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# The functional role of dorso-lateral premotor cortex during mental rotation

## An event-related fMRI study separating cognitive processing steps using a novel task paradigm

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**Subjects deciding whether two objects presented at angular disparity are identical or mirror versions of each other usually show response times that linearly increase with the angle between objects. This phenomenon has been termed mental rotation. While there is widespread agreement that parietal cortex plays a dominant role in mental rotation, reports concerning the involvement of motor areas are less consistent. From a theoretical point of view, activation in motor areas suggests that mental rotation relies upon visuo-motor rather than visuo-spatial processing alone. However, the type of information that is processed by motor areas during mental rotation remains unclear. In this study we used event-related fMRI to assess whether activation in parietal and dorsolateral premotor areas (dPM) during mental rotation is distinctively related to processing spatial orientation information. Using a newly developed task paradigm we explicitly separated the processing steps (encoding, mental rotation proper and object matching) required by mental rotation tasks and additionally modulated the amount of spatial orientation information that had to be processed. Our results show that activation in dPM during mental rotation is not strongly modulated by the processing of spatial orientation information, and that activation in dPM areas is strongest during mental rotation proper. The latter finding suggests that dPM is involved in more generalized processes such as visuo-spatial attention and movement anticipation. We propose that solving mental rotation tasks is heavily dependent upon visuo-motor processes and evokes neural processing that may be considered as an implicit simulation of actual object rotation.**

*Keywords:* Mental rotation; Visual imagery; Simulation; Spatial cognition; fMRI; Motor control

## Background

When subjects are asked to indicate whether two objects are identical or mirror versions of each other, response time usually increases linearly with the angular disparity between objects. As a linear relationship between rotation angle and rotation time is also obtained in actual object rotation, it seems plausible that object comparison relies upon simulating the rotation of one object to match it to the other. This phenomenon has been termed mental rotation. Since its first description by Shepard and Metzler (1971) mental rotation has become a task paradigm attracting enormous research interest in the field of cognitive psychology. Part of this interest was triggered by attempts to understand why object comparison using imagery seems to obey the same physical principles as overt rotation, particularly when considering that humans are capable of using imagery that is not limited by the laws of physics (see, e.g., Kosslyn, 1994).

While early attempts considered mental rotation to rely dominantly upon visuo-spatial perception and imagery (Corballis and McLaren, 1982; Shepard and Metzler, 1971), recent behavioral and neuroscientific evidence suggests that motor processes play a significant role in mental rotation. A number of behavioral studies showed specific interferences between action planning and action execution on the one hand and mental rotation on the other hand (Wexler et al., 1998; Wohlschläger, 2001; Wohlschläger and Wohlschläger, 1998). Wohlschläger (2001), for instance, demonstrated that planning manual rotation movements specifically interferes with mental rotation of objects: If the direction of planned movements was opposite to the direction of mental rotation, mental rotation speed was slowed down. Direct evidence for the relevance of motor processes in mental rotation is also derived from single cell recordings in the monkey's motor cortex. Georgopoulos et al. (1989) trained monkeys to point into a

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direction deviating from a target light with a certain angle. They found that the neuronal population vector of the motor cortex – a measure indicating the direction of upcoming movements – changed its direction already prior to the execution of the movement.

Based on these and other observations, it has been postulated (cf. Wexler et al., 1998; Wohlschläger, 2001) that mental rotation resembles an imagined (covert) action rather than a purely visual/visuo-spatial imagery skill. This assumption implies that motor areas of the human brain are involved in mental rotation – a hypothesis that has been tested using a variety of human brain research methods, such as functional magnetic resonance imaging (fMRI), event-related potentials (ERPs) and transcranial magnetic stimulation (TMS) (e.g., Carpenter et al., 1999; Cohen et al., 1996; Heil, 2002; Jordan et al., 2001, 2002; Kosslyn et al., 1998, 2001; Lamm et al., 2001b, 2005; Richter et al., 2000; Tagaris et al., 1998; Windischberger et al., 2002, 2003b). These studies unequivocally reveal that parietal cortex plays a dominant role in mental rotation, with activation being either localized in superior parietal lobe (SPL; Brodmann area BA 7), inferior parietal lobule (IPL; BA 40), and/or in intraparietal sulcus (IPS; BA 40). Results concerning contributions of brain areas involved in motor processing, though, have been less consistent. While several studies did not find activation in motor areas (e.g., Kosslyn et al., 1998; Jordan et al., 2001) a number of results suggests that lateral and medial premotor areas (lateral premotor cortex/precentral gyrus and supplementary motor area) are involved in mental rotation (e.g., Ecker et al., 2006; Kosslyn et al., 2001; Lamm et al., 2001b, 2005; Richter et al., 2000; Seurinck et al., 2004; Vingerhoets et al., 2002). Part of the inconsistencies between studies may be attributed to methodological differences in the imaging and analysis techniques used. In addition, differences in task paradigms and processing strategies also affect results (e.g., Jordan et al., 2002; Kosslyn et al., 1998, 2001; Lamm et al., 2005; Vingerhoets et al., 2002). For example, rotating body parts (like hands or feet) instead of abstract objects might trigger stronger activation in motor areas, including primary motor cortex. It has thus been argued that body parts might induce rotation from an egocentric, internal perspective – with subjects being the agent of the rotation and thus evoking motor imagery (e.g., Kosslyn et al., 1998, Parson et al., 1995).

Empirical evidence has, however, clearly shown that motor areas are also active when subjects experience themselves not to be the agent of the rotation. For example, Richter et al. (2000) used time-resolved fMRI to investigate brain activation during processing of Shepard and Metzler (1971) mental rotation tasks. They observed that the width of the hemodynamic response in lateral premotor areas significantly correlated with response time – suggesting that these areas are involved in the very performance of mental object rotation. Such task-locked activation might support the claim that mental rotation is indeed a covert, imagined object rotation rather than an image transformation relying exclusively upon visuo-spatial processing. In addition, task-specific involvement of medial and lateral premotor areas during mental rotation has been shown in a set of studies from our own group using a variety of methods and analytical approaches (Lamm et al., 2001a, 2005; Windischberger et al., 2002, 2003b). In one study (Lamm et al., 2001b) we aimed to determine whether motor areas are consistently involved in mental rotation at all, and whether this activation shows a functional relationship to aspects of task processing not related to movement preparation or execution. To this end, a combination of event-related fMRI and slow event-related cortical potentials (slow ERPs) was employed to assess the topology and the time-courses of neural activation with high temporal and spatial resolution. Consistent and clearly task-related activation was detected in lateral and medial premotor areas, but not in primary motor areas (see also Windischberger et al., 2002). Using a combination of exploratory and model-based fMRI analysis techniques, we subsequently disentangled the different contributions of primary and premotor areas to task solving (Windischberger et al., 2003b); this study corroborated our initial finding of highly task-correlated activation in premotor areas, and also confirmed that primary motor cortex was not specifically involved in mental rotation of abstract objects. Notably, this finding has recently been supported by results from various other groups (e.g., de Lange et al., 2005; Ecker et al., 2006; Seurinck et al., 2005).

In this context, it is important to define the way in which the term *premotor activation* has been used in the literature. Most papers on mental rotation (including our own so far) seem to adopt a rather loose anatomical definition, labeling activations as pertaining to premotor cortex when they are anterior to the central sulcus and in and around the dorsal parts of precentral gyrus (and sometimes even more anterior, but still in close vicinity). Hence, this constitutes a rather loose definition of what constitutes a premotor area, and part of the activations described as motor-related might not be related to motor processes in a classical sense at all (meaning that these areas are directly involved in the planning, preparation, and execution of motor acts). However, for reasons of compatibility with the literature we stick with this rather loose definition until the discussion section – where we will scrutinize the structural and functional anatomy of lateral premotor areas in more detail (see also Picard and Strick, 2001).

Despite the compelling evidence for premotor activation during mental rotation, a sound explanation of the type of computations and the information processing taking place in premotor areas is still lacking. Several, yet inconclusive hypotheses for the function of lateral premotor areas during mental rotation exist. The *motor imagery account* suggests that subjects imagine using their hands or other body parts to move the objects – as this kind of motor imagery activates a similar network as the one observed during mental rotation (e.g., Ehrsson et al., 2003). There is also some debate that premotor activation is not related to hand- or body-part related motor processes, but to *eye movements* (Carpenter et al., 1999; de Lange et al., 2005; Lamm et al., 2001b). Another explanation for premotor activation is based on the observation that the presentation of *graspable objects* activates premotor areas (e.g., Chao and Martin, 2000; Grafton et al., 1997; Grèzes and Decety, 2001). This finding has been interpreted within the framework of affordance theory (Gibson, 1979) implying that visual presentation of objects triggers components of actions that can be performed with these objects (Tucker and Ellis, 1998). Yet another hypothesis is that premotor activation during mental rotation is related to the imagined *anticipation of movement consequences*, fulfilling a similar role as during actual movement and online movement planning (see Wolpert and Kawato, 1998, for a review of related models of motor control).

It should be noted though that all these hypotheses do not explicitly consider that solving a mental rotation task is a complex skill requiring the coordinated action of a multitude of distinct cognitive processes. These processes include stimulus encoding, mental image generation, planning and “execution” of the mental rotation, subsequent comparison (matching) of the rotated stimulus

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with the second (target) stimulus, and finally entering a response. In our own studies (Lamm et al., 2001a,b, 2005; Windischberger et al., 2003b) premotor areas were active during the whole period of task processing and therefore probably during stimulus encoding and other "non-rotational" processes. The same finding most likely applies to other neuroimaging studies, because the predominant analysis approach is to integrate signal changes occurring across the whole task processing window. Notably, a recent study (Ecker et al., 2006) attempted to analytically disentangle the various processing steps triggered by mental rotation tasks. This study confirmed the previous finding by Richter et al. (2000) that dorsal premotor cortex activation is correlated with mental rotation time, while activation in visual cortex is correlated with visual perception.

We thus hypothesized that dorsal lateral premotor areas (dPM) are specifically involved in processing the visuo-spatial computations required by mental rotation tasks. Visuo-spatial computations in this framework are defined as computations of two- or three-dimensional orientation information such as the encoding of stimulus orientation as well as the computation of how that orientation changes when spatial orientation of the stimulus is changed. Apart from other mental rotation studies, indirect support for this assumption was derived from several fMRI studies and from a recent review of dorsal premotor cortex function (Schubotz and von Cramon, 2003). Schubotz and von Cramon (2001), for example, found that bilateral dorsal premotor cortex plays an important role in the attention to the spatial location and orientation of sensory events. The same group (Wolfensteller et al., 2004) recently replicated and extended this finding by demonstrating that dorsal premotor cortex is activated when subjects have to pay attention to the spatial position of visually presented stimuli, but not when they pay attention to their size.

We therefore designed a study to investigate whether dPM areas are (a) active during all task processing epochs that require the processing of spatial orientation information, and (b) whether dPM activation is modulated by the relative amount of spatial orientation information that is processed during mental rotation. We hypothesized that dPM is not only active during mental rotation, but equally active during stimulus encoding and stimulus matching – as the latter two processes also rely on spatial orientation information. In addition, we expected the relative amount of spatial orientation information to modulate activation in dPM and higher-order visual areas of the occipital and parietal cortex. To test these hypotheses, we developed a novel task paradigm allowing the separation of stimulus encoding, mental rotation and stimulus matching. In addition, the amount of relative spatial orientation information that had to be processed during mental rotation was varied by devising two different task variations (conditions). Since the timing of hemodynamic activation was critical in this paradigm, we used a novel fMRI analysis approach with no assumption about the shape of the hemodynamic response (Windischberger et al., 2004).

## Material and methods

### Subjects

Thirteen right-handed (Annett, 1985) subjects aged between 23 and 31 years giving informed written consent were included in this study which was approved by the local ethics committee. To exclude gender-related variability and to increase comparability with our previous studies the sample was restricted to male subjects. All subjects were healthy volunteers with no history of neurological or psychiatric disorders that had been recruited from various graduate and undergraduate courses of Universities in Vienna.

### Experimental paradigm

The fMRI paradigm consisted of two experimental conditions and of an eye movement control condition. Tasks of the experimental conditions required mental rotation of a two-dimensional geometrical figure presented in the center of the visual field. In the location condition, this figure contained a symmetrical object (e.g., a dot); in the orientation condition, the object was asymmetrical (e.g., an arrow). Depending upon the condition, either the object's location or its change of orientation had to be taken into account when rotating the figure (see below). In order to disentangle brain activation related to the different cognitive processes required by solving mental rotation tasks, tasks consisted of a sequence of five events (see Fig. 1): presentation of the original figure (Encoding), indication of rotation (Indicate), rotation (Rotate), presentation of the matching figure with which the mental figure had to be compared (Matching) and, finally, response execution (Response). The timing of these events – apart from the response – was fixed and as follows. The original figure was presented for 2 s, followed by marking one of the edges of the figure with an orange bar for 1 s. This bar indicated the edge on which the matching figure would be "standing"—and thus in which direction (clockwise or counter-clockwise) and how far the encoded original figure had to be rotated. Subjects were explicitly instructed to rotate the figure until this position was reached as this

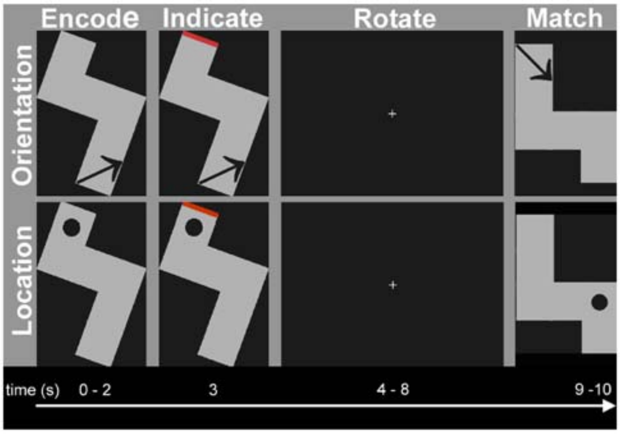

Fig. 1. Samples of the two different mental rotation tasks used in this study. Subjects first had to encode the 2D figure and the element it contained (ENCODE). Then, an orange bar (INDICATE) indicated how far and in which direction the figure had to be rotated. During rotation, subjects had to fixate a white fixation cross (ROTATE). After 5 s, a matching figure was presented which was either identical to or a mirror version of the original figure. In addition, the object contained therein could have a different orientation (orientation), or be located at a different location (location). Both examples show a mismatch between original and matching figures: the dot in the location condition is dislocated, and the arrow of the orientation condition is flipped around its vertical axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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would allow them to directly compare it to the matching figure. After showing the orange marker for 1 s, the original figure disappeared from the screen and was replaced by a crosshair displayed in the centre of the screen. This crosshair indicated to start mental rotation, and it was replaced by the matching figure after 5 s. Based on behavioral data of a pre-test (see below), 5 s were considered as sufficient to complete rotation and at the same time not to induce significant time pressure – which was considered important in our study (Lamm et al., 2001a).

The matching figure was either an identical or a mirror version of the original figure. In addition, location or orientation of the objects it contained could be identical or non-identical to those of the original figure: In the location condition, the object (e.g., a dot) could be placed at a location that was clearly distinct from its location in the original figure (see Fig. 1, in which the dot's positions are non-identical). In the orientation condition, the orientation of the element (e.g., an arrow) could differ (horizontally or vertically flipped) from the one in the original figure. Note though that it would always be placed in the same location (see Fig. 1). Hence, subjects either had to focus on changes in orientation or in object location. Subjects were explicitly instructed about this distinction between conditions and had participated in several practice trials until they were able to reliably and validly perform the tasks. Note in this context that both the orientation and the location condition inherently required the computation of spatial information – as both conditions required mental rotation of the 2D geometrical figure in which the asymmetrical or symmetrical objects were positioned. Therefore, the differences we expected resulted from *relative* differences in the amount of orientation information that had to be processed. While the orientation condition required considering the changes in orientation of the asymmetrical object, the location condition did not put additional workload with respect to computing orientation information (as the orientation of a symmetrical object does not change by rotation).

Subjects had to respond within 2 s whether the original and the matching figure were identical or non-identical. Entering the response immediately replaced the matching figure by a crosshair. If figures were non-identical, no distinction had to be made regarding the reason for the difference (which could either be due to the matching figure being a mirror version of the original figure – or due to a different location of the object in the location condition or a different object orientation in the orientation condition). All responses were entered by button press using the dominant right hand, using an MR-compatible response box attached to the subject's right thigh. Task presentation was computer-paced, with the inter-trial baseline period being randomly varied ('jittered') between 8 and 12 s to reduce stimulus predictability and for more efficient event-related signal estimation (Donaldson and Buckner, 2001).

Items were selected based upon the results of a pre-test where a large set of items with rotation angles ranging from 40° to 170° was solved by a sample of 20 subjects matched in age and education to the study population. In this pre-test subjects were instructed to press a button as soon as they had rotated the figure into the position indicated by the marker bar. This allowed determining rotation times, as well as to select only those items that showed the classical 'mental rotation' effect (i.e., a linear relationship between rotation angle and response time). In addition, we also excluded items that showed too high inter-individual variability. Based on the results of this pre-test, the rotation angles selected for the fMRI experiment were 100° and 160° clockwise, and 130° and 170° counter-clockwise. The primary motivation to select these items was to obtain rotation times of comparable length as encoding and stimulus matching times, allowing a more direct comparison between the hemodynamic responses of those different aspects of task solving. In addition, rotation times were long enough (about 2.3 s on average) to evoke reliable and pronounced signal increases.

Hemodynamic responses triggered by goal-directed eye movements (COMPARE), and by fixation (FIXATE) of a crosshair were separately assessed using an eye movement control condition. For assessing the response to saccadic eye movements, subjects had to decide whether the locations of three elements in two figures positioned next to each other were identical or not. Figures were simultaneously presented on screen and not rotated with respect to each other. The three elements were either all placed at identical locations, or one of them was very slightly displaced (by a few image pixels only). This required subjects to look back and forth between elements in order to be able to detect these minimal displacements (COMPARE). Note that this task required neither rotation nor visual imagery since figures and elements showed no angular disparity and were simultaneously presented. After 3 s, stimuli were replaced by a white fixation cross whose color changed to red after 2 s. Subjects were instructed to fixate this cross (FIXATE) and to enter their response (i.e., whether the figures were matching or not) as soon as the color changed. Note that the two different aspects (COMPARE and FIXATE) of this control task were specifically employed to control for the different types of eye movements required by the different epochs of the mental rotation task. For the encoding and the stimulus matching epochs, hemodynamic activation was controlled for saccadic eye movements (COMPARE), while the mental rotation epoch which required fixation was controlled for fixation-related activation (FIXATE).

### *Scanning procedures*

MRI and fMRI scanning was performed using a research-dedicated high-field 3 T tomograph (Medspec S300, Bruker Biospin, Ettlingen, Germany) equipped with a whole-body gradient system and a standard birdcage coil for RF excitation/reception. A single-shot, blipped gradient-recalled EPI sequence with a TE of 31 ms was used to acquire 18 axial slices with a spatial resolution of $3.28 \times 3.9 \times 4$ mm (interslice distance 1 mm), covering nearly the whole cerebrum. Slices were tilted to be approximately parallel to the line connecting the anterior and posterior commissure and repetition time (TR) for the whole image slab was 1 s. Two separate runs with 487 repetitions and 24 trials each (12 per condition) were performed for the mental rotation tasks, and a single run with 343 repetitions and 20 trials was run for the eye movement control condition. Items in the two mental rotation runs were matched with respect to response times and difficulty. Mean response times for the orientation and location trials from the pre-test were 2.35 and 2.44 s, and mean percentages of correct answers were 84.6% and 87.46%, respectively. Stimuli were presented using a back-projection system consisting of a mirror mounted on the birdcage coil and a video beamer projecting stimuli on a screen placed behind the subject's head. The sequence of the two experimental and the control runs was counter-balanced across subjects.

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### *Data analysis*

fMRI analyses were performed using a combination of in-house software written in IDL (Interactive Data Language; Research Systems, Inc., Boulder, CO) for exploratory data analyses and SPM2 (Wellcome Department of Imaging Neuroscience; London, UK) for model-based statistical analyses. Following pre-processing (motion-correction, spatial normalization, spatial smoothing using a Gaussian kernel of 9 mm full-width at half-maximum), data were modeled using the finite impulse response approach developed by Windischberger et al. (2004). With this method separate regressors are constructed for every time point (TR) within a trial, each predicting intensity changes at the corresponding time point. This approach requires no assumptions regarding the timing of cognitive processes and the corresponding neuronal and hemodynamic responses except reproducibility across trials. Based upon exploratory analyses, a hemodynamic response delay of 4 s was assumed for all subjects. Contrasts were computed to model the cognitive processes associated with the different steps of task solving. The contrast for encoding the target figure (ENCODE) included regressors 5 and 6 after stimulus presentation (which after subtraction of the hemodymamic delay would correspond to the first two images after display of the original figure). Indication of rotation angle and direction was modeled with regressor 7 (INDICATE). The mental rotation period was subdivided into three contrasts: ROTATE (regressors 8 and 9), ROTATE2 (10 and 11), and MEMORY (12). We subdivided the mental rotation period to obtain a contrast reflecting brain activation exclusively related to mental rotation itself. Based on the median rotation times of around 2 s determined in the pre-test, we assumed that the first 2 s (contrast ROTATE) would best reflect hemodynamic changes related to mental rotation proper. ROTATE2 and MEMORY modeled processes that were less clearly defined on a behavioral level. Based upon the response time range of the pre-test data, we supposed that mental rotation was probably completed in the majority of trials after 4 s, requiring the memorization of the rotated stimulus. It might still have taken place in some trials, though, introducing noise into this predictor. Thus, neither ROTATE2 nor MEMORY were systematically assessed in the analyses, but they were included into the model to increase the model fit. The comparison of original and matching figures was modeled with regressor 13 (MATCHING). The eye movement condition was analyzed in the same way, with contrasts being computed for eye movement related activation (COMPARE; regressors 5 to 7 after task presentation) and for fixation-related activation (FIXATE; regressors 8 and 9).

Activation related to the different phases of task processing then was assessed by entering the contrast images of single subjects into random effects (rfx) analyses allowing for inferences on the population level. One set of rfx analyses assessed significant activation changes compared to the pre-stimulus baseline and the corresponding eye movement control task (contrasts *ENCODE>BASELINE*, *ROTATE>BASELINE*, and *MATCHING>BASELINE*; *ROTATE>FIXATION*, and *ENCODE>COMPARE*; location and orientation conditions pooled for all contrasts). In addition, rfx *t*-tests assessing differences between activation in the orientation and location condition for the whole acquired volume during *ROTATE* and *ENCODE* were calculated. These analyses were performed as whole-brain analyses, with the aim to obtain a comprehensive view of the functional network involved in the different aspects of task solving. A second set of rfx analyses contrasted activation differences between the separate cognitive processes, and between the two task conditions (location vs. orientation). These analyses were performed using a step-wise approach combining analyses of the whole acquired brain volume with Region-of-Interest (ROI) analyses.

As a first step, activation in dPM and SPL that differed significantly from activation during the eye-movement control task was used to define two ROIs containing voxels in superior parietal lobe (SPL) and in dPM. The SPL ROI contained all voxels above threshold ($P=0.001$, uncorrected for multiple comparisons) in bilateral superior parietal lobe (SPL), and the dPM ROI contained all voxels above threshold bilaterally in the dorsal parts of lateral premotor cortex. Using these ROIs to restrict the analysis volume, we assessed whether activation in those ROIs was (a) different across the task-processing steps and (b) higher during the orientation condition than during the location condition (*SPL*: *Orientation>Location*; *dPM*: *Orientation>Location*). The goal of the ROI analyses was to investigate potential differences between conditions and processing steps with higher sensitivity, in a functionally and *a priori* defined restricted 'search space'.

Thresholds for the *whole-brain analyses* of the different processing steps were set to $P=0.01$ (corrected for multiple comparisons across the whole brain volume using false discovery rate (FDR); Genovese et al., 2002) with a cluster size threshold of $k=10$ voxels. Comparisons between the two conditions as well as between the processing steps were expected to result in smaller signal differences as the comparisons of activations against baseline. Hence, a more liberal threshold of $P=0.001$ and $k=5$ was chosen for these contrasts (both for whole-brain and ROI analyses). Structural and functional localization of activation clusters was performed using SPM-implemented toolboxes (Anatomic Automatic Labeling (AAL); Tzourio-Mazoyer et al., 2002; Anatomy Toolbox, v. 1.3c; Eickhoff et al., 2005), and the Surface Management Systems Database and the visualization software WebCaret (Van Essen, 2002; Van Essen et al., 2001; http://brainmap.wustl.edu/caret).

## Results

### *Behavioral data*

The behavioral data collected during the MR experiment revealed that the two conditions (Orientation and Location) did not differ in terms of task difficulty and response times ($P>0.30$ in both analyses, paired *t*-tests). Response times were 1.26 s±0.18 s for the orientation condition and 1.25 s±0.20 s for the location condition, respectively (mean±S.D.). The percentage of correct responses was above 90% (Orientation: 94.07%±5.21%, Location: 91.54%±7.34%).

### *fMRI data*

Analyses of the different aspects of task solving confirmed previous evidence that mental rotation tasks require a complex interplay of numerous brain regions that are sequentially activated by the different task-processing requirements. Superior parietal lobe was the only brain region that was significantly activated during all steps of task solving. Higher-order visual areas of occipital cortex (V2, V3) were predominantly activated during ENCODING and MATCHING and to a smaller extent also during ROTATE. Fig. 2 shows the contrasts between task-related and

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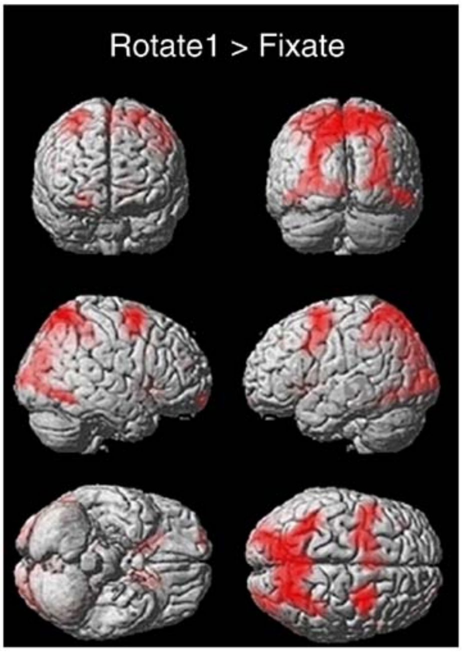

Fig. 2. Brain activation during the three task processing steps encoding, mental rotation, and matching. Images are surface-rendered maximum-intensity projections, using the single-subject brain in stereotactic space (MNI) provided in SPM2. Images are thresholded at $P=0.01$ (FDR-corrected), $k=10$, with hotter colors indicating stronger effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

baseline activation for stimulus encoding (ENCODE), rotation (ROTATE) and stimulus matching (MATCHING). The figure reveals that bilateral parietal and dorsal lateral premotor areas are active during all three processing steps. However, premotor activation during matching is considerably reduced in the right and increased in the left hemisphere, suggesting that it might be predominantly related to response preparation and movement execution with the right hand (see also below and Table 1).

### *Comparisons with saccadic and fixation-related eye movements*

As subjects had to fixate a fixation cross during the mental rotation epoch, premotor activations during ROTATE might be related to this process. However, the contrast *ROTATE>FIXATE* clearly revealed that premotor activation during mental rotation cannot exclusively be attributed to fixation-related eye movements. While both tasks activated brain networks that showed considerable overlap, activation during mental rotation was significantly higher in superior parietal lobe (BA 7), dorsal lateral and medial premotor areas (BA 6), in medial occipital and temporal lobes, as well as in various parts of the basal ganglia (see Fig. 3). Based on these results, ROIs for SPL and dorsal premotor cortex (dPM) were defined to compare activation differences in these brain regions during the three task processing steps as well as during the location and orientation conditions. The stereotactic coordinates and the location of the two ROIs are shown in Table 2 and Fig. 4. In addition, we contrasted activation during rotation with activation triggered by saccadic eye movements (ROTATE>COMPARE). The aim of this contrast was to ensure that the dPM clusters activated by mental rotation are distinct from those triggered by saccadic eye movements. This was clearly the case, as this analysis yielded large clusters in dPM that were basically identical to those of the contrast ROTATE>FIXATE (data not shown).

### *Differences between encoding, rotation and matching*

Table 1 displays results of the ROI analyses comparing activation in the dPM and SPL ROIs evoked by the three different processing steps. During the mental rotation epoch (ROTATE) activation was considerably increased – compared to both the encoding and the matching epochs – in large portions of the SPL. In addition, activation in dPM was higher during both rotation and encoding when compared to stimulus matching. No activation differences in dPM were observed when directly contrasting the encoding with the rotation epoch. Encoding activated dPM bilaterally more extensively than matching. In addition, a subcluster in left premotor cortex showing higher signal changes during matching than during encoding probably reflects activation related to motor preparation/execution. In order to assess whether the lack of differences in dPM between ENCODE and ROTATE was partially related to different eye movement requirements in the two tasks (saccades during ENCODE vs. fixation during ROTATE), we computed the difference in activation when each

Table 1
Significant clusters in superior parietal and dorsal premotor regions of interest (ROI), resulting from a region of interest analysis of activation differences between encoding, mental rotation and matching

| Contrast and ROI | *t*-value | Size | *x* | *y* | *z* |
|---|---|---|---|---|---|
| *Rotate>Encode* | | | | | |
| Dorsal premotor | No suprathreshold voxels | | | | |
| Superior parietal lobe | 9.26 | 1848 | 2 | −62 | 68 |
| | 5.56 | 122 | −42 | −52 | 58 |
| | 4.10 | 6 | −24 | −70 | 48 |
| *Encode>Rotate* | | | | | |
| Dorsal premotor | No suprathreshold voxels | | | | |
| Superior parietal lobe | No suprathreshold voxels | | | | |
| *Rotate>Matching* | | | | | |
| Dorsal premotor | 7.71 | 526 | −24 | −2 | 56 |
| | 6.22 | 543 | 32 | 2 | 54 |
| Superior parietal lobe | 8.44 | 2888 | 30 | −54 | 64 |
| | 6.95 | 139 | −28 | −48 | 50 |
| *Matching>Rotate* | | | | | |
| Dorsal premotor | No suprathreshold voxels | | | | |
| Superior parietal lobe | No suprathreshold voxels | | | | |
| *Encode>Matching* | | | | | |
| Dorsal premotor ROI | 7.89 | 456 | 24 | −4 | 64 |
| | 5.41 | 240 | −22 | −2 | 54 |
| Superior parietal lobe | 8.92 | 202 | 26 | −50 | 58 |
| | | 124 | −24 | −52 | 54 |
| *Matching>Encode* | | | | | |
| Dorsal premotor ROI | 5.26 | 5 | −32 | −6 | 68 |
| Superior parietal lobe | 6.43 | 13 | −48 | −40 | 60 |
| | 5.14 | 5 | 42 | −52 | 48 |
| | 4.51 | 7 | −24 | −56 | 70 |

*Notes.* Stereotactic coordinates and *t*-values are provided for the local maxima in the respective cluster. Thresholded at $P=0.001$ (uncorrected), $k=5$.

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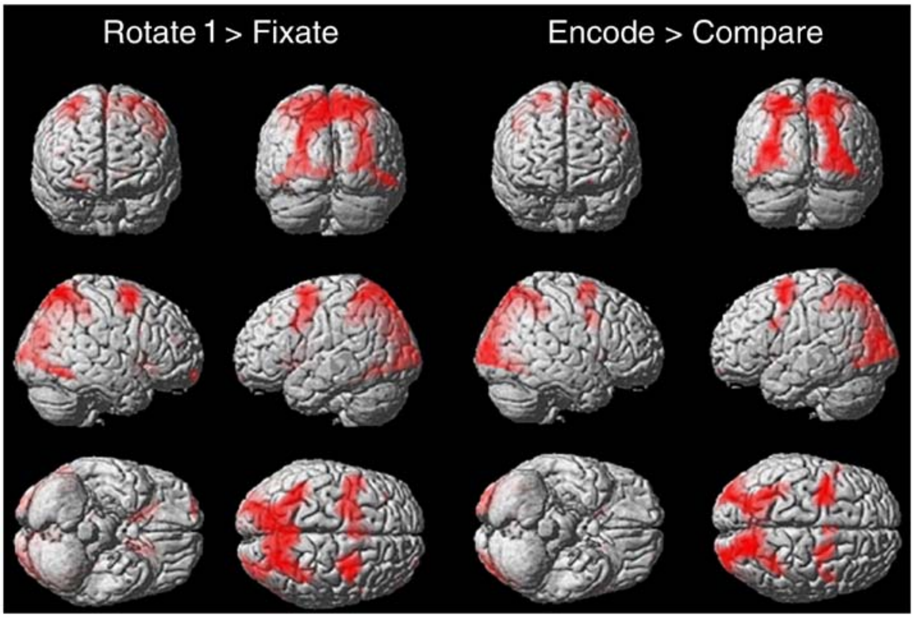

Fig. 3. Significant differences between mental rotation (epoch Rotate) and crosshair fixation (Fixate). Image characteristics as in Fig. 2.

condition was corrected for its respective eye movement control task (i.e., (ROTATE > FIXATE) > (ENCODE > COMPARE)). This revealed clearly higher signal during rotation than during encoding in bilateral dorsal lateral premotor areas, as well as in superior parietal lobe (Fig. 5). Also, contrasting encoding with the eye movement control task (ENCODE > COMPARE) resulted in a significant reduction of the dPM clusters revealed by the contrast ENCODE > BASELINE – suggesting that at least part of the latter activation is related to performing saccadic eye movements required by the detailed visual analysis of the stimuli.

### *Differences between the orientation and location conditions*

The comparison between orientation and location trials revealed that dPM activation is not modulated by the amount of spatial orientation information (Table 3). Even when lowering the threshold to $P = 0.01$, no differences in dorsal premotor cortex were obtained. However, and in line with our expectations, the orientation condition evoked stronger hemodynamic responses in superior parietal lobe, both during the rotation and during the encoding epochs (Fig. 6). In addition to these analyses tailored to test our *a priori* hypotheses we performed a whole-brain contrast between the two conditions. This contrast yielded, similar to the ROI analysis, no differences in cortical motor areas. However, differing activation in several clusters located in higher-order visual areas of the occipital lobe as well as on the border of superior occipital and parietal lobe (cuneus/precuneus; see Table 4) was detected. The location condition led to increased signal changes in subcortical areas, postcentral gyrus and the inferior frontal lobe.

Table 2
Local maximum and extent of the ROIs in left and right dorsal premotor cortex, and in superior parietal lobe

| | | *x* | *y* | *z* |
|---|---|---|---|---|
| *Dorsal premotor* | | | | |
| Left hemisphere | Maximum | −22 | 4 | 52 |
| | Extent | −36 to −12 | −14 to 12 | 51 to 72 |
| Right hemisphere | Maximum | 32 | 4 | 54 |
| | Extent | 18 to 47 | −12 to 12 | 51 to 75 |
| *Superior parietal lobe* | | | | |
| | Maximum | −2 | −52 | 60 |
| | Extent | −49 to 46 | −96 to −48 | 37 to 78 |

## Discussion

The aim of the present study was to assess the functional network involved in the different processing steps required by mental rotation tasks, and to investigate the modulation of this network's activation related to the processing of spatial orientation information. To this end, we proposed a new way to probe the various cognitive processes associated with the solving of complex cognitive tasks, and combined it with a time-sensitive event-related data analysis approach. This revealed that mental rotation tasks trigger the timed collaboration of numerous brain regions associated with visual and motor processing. Dominant among them is the superior parietal lobe which is persistently involved into all aspects of task solving, showing highest activation during mental rotation proper. In addition, higher-order visual areas in occipital and temporal lobe, as well as various motor areas – including the basal ganglia – are active during the different steps of task solving. This sequential activation of a multitude of brain regions should be considered when interpreting the results of other studies that did not explicitly separate the different cognitive processes recruited by mental rotation tasks.

Our main hypotheses were that dPM is active during all task processing epochs requiring the processing of spatial orientation information, that dPM activation is modulated by the amount of

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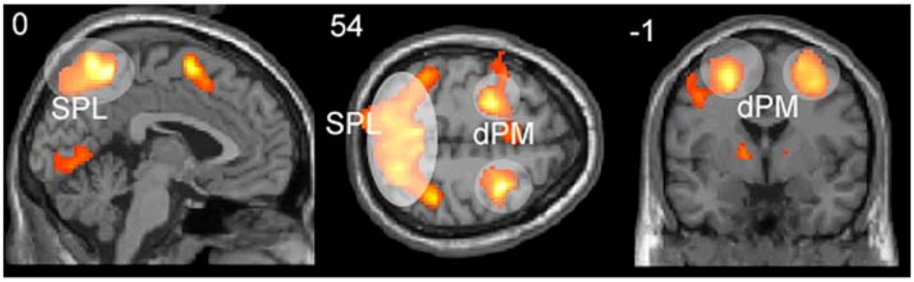

Fig. 4. Orthogonal views depicting the location and extent of the dorsal premotor (dPM) and superior parietal (SPL) regions of interest (transparent ellipses).

spatial orientation information that has to be processed, and that dPM activation is not related to eye movements. The first hypothesis receives partial support by the empirical results, as dPM was active during all processing steps. However, note that mental rotation proper seemed to recruit dPM in the most pronounced way. This conclusion is based on several observations. First, contrasting encoding and rotation with their respective eye movement control task indicated significantly higher dPM activation during rotation than during encoding. Second, both encoding and rotation activate dPM more than matching – with part of the encoding activation being related to eye movements. Third, the activation of dPM during encoding might be attributed to the display format of our task paradigm (see *limitations of this study*). We therefore suggest that dPM activation during mental rotation tasks is predominantly related to the very process of mental rotation. This conclusion receives strong support by two time-resolved fMRI analyses (Ecker et al., 2006; Richter et al., 2000), who analytically disentangled sensory, cognitive and motor processing during mental rotation tasks and also revealed stronger activation in dPM with higher rotation demands.

Analysis of the orientation and location condition did not confirm the hypothesis that motor areas are specifically involved in processing the spatial orientation information required by mental rotation. Neither the ROI analysis, nor the whole brain analysis showed any difference in premotor or primary motor areas between the orientation and the location condition. The whole-brain analysis revealed significant differences in three clusters located in higher-order visual areas. The largest of these clusters was located in higher-order visual areas such as V3a and V7 (Tootell et al., 1998). V3a is a motion-selective area that is involved in the processing of disparity information. V7 is also activated during stereopsis and was found to be active during the perception of illusory and real contours (Mendola et al., 1999). Some, but not all other studies using mental rotation paradigms also found activation in or around this area (Kosslyn et al., 2001; Barnes et al., 2000). In fact, evidence from other imaging studies using a variety of stimuli and tasks (ranging from the perception of houses to spatial deductive reasoning; e.g. Blonder et al., 2004; Knauff et al., 2002) suggests that the activation we found reflects neural computations related to the processing of edges, shapes and their spatial orientation and configuration. This would be consistent with the modulation of orientation information by the two conditions. Notably, SPL activation was not modulated by the two conditions. This might suggest that the specific spatial computations (changes in position and orientation) required by mental rotation tasks are performed in higher-order visual areas of the occipital rather than in the parietal lobe, and that the latter is more involved in visuomotor computations, in close cooperation with premotor areas. This interpretation is in line with a recent study showing that parietal activation is less directly coupled to task solving as formerly expected (Ecker et al., 2006).

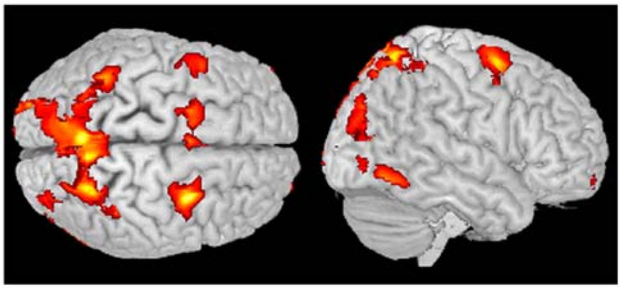

Fig. 5. Significant differences in premotor and parietal activation resulting from the contrast (ROTATE>FIXATE)>(ENCODE>COMPARE). Shown are surface-rendered maximum-intensity projections (top view and lateral view of the right hemisphere), thresholded at $P=0.001$ (uncorrected), $k=5$, with hotter colors (scale from red to yellow) indicating stronger activation differences. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In addition, comparing activation during mental rotation with activation triggered by saccadic eye movements and by fixation of a crosshair clearly revealed significant clusters in dorsal and medial premotor areas as well as in superior parietal cortex. Hence, our experimental design shows that activation in premotor and superior parietal cortex can not be explained by saccadic and fixation-related eye movement control.

On a methodological level, our study documents activation related to the different processing steps involved in a complex cognitive task – demonstrating the concerted action of a number of brain regions. This action becomes apparent only when the different processing steps are behaviorally or analytically separated. Inconsistencies in premotor activation reported by former studies might be related to differences in experimental paradigms and data analysis. For example, premotor activation might not be detected when predominantly using tasks with rather low rotation angles, or when using a block design in which the time between successive trials is not kept to a minimum (e.g., because presentation time is fixed or because breaks between trials are too long). In both cases, the amount of time in which mental rotation itself is performed is reduced. In combination with the fact

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Table 3
Significant activation differences between the location and orientation condition in ROIs in superior parietal and dorsal premotor cortex, separately for the Rotate and Encode contrasts

| Contrast and ROI | *t*-value | Size | *x* | *y* | *z* |
|---|---|---|---|---|---|
| *Rotate: Orientation > Location* | | | | | |
| Dorsal premotor ROI | No suprathreshold voxels | | | | |
| Superior parietal lobe ROI | 4.57 | 18 | −14 | −84 | 46 |
| *Rotate: Location > Orientation* | | | | | |
| Dorsal premotor ROI | No suprathreshold voxels | | | | |
| Superior parietal lobe ROI | No suprathreshold voxels | | | | |
| *Encode: Orientation > Location* | | | | | |
| Dorsal premotor ROI | No suprathreshold voxels | | | | |
| Superior parietal lobe ROI | 4.46 | 7 | 26 | −54 | 48 |
| *Encode: Location > Orientation* | | | | | |
| Dorsal premotor ROI | No suprathreshold voxels | | | | |
| Superior parietal lobe ROI | No suprathreshold voxels | | | | |

*Notes.* Stereotactic coordinates and t-values are provided for the local maxima in the respective cluster. Thresholded at $P=0.001$ (uncorrected), $k=5$.

Table 4
Brain structure, MNI coordinates (local maximum voxel) and *t*-values of significant activation differences between the location and orientation condition during mental rotation (ROTATE1)

| Hemisphere | Brain structure | *t*-value | Size | *x* | *y* | *z* |
|---|---|---|---|---|---|---|
| *Orientation > Location* | | | | | | |
| Left | Superior occipital lobe/Cuneus | 7.09 | 492 | −26 | −92 | 22 |
| Right | Calcarine sulcus/ lingual gyrus | 5.99 | 274 | 12 | −68 | 8 |
| Right | Superior occipital lobe/Cuneus | 5.82 | 99 | 24 | −68 | 32 |
| Left | Inferior occipital lobe | 5.77 | 57 | −40 | −68 | −8 |
| Right | Lingual gyrus | 5.19 | 16 | 24 | −56 | −10 |
| Right | Inferior temporal lobe | 5.08 | 35 | 52 | −68 | 10 |
| Right | Middle frontal lobe | 4.91 | 9 | 26 | 52 | −22 |
| Left | Putamen | 4.81 | 18 | −16 | 16 | −8 |
| Left | Superior occipital lobe | 4.57 | 18 | −14 | −84 | 46 |
| Right | Inferior frontal lobe | 4.11 | 7 | 32 | 32 | −6 |
| Left | Calcarine sulcus/ lingual gyrus | 4.09 | 5 | −12 | −72 | 8 |
| *Location > Orientation* | | | | | | |
| Left | Postcentral gyrus | 6.24 | 49 | −42 | −22 | 42 |
| Left | Insula | 5.39 | 22 | −34 | 10 | −2 |
| Right | Putamen | 4.92 | 9 | 34 | 4 | 0 |
| Right | Rolandic Operculum/ insula | 4.55 | 7 | 48 | −4 | 8 |
| Left | Inferior frontal lobe | 4.31 | 12 | −24 | 22 | −26 |

*Notes.* Stereotactic coordinates and *t*-values are provided for the local voxel maxima in the respective cluster. *x*=sub-peaks of a cluster. Thresholded at $P=0.001$ (uncorrected), $k=5$.

that premotor areas seem to be less involved in non-rotational processes, their activation might remain undetected by statistical analyses modeling activation to be persistent across the whole analysis time window.

## *Limitations of this study*

Mental rotation is a classical task paradigm of cognitive psychology. The exact cognitive mechanisms involved in this phenomenon have proven to be elusive so far, and despite significant efforts. In this study we devised a novel task paradigm in order to explicitly separate the various processing steps involved in mental rotation tasks. While this paradigm offers several advantages it also has its limitations. One of them is related to the inherent difficulty to separate actually contingent and functionally related processing steps. While figures during matching were aligned with respect to the horizontal image plane – and thus "standing" in a natural position – this was not the case during encoding, where stimuli were shown in a rotated position. This unusual presentation mode might automatically activate covert rotation of stimuli to a position in which the stimulus is aligned with the horizontal image plane (which is the default mode of human perception). Additionally, subjects may have started rotating the stimuli already before presentation of the orange bar. Note though that if the latter applies, our results provide even stronger support for the conclusion that activation is highest in the "core mental rotation network" (SPL and dPM) during rotation proper. Nevertheless, future studies should try to separate encoding, rotation and matching even better. Better separation might also be achieved by varying the time spent on the different processing steps (as in a time-resolved paradigm; Ecker et al., 2006; see also Ramnani and Miall, 2004). However, we decided against this measure in the present study because we considered equating processing time for the different processing steps as more

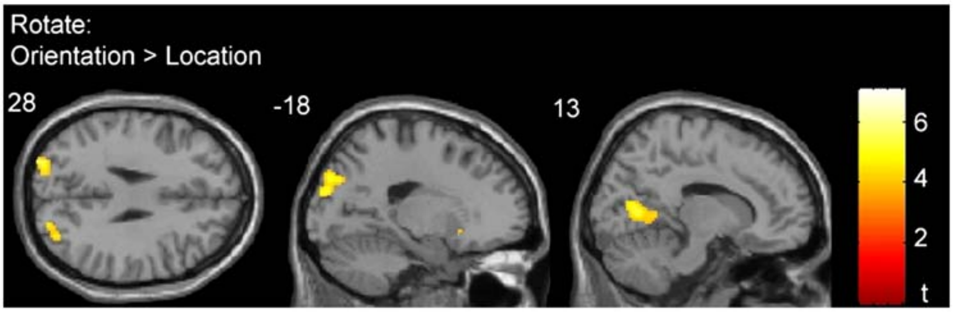

Fig. 6. Significant differences between the location and orientation condition in higher-order visual areas of the occipital and temporal lobe. Shown are coronal, sagittal and axial slices of selected clusters, with the numbers to the upper left of each image indicating the displayed slice. Thresholded at $P=0.001$, $k=5$.

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important. Furthermore, parametric variation of the amount of spatial orientation information might provide more specific insights into which brain regions are involved in processing this information. We opted against this step in the current study mainly because pretests had shown an increased working memory load and the absence of mental rotation effects when adding additional symbols or using more complex figures (e.g., with more arms). In addition, it might be worthwhile to incorporate an independent behavioral measure of the amount of orientation information that has to be processed (which was not available here because we equalized tasks for difficulty and processing time). Also, the current paradigm seems ideally suited to a TMS investigation – which would allow selective disruption of the hypothesized processing steps and an assessment of the respective contribution of the different brain regions to their completion. Finally, note that the conclusions of our study are restricted to the male gender due to our sample selection criteria.

### *General discussion – the functional relevance of dPM during mental rotation*

While initial accounts classified mental rotation as a process exclusively relying upon visuo-spatial imagery, accumulating evidence suggests a significant contribution of motor-related processes to this phenomenon. Numerous behavioral and neuroscientific studies attempted to determine the role of motor areas in mental rotation. Their main goal was to clarify if and why human motor areas are involved in solving mental rotation tasks. Available data provide clear answers for the 'if' question. A number of studies, including the present one, revealed significant and consistent activation in various motor structures of the human brain, with lateral and medial premotor areas showing most consistent involvement. These studies provide compelling evidence against the hypothesis that activation in these areas was related to "genuine" motor processes such as planning, preparation or execution of movements (as, e.g., required by pressing the response button). Rather, premotor areas seem to be involved in more "cognitive" aspects of task solving. We suggest that several hypotheses can be rejected based on the existing evidence:

#### *Eye movements*

It has been suggested that premotor activation in mental rotation is not functionally related to cognitive aspects of task solving, but reflects preparation or execution of eye movements. So far, the main arguments against this hypothesis were analyses of the localization (in terms of stereotactic coordinates) of frontal eye fields and of premotor clusters, as well as a study using a saccadic eye movement control task (Carpenter et al., 1999). Evidence from the present study suggests that dPM activities during mental rotation cannot be exclusively explained by saccadic eye movements or by fixation-related processes. When brain activation during a control task requiring eye movements and fixation was contrasted with activation during mental rotation, significantly higher and differently localized activation in bilateral dPM was clearly revealed.

#### *Graspable objects*

Another interpretation of dPM activation during mental rotation is that the presentation of graspable objects automatically triggers activation in these areas. This interpretation can be rejected based on an assessment of the localization of dPM activation during mental rotation. We computed the mean stereotactic coordinates (in MNI space)[1] of mental rotation studies reporting dPM activation (Ecker et al., 2006; Jordan et al., 2002; Kosslyn et al., 2001; Lamm et al., 2001b; Vingerhoets et al., 2002; Wraga et al., 2003, 2005). Mean MNI coordinates of left and right lateral premotor activation were −25/−7/58 and 28/−10/58, respectively. Note that this analysis is based on a variety of different task paradigms, ranging from cube comparison tasks to the rotation of tools. If these coordinates are accepted as a valid approximation of dPM activation, their localization clearly classifies as activation within dorsal lateral premotor cortex (dPM; as defined by Picard and Strick, 1996, 2001). This anatomical assignment is also in line with a recent meta-analysis of functional neuroimaging studies (Mayka et al., 2006). In contrast, premotor clusters detected during the presentation of graspable objects (Grèzes and Decety, 2001) are located considerably more ventral in an area usually classified as ventral premotor cortex.

#### *Motor imagery*

Motor imagery activates areas in dorsal premotor and possibly even in contralateral primary motor cortex (e.g., Ehrsson et al., 2003). Findings of motor activation during mental rotation promoted the hypothesis that dPM activities during mental rotation are related to imagining body or limb movements (e.g., Kosslyn et al., 2001; Vingerhoets et al., 2002; Wraga et al., 2003, 2005). While this hypothesis sounds plausible when subjects have to evaluate the laterality of body parts, such as hands or feet (but see also Sauner et al., 2006, and Thayer and Johnson, 2006), it is not convincing in the case of abstract object rotation. Here, the proponents of the motor imagery hypothesis had to suggest that subjects imagine utilizing their hands to rotate the objects. This is not a parsimonious explanation and it is in contrast to introspective reports of our subjects who usually reported objects to be moving "by themselves". In addition, empirical evidence speaks against the motor imagery account on a number of levels. When subjects were instructed to either imagine moving objects with their hands or to imagine movement by an external force, significant activation in lateral BA 6 was observed with both instructions (Kosslyn et al., 2001). Also, a recent cortical stimulation study in a patient with an implanted electrode grid over left primary motor cortex demonstrated interference effects only when the patient used motor imagery, but not during mental rotation (Tomasino et al., 2005). The lack of lateralization of premotor activities provides another argument against the motor imagery account: Most mental rotation studies show clearly bilateral dPM activation (e.g., Lamm et al., 2001b; Richter et al., 2000; Tagaris et al., 1998; Windischberger et al., 2003a,b), while movement imagery results in higher signal changes contralateral to the used limb (e.g., Ehrsson et al., 2003; Michelon et al., 2006). The strongest argument against the motor imagery hypothesis is derived from a selective review of neuroimaging studies of (hand and finger) motor imagery (Boecker et al., 2002; Dechent et al., 2004; Ehrsson et al., 2003; Hanakawa et al., 2003; Naito et al., 2002; Porro et al., 1996, 2000; Stippich et al., 2002) revealing clear differences in dPM localizations related to motor imagery and mental rotation. Motor imagery yielded mean coordinates of −24/−15/56 and 33/−8/56, showing

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[1] Coordinates reported in Talairach and Tournoux space were converted to MNI space using the non-linear transformation algorithm suggested by Mathew Brett, see http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml.

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that motor imagery clusters are located more caudally than mental rotation clusters. Note also that coordinates of the present study – which was the only study explicitly controlling for eye movements – are even more anterior in the *y* plane. Thus, we conclude that motor imagery and mental rotation activate different areas of lateral premotor cortex, and that activation during mental rotation cannot be explained by motor imagery alone.

### *Processing of spatial orientation information*

One major goal of the present study was to test whether dPM is genuinely involved in the processing of visuo-spatial orientation information. To this end we modulated the relative amount of spatial orientation information that had to be processed, using two distinct conditions. The contrast between those conditions did not reveal any significant clusters in dPM. Hence, we suggest that the relative amount of spatial orientation information that has to be processed does not modulate activation in dorsal premotor areas. Note though that both conditions led to absolute changes in dPM. This indicates that other computations relevant for task solving are performed in dPM.

### *Anticipation of movement consequences*

The present study suggests that activation in dPM is strongest during mental rotation proper. This provides some hints as to what kind of information is processed in dPM areas during mental rotation. In addressing this question it is important to determine more precisely in which part of dPM activation was observed in the current and in previous studies. Evidence from both monkey experiments and functional neuroimaging studies suggests that activities are localized in an area classified as rostral dorsal premotor cortex (PMdr; Picard and Strick, 2001). This area has much in common with so-called pre-SMA (i.e., the area of medial premotor cortex rostral to SMA-proper) and is anatomically distinct from the caudal part of dorsal premotor cortex (PMdc). The latter has direct connections to primary motor cortex (M1) and the spinal cord, and seems to be primarily involved in aspects of motor control. In contrast, PMdr and pre-SMA are not directly connected to areas involved in motor execution, including SMA-proper and PMdc. Instead, they are interconnected with areas of prefrontal cortex and the reticular formation, which led to the suggestion that pre-SMA and PMdr should be functionally classified as areas of prefrontal cortex rather than as “genuine” motor areas. This argument is supported by the observation that PMdr and pre-SMA are much more involved in “cognitive” than in motor processes. Thus, it might be questioned whether PMdr involvement during mental rotation reflects “motor” activation at all – i.e., activation related to (either real or imagined) aspects of movement planning, preparation or execution. Note also that the dorsal PM activation observed in mental rotation studies is clearly anterior to cytoarchitectonic probability maps of lateral BA 6 (Eickhoff et al., 2005).

In fact, several recent neuroimaging studies reveal activation with similar PMdr localizations as the ones detected in our study during tasks having only minimal or no specific motor components. These tasks have in common that they either require spatial attention and spatial working memory, or the mapping of sensory to (verbal or hand-movement related) motor information. Simon et al. (2002) and Boussaoud (2001), for example, found bilateral activation in PMdr in humans performing a task requiring spatial attention and spatial working memory. Subjects had to attend to stimuli presented at cued spatial locations in the peripheral visual field, with memory load being varied by means of different delays between cue and stimulus. The centers of these activities were located very close to the mean coordinates of dPM activation during mental rotation reported in the present and other studies. Notably, by means of the experimental paradigm, it could be excluded that these activities were related to movement control processes. In addition, using three different non-motor tasks Hanakawa et al. (2002) revealed activation in an area belonging to PMdr. In that study subjects had to maintain and update verbal, numerical or spatial information. Although all three tasks led to significant activation in PMdr, activation levels were highest during the spatial task which was also the only task evoking bilateral PMdr activation. This finding is also supported by a recent study combining fMRI and rTMS (Tanaka et al., 2005) demonstrating that PMdr plays an important role in the updating of spatial information.

Information about the spatial environment is conveyed to the organism both by the visual system and by the motor system. The visual system provides information about the location and orientation of objects in both allocentric and egocentric coordinate systems. It is dependent upon environmental changes and can only provide this information in real time or slightly retrospectively via sensory processing. However, vision can supervise the appropriateness of motor acts. The motor system, on the other hand, provides information about objects in egocentric coordinates. It is also in the unique position to provide prospective information about movement consequences via premotor areas involved in the planning and preparation of movements. Conveying this information to visual areas should allow for a more efficient supervision of motor acts (e.g., Wolpert and Kawato, 1998). In the case of overt object rotation, continuous exchange and updating of spatial information between visual and motor systems is particularly important. The visual system has to indicate initially in which direction the movement has to be performed. It then has to monitor whether the object is correctly moved and – if necessary – adjust movement parameters accordingly. The functional pathway allowing such a constant and prospective exchange of information in the human visuomotor system is well established in the monkey, where dorsal premotor areas are extensively interconnected with posterior parietal areas. Information between these areas is exchanged whenever the animal plans, performs or anticipates the (visual and motor) consequences of a grasping movement under visual control (e.g., Luppino et al., 1999). A similar network seems to exist in humans as well. However, overt movement planning and anticipation of movement consequences more likely takes place in PMdc rather than in PMdr.

Based upon the finding that PMdr is strongly involved in the updating of spatial attention, PMdr might therefore play a similar role in mental rotation as PMdc in overt rotation. We speculate that PMdr is involved in monitoring the mapping of visuo-spatial sensory events to motor acts and vice versa. The main difference between covert and overt object rotation then would be that the sensory information available during overt rotation is ‘replaced’ by merely imagined sensory information in mental rotation. This ‘imagined’ input, which we think is processed in superior parietal lobe and possibly also in higher-order areas of the occipital lobe, is relayed to premotor neurons. We speculate that these neurons are located in PMdc during overt rotation, while their sensory–motor attention and mapping function is processed in PMdr during mental rotation.

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## Conclusion

Using a tailored experimental paradigm, we were able to achieve a separation of the numerous processing steps involved in mental rotation tasks. This approach suggests that dPM activation during mental rotation proper is neither related to eye movement control nor modified significantly by the amount of spatial orientation information to be processed. Rather, our results indicate that dPM activation reflects generalized processes related to the imagined anticipation of movement consequences. We conclude that mental rotation in fact shows a high degree of functional equivalence with overt object rotation, relying upon the usage of similar, but only partially overlapping functional modules in the human brain.

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