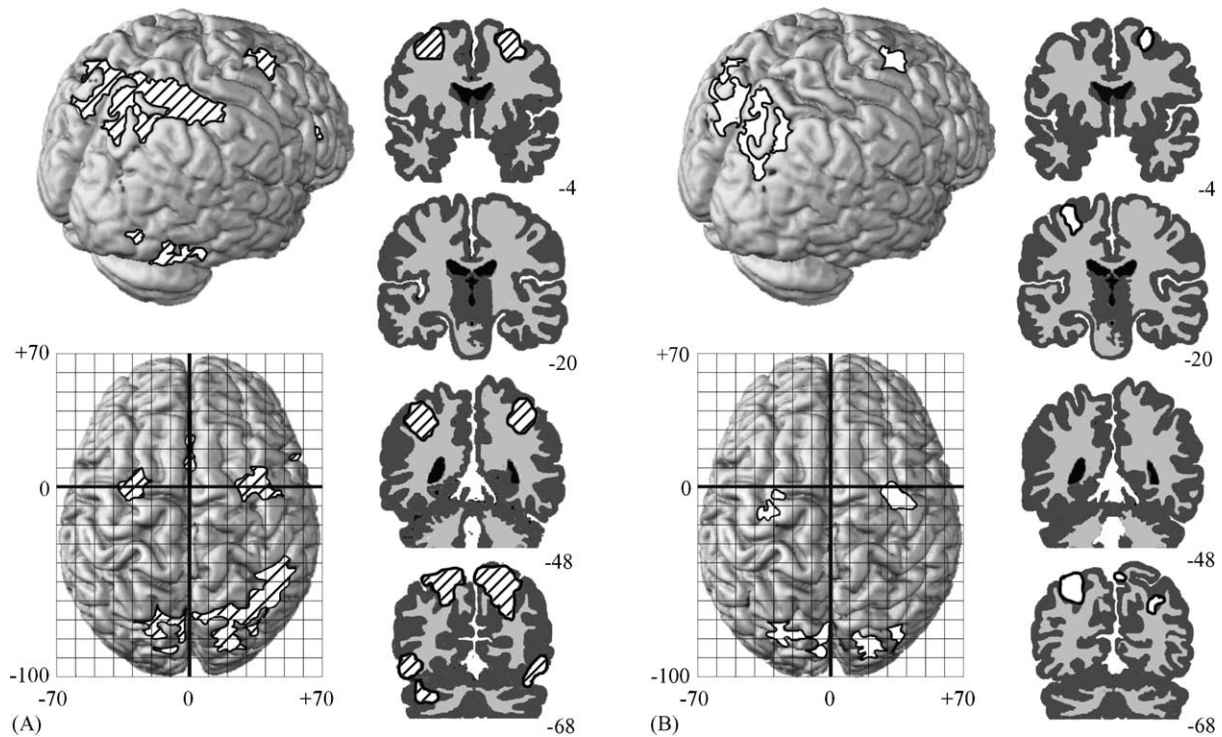


Fig. 4. Areas of significant activations obtained for all mental rotation conditions compared to the control condition superimposed on a MNI-normalized brain. (A) Women, striped; (B) men, white. Schematic coronal sections show activations in the following areas: PMdc ( $y = -4$ ), M1 ( $y = -20$ ), IPS ( $y = -48$ ), SPL and ITG ( $y = -68$ ).

representing the standardized difference between the mental rotation task and the control condition.

In Table 5, the results of the MANOVA and the subsequent ANOVAs are shown. There were significant effects for SEX and CONDITION but no significant interaction between these factors. The ANOVAs revealed significant

effects for the factor SEX in 8 of the 15 regions. In order to “unpack” the SEX-effect, subsequent Bonferroni-corrected  $t$ -tests for independent samples were computed revealing stronger activations for women than for men in the right SPL, the left aIPS and the left ITG for all three mental rotation conditions ( $P < 0.05$ ). For the right ITG and the

Table 4

Brain areas and their stereotaxic coordinates for the comparisons: women vs. men and vice versa, for the combined mental rotation conditions vs. the CONTROL conditions

Comparison	Anatomical region		$x$	$y$	$z$	$T$	$P$
Women vs. men	Superior parietal lobule	R	20	-68	56	6.2	**
	Posterior intraparietal sulcus	R	20	-60	48	6.1	**
	Anterior intraparietal sulcus	R	36	-44	48	3.7	*
	Inferior temporal gyrus	L	-48	-68	-8	5.8	**
	Precentral gyrus, PMdc	L	-36	-4	52	5.7	**
	Anterior intraparietal sulcus	L	-36	-48	48	5.5	**
	Inferior parietal lobule	L	-60	-28	36	4.3	*
	Inferior temporal gyrus	R	52	-60	-4	5.2	**
	Middle occipital gyrus	R	48	-72	-16	4.1	*
	Precentral gyrus, PMdc	R	32	0	52	4.4	*
Men vs. women	Precentral gyrus, M1	L	-32	-20	68	6.2	**
	Posterior intraparietal sulcus	L	-36	-72	40	5.7	**
	Parieto-occipital sulcus	R	16	-88	40	5.7	**
	Precentral sulcus, M1	R	32	-24	52	4.6	*

Note:  $T$ -values of the maxima from the comparisons are given.  $x$ ,  $y$ ,  $z$ : MNI coordinates in mm. L, R: left and right hemisphere. M1, motor cortex; PMdc, caudal part of the premotor cortex.

\*  $P < 0.001$  (uncorrected).

\*\*  $P < 0.05$  (corrected).

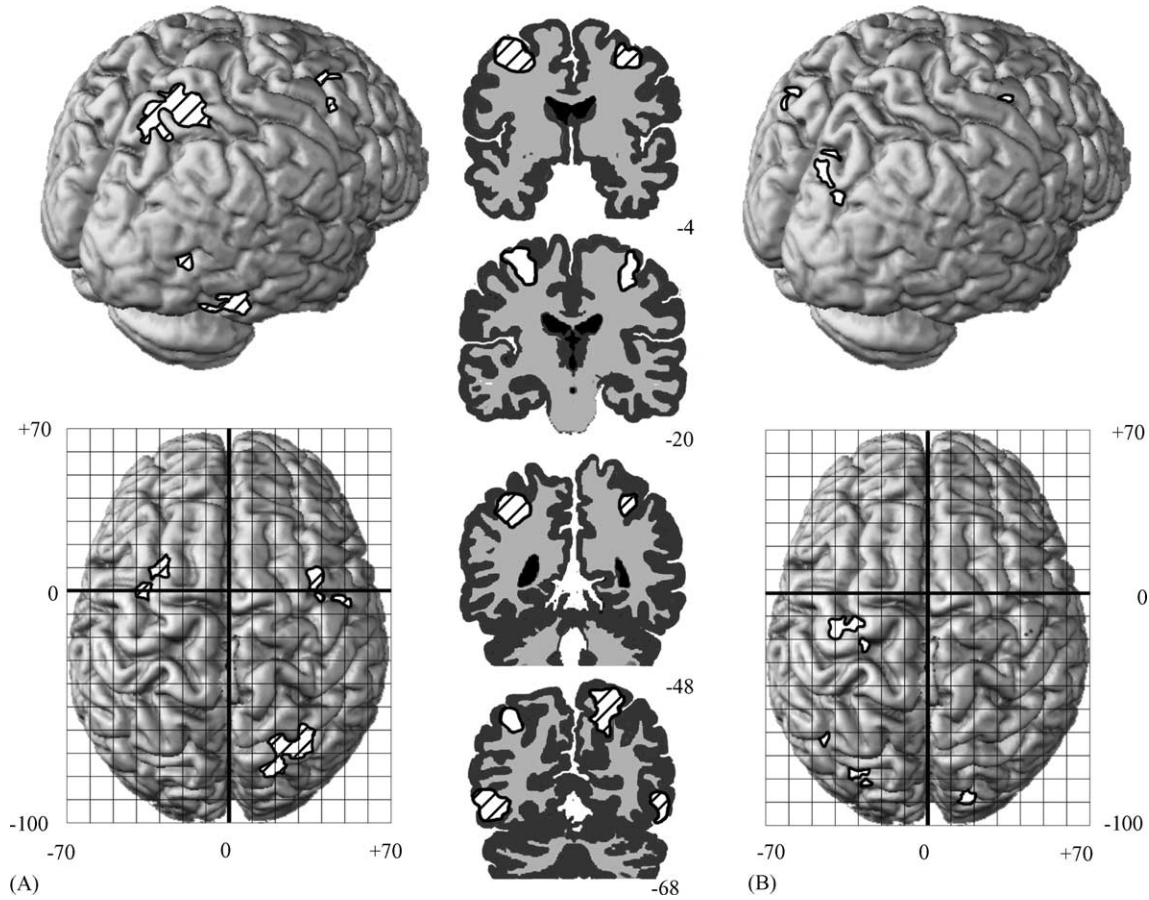


Fig. 5. Areas of significant activations for the comparisons: women vs. men and vice versa, for the combined mental rotation conditions vs. the CONTROL conditions superimposed on a MNI-normalized brain. (A) Significantly stronger activations in women than in men, striped; (B) significantly stronger activations in men than in women, white. Schematic coronal sections show activations in the following areas: PMdc ( $y = -4$ ), M1 ( $y = -20$ ), IPS ( $y = -48$ ), SPL and ITG ( $y = -68$ ).

Table 5

MANOVA and subsequent ANOVAs with repeated measurements for the CONDITION factor and the hemodynamic responses obtained from the volume of interests (peak activations taken from Table 2)

Region (voxel of interest)	Factor		SEX $\times$ CONDITION
	SEX	CONDITION	
Main effect	$F_{\text{Wilks-Lambda}}(8, 15) = 3.9, \eta^2 = 0.88^*$	$f_{\text{Wilks-Lambda}}(30, 60) = 4.4, \eta^2 = 0.69^{**}$	$F_{\text{Wilks-Lambda}}(30, 60) = 1.2, \eta^2 = 0.37 \text{ n.s.}$
Right SPL	$F(1, 22) = 15.2, \eta^2 = 0.41^{**}$	$F(1.4, 30.1) = 9.7, \eta^2 = 0.31^*$	
Left SPL	$F(1, 22) = 0.73, \eta^2 = 0.03 \text{ n.s.}$	$F(1.8, 40.4) = 11.6, \eta^2 = 0.35^{**}$	
Right POS	$F(1, 22) = 17.4, \eta^2 = 0.44^{**}$	$F(1.3, 28.5) = 5.9, \eta^2 = 0.21^*$	
Left POS	$F(1, 22) = 3.4, \eta^2 = 0.14 \text{ n.s.}$	$F(1.7, 36.7) = 1.4, \eta^2 = 0.06 \text{ n.s.}$	
Left aIPS	$F(1, 22) = 15.8, \eta^2 = 0.42^{**}$	$F(1.9, 42.6) = 5.6, \eta^2 = 0.20^*$	
Left pIPS	$F(1, 22) = 0.7, \eta^2 = 0.03 \text{ n.s.}$	$F(1.9, 42.6) = 5.4, \eta^2 = 0.20^*$	
Right MOG	$F(1, 22) = 3.2, \eta^2 = 0.13 \text{ n.s.}$	$F(1.7, 37.9) = 23.1, \eta^2 = 0.51^{**}$	
Right ITG	$F(1, 22) = 7.2, \eta^2 = 0.25^*$	$F(1.6, 35.0) = 3.9, \eta^2 = 0.15^*$	
Left ITG	$F(1, 22) = 14.3, \eta^2 = 0.40^{**}$	$F(1.6, 34.5) = 2.3, \eta^2 = 0.1 \text{ n.s.}$	
Right IFG	$F(1, 22) = 4.1, \eta^2 = 0.16 \text{ n.s.}$	$F(1.7, 37.4) = 7.2, \eta^2 = 0.25^*$	
Left pCB	$F(1, 22) = 8.6, \eta^2 = 0.28^*$	$F(1.9, 41.1) = 17.8, \eta^2 = 0.45^{**}$	
Right PMdc	$F(1, 22) = 0.8, \eta^2 = 0.03 \text{ n.s.}$	$F(1.8, 39.6) = 9.8, \eta^2 = 0.31^{**}$	
Left PMdc	$F(1, 22) = 4.9, \eta^2 = 0.18^*$	$F(1.9, 42.5) = 9.0, \eta^2 = 0.29^{**}$	
Left M1	$F(1, 22) = 8.6, \eta^2 = 0.28^*$	$F(1.9, 41.0) = 1.5, \eta^2 = 0.1 \text{ n.s.}$	
Pre-SMA	$F(1, 22) = 3.2, \eta^2 = 0.13 \text{ n.s.}$	$F(1.9, 42.4) = 14.4, \eta^2 = 0.40^{**}$	

SPL: superior parietal lobule, POS: parieto-occipital sulcus, aIPS: anterior part of the intraparietal sulcus, pIPS: posterior part of the intraparietal sulcus, MOG: middle occipital gyrus, ITG: inferior temporal gyrus, IFG: inferior frontal gyrus, pCB: posterior cerebellum, PMdc: dorsal premotor cortex, M1: primary motor cortex, pre-SMA: supplementary motor area.

\*  $P < 0.05$ .

\*\*  $P < 0.001$ .



left PMdc these differences were seen only in the 3D- and ABSTRACT-conditions ( $P < 0.05$ ). For the pCB, women exhibit only in the 3D-condition stronger activation than men ( $P < 0.05$ ). Men revealed stronger activations in the right POS for all three mental rotation conditions, and in the left M1 in the ABSTRACT and 3D-condition ( $P < 0.05$ ). Regarding the factor CONDITION, 12 of the 15 VOIs revealed significant effects (Greenhouse–Geisser correction was used in case of heterogeneous variances). Subsequent *t*-tests for dependent samples revealed stronger activation for the 3D-condition than for the LETTER- and ABSTRACT-conditions in most of the analysed VOIs ( $P < 0.05$ ). Only in the right MOG the mental rotation of letters evoked stronger hemodynamic responses than mental rotation of abstract figures ( $P < 0.05$ ), no other region showed differences between these two conditions.

This VOI analysis supported our earlier mentioned results based on conventional SPM analysis and showed that there was no interaction between SEX and mental rotation task.

#### 4. Discussion

The present study was designed to measure cortical activation patterns in women and men who did not differ significantly in mental rotation task performance. As expected, mental rotation of 3D-figures was more difficult than the other tasks as indexed by longer reaction times and more errors.

In general mental rotation evoked cortical activation bilaterally in the superior and inferior parietal lobule, including the intraparietal sulcus, in the parieto-occipital sulcus and the middle occipital gyrus. Additional significant activations were found in the inferior temporal gyrus, the inferior frontal gyrus, the dorsal premotor cortex and the primary motor area. The mental rotation of 3D-figures evoked significant stronger cortical hemodynamic responses than the mental rotation of ABSTRACT-figures or LETTERS in all activated areas. However, there were significant sex differences in cortical activations, with women showing stronger activation than men bilaterally in ITG and the PMdc, in the right SPL and IPS and in the left IPL and aIPS. Men, in contrast, exhibited stronger activation bilaterally in the primary motor cortex, in the left pIPS and the right POS.

The results of this study demonstrate that different mental rotation conditions did not inevitably evoke different cortical activation patterns. We only found stronger activations for the 3D-condition in some areas. This activation finding is in marked contrast with the behavioral findings, where there was a marked rank order of difficulty, with the performance levels best in the LETTER- and ABSTRACT-conditions and worst in the 3D-condition. These results support our previous study, where we did not find significant differences with respect to the cortical hemodynamic responses either in terms of intensity or in terms of spatial extend in spite of strong performance differences between the different mental

rotation tasks [31] (for a related finding see Podzebenko et al. [45]).

The most essential aspect of our study is that sex-specific activation patterns during mental rotation were observed in the absence of performance differences between the sexes. Three principal, not mutually exclusive, hypotheses can be offered to account for the sex differences:

- (1) The sexes apply different strategies in solving the mental rotation tasks.
- (2) In interaction with (1), the sexes may focus attention differently on the mental rotation tasks.
- (3) There is a sex-specific topographical organization of neural networks involved in mental rotation.

In support of (1) and (3), there are stronger activations of ITG and MOG in women than in men. These are part of a system known to be involved in various higher cognitive processes including object identification, object categorization, object memory, spatial analysis, spatial memory, selective attention to objects, and covert attention [6]. Carpenter et al. [7] associated their activation within the fusiform gyrus and the inferior temporal gyrus in mental rotation mainly with processes of object and object-part identification (as a part of the “what” system). A parsimonious interpretation for the activation of the inferior temporal gyrus in women would be that women expend more effort in dealing with the identity of the visual objects, which could include attempts of identification of parts of the objects, while men are more active in responding to the surface visual-spatial characteristics. Fig. 6 shows, at a speculative level, these possible processing strategies in women and men during mental rotation tasks. The activation of areas as the ITG known for object recognition as mentioned earlier in women also correspond to the known preferences of women for the verbal-analytic or more piecemeal strategies in mental rotation tasks [10,44]. Because of the lack of differences in performance between both sexes we attribute the differences to a preference for different strategies. Thomsen et al. [60] suggested a “gestalt” strategy for men and a “serial” reasoning strategy for women, based on their findings of a more frontal inferior activation for the women than for the men. We, too, found a small activation of the right inferior frontal gyrus for the women. However, there is no agreement in the involvement of the inferior frontal areas in mental rotation tasks. Cohen et al. [11], Thomsen et al. [60], Jordan et al. [31] and Podzebenko et al. [45] described bilateral activation of the inferior frontal areas, whereas others, e.g. Tagaris et al. [58,59], Kosslyn et al. [35], Richter et al. [47] and Dietrich et al. [17] failed to show hemodynamic responses in these cortical areas. We assume, that these differences may be related not only to different methods but also to different individual strategies of the Ss. For example, the inferior frontal gyrus is reported to be involved in working memory tasks. According to the “hemispheric encoding retrieval asymmetry” model (HERA) the left IFG is more involved in encoding, whereas the right IFG seems to be activated more

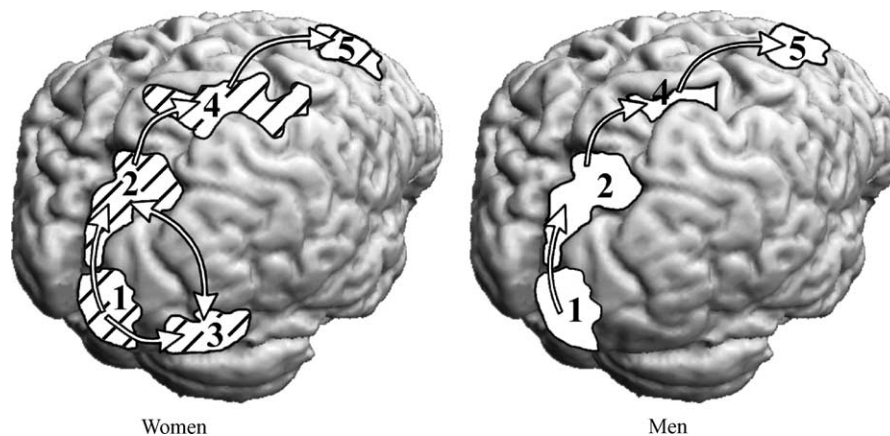


Fig. 6. Hypothetical pathways for solving mental rotation tasks in women and men: (1) primary visual area, (2) extrastriate cortex, (3) inferior temporal/inferior occipital regions, (4) parietal regions (intraparietal sulcus), (5) premotor cortex.

during retrieval. Tasks requiring processes like object decision [21] or object selection in association with sustained attention [13] could also evoke activations within the right inferior frontal gyrus. A possible interpretation for the activation of the right IFG in our study may be that women place more effort on the mental rotation tasks by picturing the figures in their mind. Thus, it may be that we measured a variant of the spatial working memory.

We did not find any activation in cortical areas usually involved in verbal or phonetic processing (left frontal and left temporal areas) [4,19,22,30,64], which would be expected if some kind of “verbal-analytic” strategy were the principal strategy applied by women during mental rotation tasks. The failure to find activation in areas concerned with verbal function, when performing mental rotation tasks, is in line with other studies [6]. Thus, we conclude that explicit “verbal” strategies are uncommon during mental rotation. Regarding the activation of the inferior temporal and the right inferior frontal areas, this is consistent with a more piecemeal and analytic and/or serial strategy for women.

Sex-specific processing strategies are also suggested by the different activations in the frontal motor areas (PMdc and M1). Area PMdc (especially the left) is thought to play an important role in the recalibration of visual and motor coordinates (especially in body-part-centered coordinates), while generating motor programs [48]. The differences in regional patterns suggest a difference in the way in which motor systems are recruited in solving spatial problems. Recent work [35,47] suggests that mental rotation problems can be solved with and without involvement of the motor system, an observation that is indirectly confirmed by the study of patients with apraxia, some of whom have problems in imagining movements while showing intact spatial imagery [41]. Because Richter et al. found a positive correlation between the onset times and width of the activation peaks in the premotor and other motor areas and the response time, they proposed a relation of the premotor areas to the very execution of the mental rotation task, and not only to an

aspect of the task which is only peripherally related to mental rotation, such as, for example, the response selection or the actual pushing of the answer button at the end of the task [47]. The authors assumed that the involvement of motor areas in mental rotation tasks could depend on subject’s perspectives during the dynamic imagery, e.g. an internal or an external perspective. The internal perspective, e.g. “imagine you are manipulating an object”, would evoke the activation in the motor areas, whereas the external perspective, e.g. “imagine somebody else’s manipulation of an object” would not. Therefore, the subjects in our study could have used a more internal perspective but at different levels. As preliminary testable hypothesis, it might be suggested that men take a more concrete, and, literally “hands on” approach, as evidenced by activation of the primary motor cortex. This hypothesis is supported by a study of Kosslyn et al. [36] who recently demonstrated the involvement of the primary motor cortex in a mental rotation task when subjects imagined the rotations as a consequence of earlier manual activity with the objects [36]. Additionally, Sadato et al. showed that women exhibit a more symmetric activation of the premotor cortices in an active tactile discrimination task. They suggested differences in motor programs for exploration in manipulospatial tasks possibly by greater interhemispheric interaction through the dorsal premotor cortices in women than in men [49].

The sex-specific activations in the posterior cortical regions could represent sex-specific attentional strategies and or sex-specific cortical organization patterns of functions located in this region [23,24,40,54,57]. While SPL and especially the IPS are the core regions involved in mental rotation performance, subdivisions of these areas are under discussion. For instance, it is hypothesized that the caudal IPS receives input from the visual cortex in order to process 3D-visual information [50,51]. From there, information is thought to pass to the more anterior parts of the IPS [39] linking the visual information to the frontal motor and premotor areas. The bilateral activation of the aIPS and the

PMdc found for the women of our study could represent these processes, whereas the activation of the posterior IPS in men may emphasize the processing of the 3D-information of the stimuli. In addition to these specific perceptual functions there are also the so-called “cognitive intermediates”, such as spatial attention or spatial memory, which might be at least partly controlled by neural networks within or in the vicinity of the SPL and IPS, predominantly in the right hemisphere [14–16]. It remains to be determined what differences in attentional strategies or their interactions with underlying differences in organization lead to the differences in activation patterns in the sexes.

In conclusion, the observed sex differences in cerebral activation included differences with respect to the level of activation for regions active in both sexes, differences in lateralization of areas that were more strongly activated in one sex than in the other, and areas that were significantly active in one sex but not the other. Our interpretation allows for the possibility of marked plasticity in regional activation patterns, depending on strategies in solving mental rotation problems. For instance, practice with such problems may result in strategy changes that in turn produce different activation patterns. The sex differences are, in this view, not immutable and attributable to fixed differences in cerebral organization but rather may result from sex-specific preferred strategies and reactions to certain classes of cognitive problems. Thus, it may be an interesting question for future research to explore whether different strategies and their concomitant cortical activations might be changed by experience in solving mental rotation problems.

## Acknowledgements

We thank two anonymous reviewer for most helpful suggestions.

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