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Does egocentric mental rotation elicit sex differences?

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Mental rotation tests traditionally show a male performance advantage. Some neuroimaging studies have reported sex-specific cortical activation patterns during mental rotation. However, these experiments used abstract stimuli and some studies did not systematically exclude performance as a confounding variable. The mental rotation of hands and hand-related objects, compared to abstract objects, is known to evoke an egocentric motor strategy. In this study, we used fMRI to explore potential gender-specific cortical activation patterns for the mental rotation of hands and tools in a sample with an adequate and equal performance for men and women. We found a common neural substrate for men and women comprising superior parietal lobe, dorsolateral premotor cortex, and extrastriate occipital areas, compatible with an egocentric motor strategy for the mental rotation of hands and tools. Sex differences were modest and limited to the mental rotation of hands. Women recruited more left ventral premotor cortex, which could imply that women rely more on imitation or use more perceptual comparisons. Men, on the other hand, drafted more the lingual gyrus, possibly referring to more extensive semantic or early visual processing. We conclude that men and women use a very similar motor strategy during egocentric mental rotation with a potential gender-specific accent.

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Introduction

Men outperform women on several spatial ability measures. Particularly, the Mental Rotations Test (MRT) shows a robust sex difference (Crucian and Berenbaum, 1998; Halpern and Tan, 2001; Masters, 1998; Parsons et al., 2004; Siegel-Hinson and McKeever, 2002; Vandenberg and Kuse, 1978; Voyer et al.,

1995). The MRT is a paper-and-pencil test based on the mental imagery study of Shepard and Metzler (1971). This test shows that the response time, associated with deciding whether two objects at different orientations are identical or mirror images, increases with angular disparity. Similar behavioral experiments have revealed that mentally rotating a visual image is very similar to physically manipulating an actual object (Cooper and Shepard, 1984; Kosslyn and Ochsner, 1994). Why does this specific implementation of an imagery-based problem solving strategy elicit sex differences?

A number of explanations have been offered within the nature or nurture debate. An illustration of the environmental approach, related to sex stereotyping, is the effect of spatial experience (Cerone and McKeever, 1998). The biological line of research, on the other hand, suggests that genetics, hormonal exposure, and cerebral organization may cause the sex difference. Kimura (1999), for example, stresses the importance of prenatal events and early or current hormonal environments, possibly mediated by brain structure and function. Up to this point, there is no consensus on the relative contribution of these two viewpoints. Though there seems to be a dominance of biological causes in the literature as illustrated by a tachistoscopic study, revealing that sex differences on the MRT were primarily due to right hemispheric specialization while spatial activity experiences were only secondarily involved (Siegel-Hinson and McKeever, 2002).

A recent study distinguishes task variables besides environmental causes and biological factors (Parsons et al., 2004). Task variables have long been discarded but may prove to be important. For instance, the manner of administering and scoring the MRT influences the effect size of the sex difference (Voyer et al., 1995). One could also wonder if the nature of the stimulus, employed in the mental rotation task, has an impact. The MRT consists of images of three-dimensional multiarmed cube shapes, originally used in the Shepard–Metzler experiment. Adjusting the complexity of these Shepard–Metzler objects still elicits sex differences (Bryden et al., 1990), but they disappear when real three-dimensional models of the original images are used (Bryden et al., 1990; McWilliams et al., 1997). Studies reporting mental rotation of pictures of completely different objects, such as hands or a manikin, result in a male advantage too (Karadi et al., 1999;

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Richardson, 1994). Of particular interest is the study of Collins and Kimura (1997), which implies that even a two-dimensional mental rotation task utilizing simple abstract figures could bring forth a sex difference as large as on the MRT, but only if the task was difficult enough (e.g., large angular disparity). We conclude that images of a wide variety of objects can lead to sex differences in mental rotation performance, provided that the task difficulty is sufficiently high.

Underlying sex differences in brain organization are often regarded as an indication of a biological explanation for the male advantage in mental rotation. The emergence of functional brain imaging offers the possibility to directly verify if females recruit other brain regions while performing mental rotation, associated with gender-specific strategies. To our knowledge, up to now, four studies have explored sex differences in cortical activation patterns while performing a mental rotation task very similar to the MRT (Dietrich et al., 2001; Jordan et al., 2002; Thomson et al., 2000; Weiss et al., 2003). One study found larger cortical activation patterns in females, compared to males, but only during the high estrogen phase (Dietrich et al., 2001). The level of estrogen had no effect on the lateralization or localization of the cortical activation pattern.

The other three experiments report gender-specific cortical activation patterns, but there is no consensus on the nature of these differences (Jordan et al., 2002; Thomson et al., 2000; Weiss et al., 2003). Two studies suggest that men show increased activation of parietal areas, reflecting a gestalt strategy, while women would rather recruit right inferior frontal cortex, indicating a more analytic or serial strategy (Thomson et al., 2000; Weiss et al., 2003). Jordan et al. (2002), on the other hand, find stronger activity for women in the inferior temporal gyrus, premotor cortex, and certain parietal areas, while the men demonstrate more involvement of the primary motor cortex, a part of the left intraparietal sulcus, and the parieto-occipital sulcus. In the following, we wish to focus on two aspects of these three studies: the stimuli employed and the behavioral measures reported.

First, the abovementioned experiments are limited to the mental rotation of abstract stimuli. All three studies used Shepard–Metzler objects in their experimental condition. One study also included two-dimensional abstract objects and letters (Jordan et al., 2002). Mental rotation of other objects, particularly hand-related stimuli, may result in a different cortical activation pattern. A PET study, comparing the mental rotation of hands and Shepard–Metzler objects, resulted in stimulus-specific cortical activation patterns with motor and premotor cortex activation limited to the hands condition, reflecting a differential strategy (Kosslyn et al., 1998). Mental rotation of stimuli such as hands preferably evoke a motor strategy with imaginary limb movement, resulting in additional activation of motor areas, while abstract stimuli (e.g., Shepard–Metzler objects) are more prone to elicit a visual object transformation. These motor strategies in mental rotation could also be called egocentric strategies since it has been suggested that motor strategies are not limited to the mental rotation of body parts but are rather required by egocentric mental transformations in general (Wraga et al., 2003). The term “egocentric” refers in this definition to an egocentric frame of reference in both action and space, as the participant imagines the mental rotation from the first-person-perspective and experiences oneself as the agent of the mental rotation (Vogele and Fink, 2003). In a second PET study (Kosslyn et al., 2001),

subjects were instructed to adopt two different strategies while mentally rotating the same Shepard–Metzler objects, an egocentric strategy in which one imagines oneself as the agent of rotation or a strategy where the object is being rotated by an external or nonbody source. A direct comparison of both strategies revealed only motor cortex activity when using an egocentric strategy. A recent fMRI study comparing the mental rotation of hands and tools in a male sample, further demonstrated that these egocentric or motor strategies can also be implicitly evoked by graspable, hand-related objects (Vingerhoets et al., 2002). The mental rotation of hands evoked bilateral premotor involvement, suggesting imaginary movement for both hands to solve the task, while the mental rotation of tools revealed unilateral premotor activation associated with the dominant hand, implying imaginary manipulation of the tool with this hand. We can summarize that an egocentric strategy in mental rotation implies imaginary limb movement with its corresponding cortical activation pattern and can be elicited implicitly through hand-related stimuli.

Second, these three studies report behavioral data pertaining to the performance on the mental rotation task. Behavioral measures are important for two reasons. To start with, they allow to control whether participants actually used mental rotation to solve the task. In other words, is the error rate sufficiently small and does the response time increase with angular disparity? Second, a SPECT study, using a related visuospatial task, suggests that quality of performance, rather than gender, has an effect on the cortical activation pattern (Unterrainer et al., 2000). While the abovementioned studies reported equal performance for men and women, none met both requirements for an adequate (high accuracy and typical response time profile) behavioral performance. Accuracy, for example, was only satisfactory in one study that did not describe the response time profiles (Weiss et al., 2003).

In the present study, we want to explore sex-specific cortical activation patterns during egocentric mental rotation of hands and tools, in a sample with an adequate and equal performance. Or in other words, will sex-specific strategies supersede an implicitly evoked egocentric strategy when performance is controlled for? Eleven female participants carried out the mental rotation experiment of Vingerhoets et al. (2002). Next, we compared these results with the data of 11 male subjects who participated in the original study of Vingerhoets et al. (2002).¹ We expect the mental rotation of hands and tools to show very similar cortical activation patterns. More specifically, we anticipate recruitment of motor areas besides the classic parietal involvement, compatible with a common egocentric strategy to solve both mental rotation tasks. Furthermore, we presume no important differences in the behavioral data according stimulus type as they elicit the same mental rotation strategy. In addition, we suppose the potential gender-specific involvement of brain regions to be comparable for hands and tools.

¹ There may be mild differences in the results for the male participants compared to the published findings of Vingerhoets et al. (2002). We did not include all 12 subjects from the original study. The spatial preprocessing and statistical thresholding were also slightly different in this study.

Methods

Participants

Twenty-two healthy right-handed volunteers (eleven females) participated in this study, following written informed consent according to the institutional guidelines of the Ethics Committee of the Ghent University Hospital. All participants were between 19 and 40 years old (mean \pm SD: overall 25.4 ± 5.2 years; women 24.7 ± 3.1 years; men 26.1 ± 6.7 years; $df = 13.96$, $t = 0.61$, $P = 0.55$). Most participants were graduate students or had an equal level of education as employees of the Ghent University or Hospital. Before scanning, the participants were familiarized with the mental rotation task using a block of practice trials. Because men are known to outperform women on mental rotation tasks, our female participants received more practice trials to remove possible gender differences in performance. It was pointed out that before a comparative judgment could be made in the rotated condition, subjects had to mentally rotate one of the two images to alleviate the angular disparity. Subjects were also asked to describe and show how they did this. All made grasping and manipulating gestures and described some kind of hand movement to execute the task. On every trial, the subjects received feedback and were given the chance to repeat the mental rotation when their initial answer was wrong. At the end of the training session, all subjects were able to correctly answer the trials in a reasonable amount of time.

Experimental design

All participants performed four conditions, of which two were mental rotation tasks and two their respective control conditions: (1) nonrotated hands (control hands, CH), (2) rotated hands (experimental hands, EH), (3) nonrotated tools (control tools, CT), and (4) rotated tools (experimental tools, ET). The task was identical for all four conditions: judging whether the two figures are identical or mirror images.

Stimuli consisted of realistic pictures of hands in four different positions (e.g., finger snapping) or four different tools (e.g., can opener), constructed with a digital camera (Kodak DC290 Zoom) and picture-editing software (Adobe PhotoShop 5). The depicted stimuli were asymmetric in all three dimensions. Next, the pictures were paired up with a copy or a mirror image, so that half of the stimuli consisted of the same pairs of figures, while the other half contained mirror image pairs. Half of the stimuli in both hand conditions had a left hand in the left corner. All pictures were presented in four different orientations (0° , 90° , 180° , and 270°). For the control conditions, the angular disparity between both pictures of a stimulus was 0° . In the experimental stimuli, one of the pictures was rotated in the plane of the picture, starting with an

angular disparity of 90° , raised up to 270° in incremental steps of 30° . This finally resulted in 64 different stimuli for each condition. A sample of the stimuli is shown in Fig. 1.

The conditions were presented in a semirandomized block design. Each condition was divided into eight blocks, lasting 32 s each. The control condition preceded the respective experimental condition just as often as the control condition preceded the respective experimental condition, and all conditions had appeared once before a new set of blocks was presented. Stimulus presentation was fixed with a new stimulus appearing every 4 s regardless of the behavioral response, resulting in eight stimuli per block.

Participants answered by pressing an fMRI-compatible button box with either the index or the middle finger of their left hand. In-house software controlled stimulus presentation, recording of the response times, hit rates and errors.

Scanning procedure

Scanning was performed at 1.5 T on a Siemens Symphony MRI scanner equipped with echo planar imaging (EPI) capabilities, using the standard head coil for radio frequency transmission and signal reception. A 3D high-resolution T_1 -anatomical image of the whole brain (3D MPRAGE, 128 slices, slice thickness = 1.25 mm, in-plane resolution = 0.9×0.9 mm, TR = 2010 ms, TE = 5.13) was acquired for coregistration with the functional images after automatic shimming of the magnetic field on each participant. Finally, 384 functional EPI images were obtained during stimulus presentation (TR = 4 s, TE = 60 ms; flip angle = 90° , 33 slices, slice thickness = 5 mm, FOV = 192 mm, and matrix = 64×64 , resulting in a resolution of $3 \times 3 \times 5$ mm).

Image analysis

We conducted all image processing and analysis on a PC workstation using MATLAB and statistical parametric mapping (SPM99) (URL <http://www.fil.ion.ucl.ac.uk/spm>). On a single-subject level, all images were coregistered with the participants corresponding anatomical (T_1 -weighted) images, realigned to the first volume and corrected for motion artifacts, using a sinc interpolation. The resulting images were normalized into MNI stereotaxic space ($2 \times 2 \times 2$ mm) using the corresponding anatomical image as a reference and smoothed using a 10-mm full width at half-maximum Gaussian kernel. The BOLD response in each condition was modeled by convolving these neural functions with a canonical hemodynamic response function to form covariates in a general linear model (Friston et al., 1995). Also included was a single covariate representing the mean over scans. Parameters for each covariate were estimated by a least squares fit to the data. Linear contrasts of these parameter estimates, averaged across sessions within each participant, composed the data for the

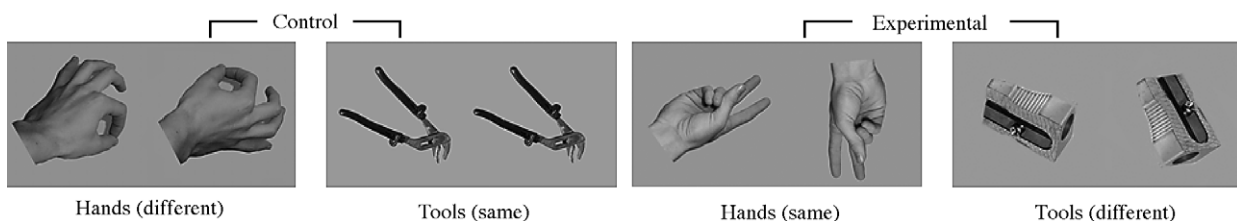


Fig. 1. Examples of stimuli used in the experimental design.

Table 1
Response times (in ms) and percentages of correct answers, Mean (SD)

		Hands		Tools	
		Control	Experiment	Control	Experiment
Women	Response time	1766 (261)	2299 (245)	1780 (209)	2478 (212)
	% correct	92 (2)	89 (7)	95 (3)	85 (9)
Men	Response time	2112 (264)*	2587 (189)*	2075 (240)*	2756 (229)*
	% correct	92 (9)	84 (12)	91 (6)	78 (11)

* Sex difference is significant with $P < 0.01$.

second stage of analysis, treating subjects as a random variable (Friston et al., 1999).

We defined the following contrasts to test hypotheses on the mental rotation of the two different stimulus types: (1) EH > CH, (2) ET > CT. Next, four group SPMs were generated to assess main effects for the mental rotation of each stimulus type in both males and females, using a one-sample t test with a threshold of $P < 0.0001$ and an extent voxel size of $k = 10$. Potential gender-specific cortical activation patterns were explored with a two-sample t test for the mental rotation of hands and tools separately using a more liberal threshold at the voxel level ($P < 0.001$), but with a corrected extent threshold of $P < 0.05$. In a similar manner as for the main effects of mental rotation, we also looked at the effect of stimulus type. The contrasts EH > ET and ET > EH were calculated, after masking them with their respective main contrasts EH > CH and ET > CT (mask threshold $P = 0.001$). Finally, these contrasts were entered in a two-sample t test as well to assess which brain regions show a possible interaction effect between gender and stimulus type, resulting in four new group SPMs [e.g., female > male (EH > ET) masked with female (EH > CH)].

The activated cortical voxels surviving these procedures were superimposed on a stereotaxically normalized high-resolution MR-anatomical scan, obtained by averaging the anatomical scans of the subjects included in the corresponding SPM, to identify the matching anatomical regions. Coordinates of regions with significantly activated clusters of voxels in SPM were projected into the standard stereotaxic space of Talairach and Tournoux (1988). In order to obtain atlas brain or Talairach coordinates, the nonlinear

transform of MNI to Talairach brain as described by M. Brett (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>) was applied.

Results

Behavioral data

Mean response times and accuracy rates are shown in Table 1. For 6.2% of the trials, subjects failed to respond within the 4 s of stimulus presentation. Trials with response times lower than 500 ms were included in this amount because we consider these low response times to have occurred when participants accidentally answered the previous trial, while the next trial was already presented.

In order to assess possible sex differences in the quality of performance, we conducted a repeated measures analysis for mean accuracy rate and response time, with stimulus type and condition as within-subject factors and gender as between-subject factor. There were significant linear effects of stimulus and condition on accuracy rate [$F(1,20) = 5.21$, $P < 0.05$; $F(1,20) = 40.58$, $P < 0.01$] and response time [$F(1,20) = 6.36$, $P < 0.05$; $F(1,20) = 204.13$, $P < 0.001$], with fewer errors and faster response times in the control condition in comparison with the experimental condition, and for the tasks using hands as stimuli compared with the tools. An interaction effect between stimulus and condition showed an even stronger increase of error rates and response times in the experimental condition of the tools [$F(1,20) = 15.68$, $P <$

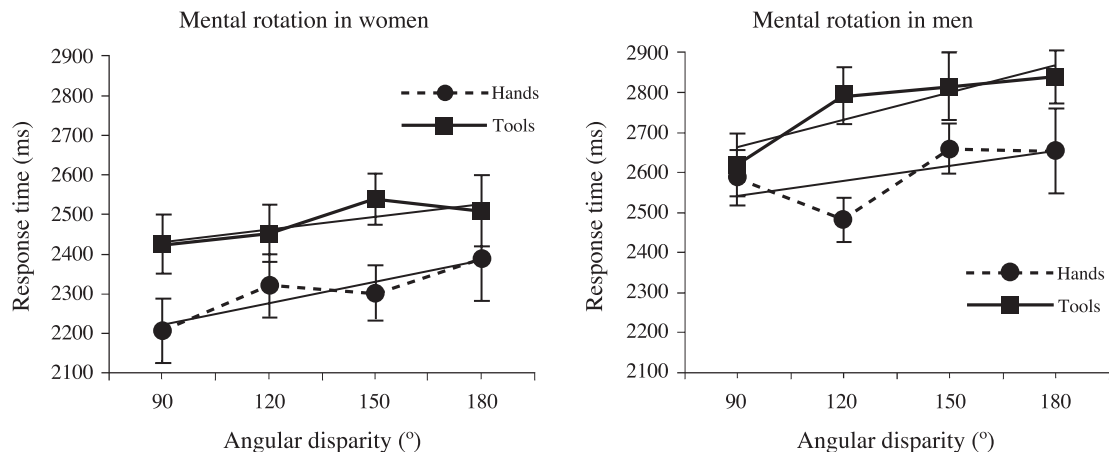


Fig. 2. Response time profiles measured during the mental rotation of hands and tools (mean RT \pm SEM). A significant linear trend is present, irrespective of stimulus type or gender. We also observe higher response times in men compared to women.

0.01; $F(1,20) = 17.92$, $P < 0.01$]. There was no effect of gender on accuracy [$F(1,20) = 1.94$, $P = 0.18$], but there was a significant influence on response time [$F(1,20) = 13.84$, $P < 0.01$] with women responding faster. Separate t tests confirmed this trend for both conditions of each stimulus type. To further assess the possible confounding role of response time on the cortical activation patterns in our subtraction design, we conducted a supplementary analysis on the differences in response time between the control and experimental task. These showed no sex differences, regardless what type of stimulus was employed in the mental rotation task [$F(1,20) = 0.2$, $P = 0.66$]. No other interaction effects were significant.

All subjects reported mental rotation as their applied strategy. Furthermore, they described imagery hand motion to perform the rotation, compatible with an egocentric strategy. We explored the data to see if they actually reflect the typical response time profile, associated with mental rotation. The results are shown in Fig. 2. Given the effect of stimulus type on response time, we conducted separate repeated measure analyses for each stimulus type, with angular disparity as within-subject factor and gender as between-subject factor. The results for mental rotation of hands and tools were very similar. There was a significant effect of angular disparity [hands: $F(3,60) = 3.19$, $P < 0.05$; tools: $F(3,60) = 5.90$,

$P < 0.01$] showing a linear trend [hands: $F(1,20) = 8.81$, $P < 0.01$; tools: $F(1,20) = 15.90$, $P < 0.01$]. Gender did influence the response time profile [hands: $F(1,20) = 8.90$, $P < 0.01$; tools: $F(1,20) = 9.22$, $P < 0.01$], showing overall faster response times for women. However, there was no interaction effect between gender and angular disparity, suggesting a similar trend in the response time profile.

Imaging data

The separate group results for males and females during the mental rotation of hands and tools are summarized in Tables 2 and 3 and shown in Fig. 3. Starting with the mental rotation of hands, we see a common neural network comprising bilateral activation of the middle frontal gyrus, the superior parietal lobe, and the parieto-occipital junction. There is a significant effect of gender for only two brain regions; women show increased activation of a left frontal area situated on the border of the inferior frontal gyrus with the precentral gyrus when mentally rotating hands, while men draw more upon a medial part of the lingual gyrus (see Table 4 and Fig. 3).

Mental rotation of tools reveals a more widespread cortical activation pattern, again with an observable overlap for men and women. They both recruit the bilateral superior parietal lobe,

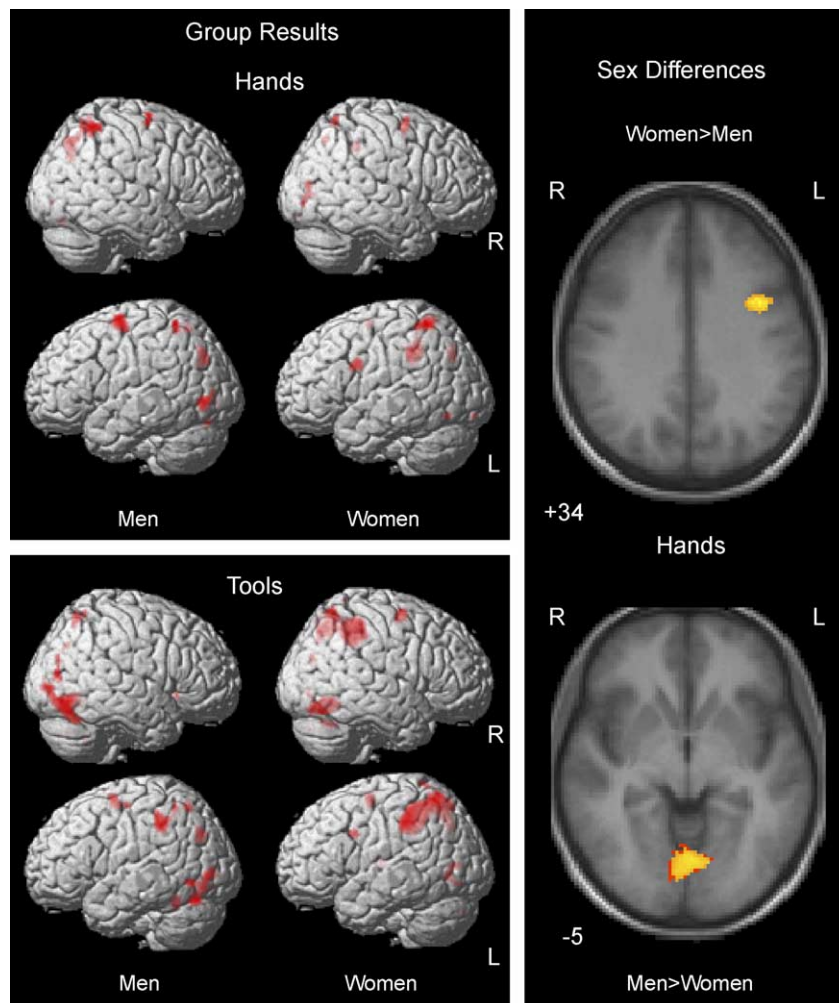


Fig. 3. Visual representation of the SPMs for the mental rotation of hands (top panel) and tools (bottom panel). The horizontal sections show the small brain regions with a gender-specific activation pattern during the mental rotation of hands.

Table 2

Cortical activation patterns associated with the mental rotation of hands: foci of significant activation (tentative Brodmann areas) and their stereotaxic coordinates

Hands	Men					Women				
	Cluster size	Max Z score	Coordinates			Cluster size	Max Z score	Coordinates		
			x	y	z			x	y	z
Frontal regions										
Right middle frontal gyrus (6)	57	4.48	20	−3	63	66	4.18	28	1	55
Left middle frontal gyrus (6)	169	4.88	−28	−5	57	13	3.97	−20	−3	57
Left precentral gyrus (6)/ inferior frontal gyrus (44)						86	4.99	−48	7	27
Parietal regions										
Right superior parietal lobe (7)	268	4.24	26	−68	46	55	4.12	20	−55	62
Right intraparietal sulcus (7/40)	268	5.10	28	−50	54					
Left superior parietal lobe (7)	39	4.13	−36	−52	62	421	3.76	−20	−50	54
Left inferior parietal lobe (40)						421	4.10	−38	−35	39
Occipital regions										
Right middle occipital gyrus (18)						53	4.25	34	−83	1
Left fusiform gyrus (19)						11	4.03	−42	−68	−8
Left middle occipital gyrus (19)	69	4.48	−48	−74	4					
Left parieto-occipital junction (7/19)	74	4.22	−26	−72	37	34	4.21	−26	−71	39
Right lingual gyrus (BA 18)	10	3.85	4	−83	1					
Left inferior occipital cortex (17)						12	4.67	−12	−90	−6

extending into the inferior parietal lobe on the left side; extrastriate cortex, comprising occipital gyri (bilateral inferior, left middle, and right superior), bilateral parieto-occipital junction, and right fusiform gyrus; and the left middle frontal gyrus. Contrary to the mental rotation of hands, the mental rotation of tools shows no significant sex differences.

Stimulus-specific activation patterns for men and women are presented in Table 5. A comparison for stimulus type shows a differential involvement of visual cortex for men. The mental rotation of hands draws more upon the left middle occipital gyrus

and a medial part of the lingual gyrus, while the same task employing tools elicits stronger involvement of other more lateral visual brain regions. The effect of stimulus type looks somewhat different in the female sample. We see a stronger recruitment of the right middle occipital gyrus when mentally rotating hands. However, right superior parietal and bilateral inferior regions together with the right fusiform gyrus participate more in the mental rotation of tools. A final analysis reveals a significant two-way interaction effect between stimulus type and gender in the medial part of the right lingual gyrus (BA 18; 8 −74 2). This

Table 3

Cortical activation patterns related with the mental rotation of tools

Tools	Men					Women				
	Cluster size	Max Z score	Coordinates			Cluster size	Max Z score	Coordinates		
			x	y	z			x	y	z
Frontal regions										
Right middle frontal gyrus (6)						96	4.84	26	1	55
Left middle frontal gyrus (6)	92	4.27	−30	3	59	84	4.44	−20	−3	55
Right inferior frontal gyrus (47)	11	3.94	34	18	−4					
Left precentral gyrus (6)/ inferior frontal gyrus (44)						29	4.11	−50	9	29
Parietal regions										
Left postcentral gyrus (5/7)						19	4.19	−16	−43	70
Right superior parietal lobe (7)	83	3.94	30	−51	58	927	4.62	24	−55	60
Right inferior parietal lobe (40)						927	4.69	40	−40	48
Left superior parietal lobe (7)	50	4.20	−20	−57	56	1470	4.89	−20	−57	62
Left inferior parietal lobe (40)	182	4.28	−48	−39	41	1470	5.71	−44	−31	38
Occipital regions										
Left parieto-occipital junction (7/19)	67	4.31	−30	−70	33	1470	4.01	−24	−66	38
Right parieto-occipital junction (7/19)	10	3.92	28	−66	38	927	3.91	26	−68	40
Right lingual gyrus (18/19)	657	4.90	28	−64	−2					
Right fusiform gyrus (19)	657	4.85	34	−70	−5	257	4.66	38	−72	−10
Right inferior occipital gyrus (18/19)	657	4.70	38	−72	−8	257	3.76	36	−74	−5
Right middle occipital gyrus (18/19)	657	4.09	30	−83	6					
Right superior occipital gyrus (19)	71	4.01	34	−74	28	12	4.09	28	−74	28
Left inferior occipital gyrus (18/19)	255	4.37	−44	−76	−1	69	3.80	−38	−78	−10
Left middle occipital gyrus (18/19)	255	4.24	−40	−79	4	69	4.01	−36	−76	2

Table 4
Gender-specific cortical activation patterns

Hands	Men > women			Women > men						
	Cluster size	Max Z score	Coordinates			Cluster size	Max Z score	Coordinates		
			x	y	z			x	y	z
Left precentral gyrus (6)/inferior frontal gyrus (44)						186	4.05	–40	7	29
Left lingual gyrus (18)	462	3.85	–4	–72	–1					
Right lingual gyrus (18)	462	3.69	10	–80	–3					

region is more involved in the male sample during the mental rotation of hands compared to tools.

Discussion

Behavioral data

An adequate and equal behavioral performance for men and women was an important requirement in this experiment. Previous imaging studies on mental rotation did not systematically report matching behavioral data. It has also been suggested that performance might be a confounding factor when analyzing gender-specific cortical activation patterns. In our sample, the error rates were low throughout all conditions. Furthermore, men and women showed an equivalent amount of correct answers. The response time profiles, associated with the experimental condition of both hands and tools, corresponded with the act of mental rotation. They increased linearly with angular disparity and this trend was not influenced by gender. However, women completed the trials systematically faster, regardless of condition or stimulus type. This is most likely a result of the longer training our female subjects received to alleviate potential sex differences. Since the difference also appeared in the control conditions, it is probably related to other processes than the transformation process of mental rotation in itself, such as visual encoding, comparison, decision making, or motor response generation. Still these response time differences might influence the cortical activation pattern since the men in our sample were longer on task than the women. Given that we compared the contrasts of the experimental condition with the matching control condition to trace potential sex differences, the relative difference in response time between both conditions may be more interesting. In subtraction designs where trial pacing is fixed, such as our current

study, the difference in time on task between the experimental and control condition can have an important impact on the imaging data (D'Esposito et al., 1997). Since these response time differences were equivalent for men and women, we can conclude that our sample indeed shows an equal performance for men and women, compatible with the act of mental rotation.

Imaging data

Egocentric mental rotation

The imaging data revealed a common cortical activation pattern for men and women comprising superior parietal lobe, middle frontal gyrus, and extrastriate occipital areas for the mental rotation of both hands and tools.

The superior parietal cortex is by far the area that has been most implicated in the act of mental rotation. As a center for visuospatial transformations, it is regarded as an essential brain region for mental rotation. However, much discussion remains on the lateralization of the contribution of this brain region. Mental rotation has long been regarded as a prototypical right-hemispheric function (Corballis, 1997). Many neuroimaging studies failed to corroborate this by reporting bilateral or left parietal activation. We found bilateral recruitment of superior parietal cortex, regardless of gender or stimulus type. Stimulus characteristics might offer an explanation. One PET study suggests a preferential role for the right parietal cortex in mental rotation when the task employs single characters (Harris et al., 2000). Though the results could not be replicated with fMRI (Podzbenko et al., 2002), a recent rTMS study did confirm the notion that only right superior parietal cortex is essential during the mental rotation of these singular stimuli (Harris and Miniussi, 2003). The stimulus pairs we used require more attention shifts and eye movements, potentially resulting in bilateral superior parietal activation. A different line of research

Table 5
Stimulus-specific cortical activation patterns

	Men			Women						
	Cluster size	Max Z score	Coordinates			Cluster size	Max Z score	Coordinates		
			x	y	z			x	y	z
Hands > tools										
Right lingual gyrus (18)	206	5.36	8	–74	2					
Left middle occipital gyrus (19/37)	31	4.47	–48	–72	5					
Right middle occipital gyrus (19/37)						64	6.18	46	–68	5
Tools > hands										
Right inferior parietal lobe (40)						93	4.22	38	–43	43
Left inferior parietal lobe (40)						59	4.87	–42	–33	38
Right superior parietal lobe (7)						160	4.68	22	–66	47
Right fusiform gyrus (37)						249	5.03	30	–49	–9
Left fusiform gyrus (37)	150	5.41	–34	–49	–6					
Right lingual gyrus (19)	263	4.54	28	–61	–4					
Right middle occipital gyrus (18)	263	5.13	30	–80	–6					

focuses on the type of stimulus and considers an area in right superior parietal cortex to be crucial for the mental rotation of external objects, but not if the task implies mentally rotating one's whole body (Parsons, 2003; Zacks et al., 2002, 2003). Since it matters what one rotates, it cannot be excluded that egocentric mental rotation, employing hands and hand-related objects, induces a specific, more bilateral, parietal activation pattern.

Of special interest for egocentric mental rotation is the involvement of premotor cortex. Egocentric motor strategies for the mental rotation of hands and tools were illustrated with a respective bilateral and unilateral recruitment of dorsolateral premotor cortex for the male sample in a previous study (Vingerhoets et al., 2002). Our female sample also displayed premotor activation, compatible with egocentric motor strategies. The activation pattern, however, was rather different. Women showed bilateral dorsolateral premotor participation during the mental rotation of both hands and tools. A plausible explanation is the view that women have a more bilateral cortical organization. Recent studies confirm this notion for spatial abilities (Vogel et al., 2003) and mental rotation in particular (Johnson et al., 2002). However, the unilateral activation of dorsolateral premotor cortex during the mental rotation of tools in the study by Vingerhoets et al. (2002) might be a threshold effect since this brain region showed no effect of stimulus type.

There is still debate on what the involvement of dorsolateral premotor cortex reflects in mental rotation. Task-specific differential activity has been observed within the dorsolateral premotor cortex, associated with several other cognitive functions besides imagining hand movement or manipulation. One possibility is eye movement as an inherent aspect of visual imagery (Laeng and Teodorescu, 2002). An alternative view focuses on the functional resemblance of the rostral part of the dorsolateral premotor cortex with prefrontal rather than motor cortex (Picard and Strick, 2001). A recent neuroimaging study for example suggests that this rostral brain region is implicated in nonmotor cognitive tasks and can be situated dorsomedial of the presumptive frontal eye fields (Hanakawa et al., 2002). Finally, the involvement of premotor cortex has also been attributed to the generation of the motor response. Nevertheless, we consider imaginary hand movement associated with an egocentric strategy to be the most plausible explanation for the involvement of dorsolateral premotor cortex in our particular study for a number of reasons. First of all, our stimuli were selected to evoke an egocentric strategy. To our knowledge, only the manipulation of strategy has been systematically correlated with (pre)motor cortex involvement in mental rotation up to this date and hands have been specifically used for this purpose before (Kosslyn et al., 1998, 2001; Wraga et al., 2003). We regard it most likely that tools would elicit a similar egocentric strategy. An earlier neuroimaging study has shown that tools are a special category of objects that are strongly associated with movement since the mere observation of tools already can elicit strong activation of premotor cortex (Grafton et al., 1997). Second, behavioral studies suggest that imaginary limb movement is an underlying process of mental rotation. When performing a motor rotation during a mental rotation task, this results in faster response times and fewer errors, but only when the motor rotation is compatible with the mental rotation (Wexler et al., 1998). Furthermore, during the mental rotation of hands, the response time profiles deviate from the traditional linear relationship with angular disparity when the posture of the hand is more awkward to imagine due to sensorimotor restrictions (Parsons, 1994). Third,

our participants reported using imaginary hand movements to solve the mental rotation problem. Fourth, our results show recruitment of premotor cortex but not M1. It has been suggested that M1 is implicated in the generation of the motor response rather than premotor cortex (Richter et al., 2000). A recent fMRI study corroborated this view by showing that premotor cortex was activated throughout the spatial transformation phase of a mental rotation task while M1 was only correlated with the button press response (Windischberger et al., 2003).

A number of mental rotation studies report occipital activation. An fMRI study found widespread dorsal stream activation while performing a simple mental rotation task (Podzebenko et al., 2002). Our results show a great variety of extrastriate activation. Only the left parieto-occipital junction was involved regardless of gender or stimulus type. This brain region has been associated with the processing of visual motion (Paradis et al., 2000) and reach to grasp (Chapman et al., 2002). Since egocentric mental rotation requires imagining movement induced by the own hand, it is highly plausible that these two functions are implicated in the visual transformation phase of mental rotation. In conclusion, the results reveal a common neural substrate for men and women, compatible with egocentric mental rotation.

The mental rotation of hands and tools showed a fairly similar neural network. A direct comparison for the effect of stimulus type confirmed this. Women did exhibit a more profound activation of the parietal cortex during the mental rotation of tools compared to hands. All other effects of stimulus type were confined to the visual cortex. Overall, the mental rotation of tools resulted in stronger cortical activation possibly indicating a higher task demand. The behavioral data reporting more errors and slower response times for the mental rotation of tools match this finding since slower response times in a mental rotation task have been correlated with greater cortical activation (Zacks et al., 2002). Although mental rotation of hands and tools both recruit an egocentric strategy, there might be differences making the mental rotation of tools more difficult. We offer two possible but not exclusive explanations. Tools could be perceived as more complex stimuli since most stimulus-specific cortical activation patterns are situated within visual cortex. However, the behavioral data show a more distinct increase of error rates and response times during the mental rotation of tools compared to all other conditions. This implies that processes equally present in the control condition, such as visual encoding, alone cannot explain the performance difference. An alternative might be found in the mental rotation strategy. Using an egocentric mental rotation strategy implies an egocentric frame of reference or centering one's own multimodal experiential space upon one's own body (Vogeley and Fink, 2003). Within this framework, hands as body parts would require less resources than external objects such as tools because these latter still have to be related to one's own body. In other words, mental rotation of tools would be a more indirect form of egocentric mental rotation as they are mediated by hand manipulation, resulting in a poorer behavioral performance and stronger cortical activation patterns than the mental rotation of hands.

Sex differences

Besides a common neural substrate, our group results show gender-specific involvement of various brain regions. On the other hand, most of these apparent differences could not be observed in a direct statistical comparison. Just two brain regions showed significant sex differences, but only for the mental rotation of

hands. Women recruited more left inferior frontal cortex, while men drew more upon a medial part of the lingual gyrus.

The left inferior frontal area is located within ventral premotor cortex. More precisely, it is centered on the inferior precentral sulcus, extending into the precentral gyrus and the inferior frontal gyrus. A similar area could be seen in the female, but not the male, sample for the mental rotation of tools, suggesting a common role for both forms of egocentric mental rotation. Two previous imaging studies focusing on sex differences in mental rotation found stronger involvement of right inferior frontal gyrus in women, associated with a more analytical or serial strategy in the task (Jordan et al., 2002; Thomson et al., 2000; Weiss et al., 2003). Our results, on the other hand, situate the significant cluster more posterior in the left hemisphere. Rizzolatti et al. (2002) attribute both motor and cognitive functions to the ventral premotor cortex. These functions can vary from grasp-related motor behavior, over imitation, to the complex process of decision making. It has been suggested that ventral premotor cortex is a functional homologue for monkey area F5 comprising mirror and canonical neurons (Rizzolatti et al., 2002). Canonical neurons fire both during seeing and grasping of an object. Mirror neurons are triggered while grasping an object and seeing it being grasped. The mirror system has been implied in the understanding and imitation of action (Rizzolatti et al., 2001). A recent fMRI study addressed the localization in the human brain and found activation related to mirror and canonical neurons in the ventral premotor cortex, situating the human homologue of F5 on the ventral limb of the precentral sulcus (Grezes et al., 2003). Ventral premotor cortex might in addition be important for perceptual decisions. Neurons of the ventral premotor cortex in monkeys during a sensory decision task reflected current and remembered sensory inputs, their comparison, and the motor commands expressing the result (Romo et al., 2004).

To our knowledge, this is the first time that the lingual gyrus demonstrates a gender-specific activation during a mental rotation task. Although this brain region has been implicated in semantic processing (Bellgowan et al., 2003; Hinojosa et al., 2000; Martin-Loeches et al., 2001), the abovementioned result might reflect a more basic underlying sex difference in handling visual information. An fMRI study demonstrated that men activated more the right lingual gyrus during the early visual processing of a dartboard stimulus (Kaufmann et al., 2001).

Based on our results, differential strategies during egocentric mental rotation of hands seem possible. Women would rely more on imitation or use more perceptual comparisons (left ventral premotor cortex), whereas early visual or semantic processing would be more important for men (lingual gyrus). However, this point of view needs further consideration.

First, we want to emphasize the relative small nature of the sex differences. The cortical network for egocentric mental rotation is to a high degree similar for men and women, except two small brain regions for the mental rotation of hands. Furthermore, gender differences could not be found when using tools as stimuli instead, despite largely parallel cortical activation patterns. These sex differences may not even reflect a gender-specific cortical activation pattern. Instead they may be caused by a structural brain difference. For example, men in general have larger and heavier brains than women (Kimura, 1999). Before comparison, we normalized all images with the same, balanced template. This should considerably limit the chance of structural-related artifacts. Second, what do these sex-specific cortical activation patterns indicate? Within a causal biological framework, they may refer to

fixed differences in cerebral organization. We tend to agree with Jordan et al. (2002) who rather attribute these differences to flexible sex-specific preferred strategies. Individuals may display a wide variety of different strategies regardless of gender, overestimating the effect of sex-specific strategies.

We conclude that egocentric mental rotation in a sample with a good and equal performance elicits only modest sex differences. In our interpretation, this suggests that men and women use a very similar motor strategy for the mental rotation of hands and tools, with some gender-specific accents for the former stimuli. In this particular study, performance was excluded as a possible confound at the neural level. It would be interesting to explore whether the sex-specific cortical activation patterns we found correspond with performance-related strategies in a design where gender is ruled out as a variable of interest.

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