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Rotated alphanumeric characters do not automatically activate frontoparietal areas subserving mental rotation

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ABSTRACT

Functional neuroimaging studies have identified a set of areas in the intraparietal sulcus and dorsal precentral cortex which show a linear increase in activity with the angle of rotation across a variety of mental rotation tasks. This linear increase in activity with angular disparity suggests that these frontoparietal regions compute rotational transformations. An open question is whether rotated target stimuli automatically activate these frontoparietal regions, even if the task does not require rotational transformations. To address this question, we performed functional MRI while healthy male volunteers made two-choice reaction-time judgements on canonical or mirror images of two-dimensional alphanumeric characters presented at various angles of rotation. Participants had either to decide whether characters were normal or mirror-reversed (i.e., mental rotation) or judge whether the stimulus was a letter or a number (i.e., stimulus categorization). Reaction times and error rates linearly increased with the angle of rotation for mirror-reversed judgements but not for number–letter judgements, showing that only the mental rotation task required rotational transformations of the characters. The mental rotation task was associated with a linear increase in neuronal activity with angular disparity in a bilateral set of frontoparietal areas, comprising the rostral dorsal premotor cortex, frontal eye field, ventral and medial intraparietal sulcus. Neuronal activity in these regions was neither increased nor modulated by angular disparity during the stimulus categorization task. These results suggest that at least for alphanumerical characters, areas implicated in mental rotation will only be called into action if the task requires a rotational transformation.

Introduction

Mental rotation (MR) tasks test the ability to imagine the rotation of an object in the absence of overt sensorimotor rotation. The active mental manipulation of the presented stimuli is reflected in the reaction times (RT) which show a monotonic increase with the required angle of rotation (Shepard and Metzler, 1971). This linear increase in RT was replicated across a wide range of tasks including MR of tools, hands, characters or scenes (Hochberg and Gellman, 1977; Parsons, 1987b). The robust linear relationship between RT and angular disparity prompted a series of functional neuroimaging studies which parametrically manipulated the angle of rotation (Zacks, 2008). It has been shown that the intraparietal sulcus (IPS) and adjacent parietal areas showed a linear increase in activity with the angle of rotation during in-plane MR of two-dimensional alphanumeric characters (de Lange et al., 2005; Podzebenko et al., 2002), hands (de Lange et al., 2005) or abstract three-dimensional objects along the *x*-, *y*- or *z*-axis (Gauthier et al., 2002). These results support the notion that the IPS is critically involved in computing rotational transformations during MR tasks. Linear increases in neuronal activity with angular disparity were also observed in dorsal precentral areas, especially when MR tasks favoured motor simulation (Zacks, 2008).

While previous neuroimaging studies identified a set of frontoparietal areas which become increasingly active with angular disparity during a wide variety of MR tasks, they did not address the question how much of this neuronal response pattern was driven by the perception of rotated stimuli. If objects have a preferred spatial orientation, neuronal systems involved in rotational transformation may “by default” map rotated objects onto their normal spatial

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orientation. Such automatic mapping should cause a linear increase in neuronal activity in areas implicated in rotational transformations, even if the task does not require MR.

Here we used event-related MRI to test whether the perception of rotated stimuli automatically activates frontoparietal areas subserving rotational spatial transformations. Healthy male volunteers performed two two-choice reaction time tasks which were matched in terms of sensory input and motor output. Canonical or mirror images of two-dimensional alphanumeric characters were presented at various angles of rotation in the centre of the visual field. Participants had either to indicate whether characters were normal or mirror-reversed (i.e., MR task) or whether stimuli were letters or numbers (i.e. stimulus categorization task). This enabled us to test two alternative hypotheses: (i) If rotated alphanumerical characters automatically trigger “rotational mapping”, the presentation of rotated numbers or letters will produce a linear increase with angular disparity in frontoparietal areas computing rotational transformations during stimulus categorization and mental rotation (Bode et al., 2007; Eisenegger et al., 2007). (ii) Alternatively, rotational transformations may represent a non-routine process that is only called into action when rotational transformations are crucial to task performance. In this case, a linear increase in neuronal activity with angular disparity should only occur with mental rotation but not with stimulus categorization.

Materials and methods

Subjects

Sixteen young healthy men (age range: 20 to 39 years) were recruited from a database of healthy volunteers at NeuroImageNord. Because of gender-specific differences in performance (Linn and Petersen, 1985; Voyer et al., 1995) and cortical activation pattern (Hugdahl et al., 2006; Jordan et al., 2002) with MR, we only studied males to minimize inter-subject variability. Participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971) and naive to the purpose of the study. Written informed consent was obtained before the experiment. The experimental procedures were approved by the local ethics committee.

Experimental design

The time line of the experiment is illustrated in Fig. 1A. We first obtained a T1-weighted structural MRI to exclude anatomical abnormalities. After structural MRI, participants underwent two fMRI sessions during which they made a two-choice reaction-time judgement on alphanumerical characters. We chose two-dimensional alphanumeric stimuli because numbers and letters are highly familiar stimuli that are usually presented in an upright position. In one

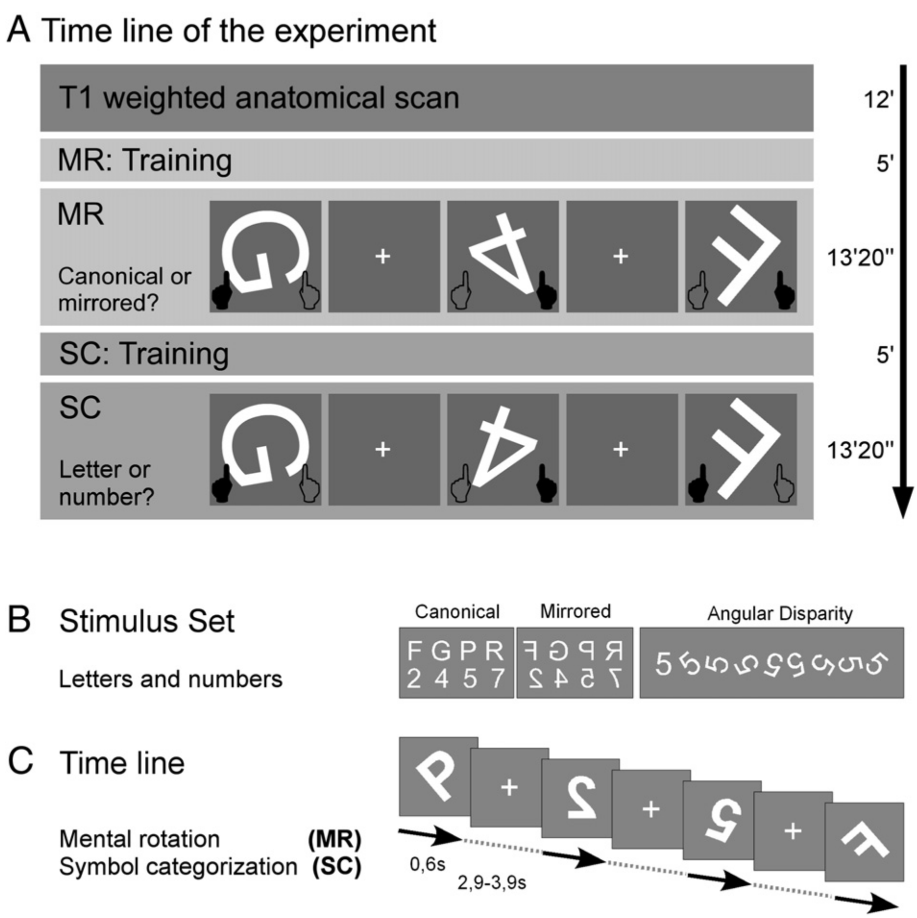

Fig. 1. Experimental design: (A) Time line of the experiment. A T1-weighted structural MRI was obtained followed by the two experimental fMRI sessions during which participants either performed a mental rotation (MR) or stimulus categorization (SC) task. The order of fMRI sessions was balanced across subjects. Each fMRI session was preceded by a training session in the MR scanner without imaging. The duration of each experimental section is given on the right. (B) Set of stimuli. A set of eight alphanumeric characters and their mirror images were pseudorandomly presented. Stimuli were rotated in steps of 40° clockwise to the canonical up-right. (C) Time line of a single trial: a picture of a letter or number was presented in the centre of the visual field. After 0.6 s, the target stimulus was replaced by a central fixation cross. The cross was presented for 2.9 to 3.9 s until the beginning of the next trial. During the MR task, participants had to report whether the picture was an alphanumeric or mirror image. During the SC task, participants had to indicate whether the picture was a letter or number. Responses were made with the left or right index finger.