

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.

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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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