Neuropsychologia 48 (2010) 529–535

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Greater superior than inferior parietal lobule activation with increasing rotation angle during mental rotation: An fMRI study

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ARTICLE INFO

Article history:
Received 18 February 2009
Received in revised form 18 June 2009
Accepted 12 October 2009
Available online 20 October 2009

Keywords:
Alphanumeric characters
Parametric
Posterior parietal lobules

ABSTRACT

Mental rotation is a task known to activate the parietal cortical regions. The present study aimed to investigate whether there is differential activation of regions within the parietal lobe and to reveal functional subspecialisation of this region by examining the effects of increasing angle of rotation. Functional magnetic resonance imaging was performed in nine healthy female subjects whilst undertaking a parametric mental rotation task. The task comprised 6 alphanumeric characters presented in their normal or mirror-reversed orientation. Behaviourally, subjects showed increased reaction times with increased angle of rotation, with differential effects between the alphanumeric characters; numbers having greater reaction times than letters. BOLD signal increase was observed bilaterally in the middle occipital gyrus and medial frontal gyrus, in the right superior and inferior parietal lobules and in the left superior temporal gyrus. Parametric increases in activation with increasing angle of rotation were observed bilaterally in the superior and inferior parietal lobules and in the right medial frontal gyrus, with greater parametric effects in the superior parietal lobules compared to the inferior parietal lobules. Our findings suggest subspecialisation of the posterior parietal lobules during mental rotation, with differential responses in the superior and inferior regions.

1. Introduction

Mental rotation is a well-studied global task of visuospatial ability (Booth et al., 2000; Zacks, 2008). Mental rotation is the act of imagining the re-orientation of a visual image until it matches a known or memorised comparison image or target image (Cohen et al., 1996; Corballis, 1997; Podzebenko, Egan, & Watson, 2002; Shepard & Metzler, 1971). Mental rotation requires a number of steps: the visual recognition and encoding of an object, the imagined rotation of the object, holding the mentally rotated representation of the object in spatial working memory, and a decision process as to whether the object matches a target object (Booth et al., 2000). Shepard and Metzler (1971) were the first to show that there was a linear relationship between task performance and angle of rotation.

The mental rotation task has been well adapted for use in functional magnetic resonance imaging (fMRI) studies and is a robust method by which the functioning of prefrontal and parietal brain regions can be investigated (Cohen et al., 1996; Koshino, Carpenter, Keller, & Just, 2005; Podzebenko et al., 2002; Podzebenko, Egan, & Watson, 2005). Several neuroimaging studies have identified a network of regions involved in mental rotation; object recognition activates the ventral occipital–temporal pathway or the 'what' system and spatial processing activates the dorsal occipital-parietal pathway or the 'where' system (Booth et al., 2000; Koshino et al., 2005; Mishkin, Ungerleider, & Macko, 1983; Ungerleider, Courtney, & Haxby, 1998).

The posterior parietal lobes have been suggested to be the main regions mediating mental rotation (Alivisatos & Petrides, 1997; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Cohen et al., 1996; Harris et al., 2000; Jordan, Heinze, Lutz, Kanowski, & Jancke, 2001; Koshino et al., 2005; Milivojevic, Hamm, & Corballis, 2009; Podzebenko et al., 2002; Zacks, 2008), whereas activation of prefrontal regions during mental rotation is thought to be associated with the comparison of the mentally rotated stimulus with a known target stimulus and thus represents spatial working memory and attentional demands (Carpenter et al., 1999; Cohen et al., 1996;

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doi:10.1016/j.neuropsychologia.2009.10.013

Koshino et al., 2005; Podzebenko et al., 2002). The parietal lobe integrates visual and somatosensory information and is involved in the generation of visually guided movement. The parietal lobe is thought to form a representation of visual space by extrapolation of visual information concerning the spatial properties of the surrounding environment transformed into motor plans and responses (Podzebenko et al., 2002).

In the present study, the mental rotation task comprised alphanumeric characters, following Podzebenko et al. (2002) and others (Alivisatos & Petrides, 1997; Booth et al., 2000; Harris et al., 2000; Milivojevic et al., 2009). Mental rotation studies using alphanumeric characters have found that behavioural task performance is linearly related to the angle of rotation (Booth et al., 2000; Harris et al., 2000; Jordan et al., 2001; Milivojevic et al., 2009; Podzebenko et al., 2002, 2005; Rilea, 2008). In the study by Podzebenko et al. (2002), brain activation associated with mental rotation was investigated using a parametric design. The design allowed the identification of brain regions that showed a linear relationship between increased BOLD signal response and increasing task difficulty, where difficulty referred to the proportion of characters rotated. They reported robust bilateral activation in the intraparietal sulcus, and superior (Brodmann Area, BA 7) and inferior (BA 40) parietal lobules, with a right hemisphere dominance (Podzebenko et al., 2002). Carpenter et al. (1999) examined the effect of increasing angle of rotation on brain activation, however they used the 3D Shepard and Metzler (1971) figures and not the alphanumeric characters. They found significant activation in parietal regions as well as temporal and frontal regions, with increasing angle of rotation. Carpenter et al. (1999) used a region of interest approach; one region of interest was the parietal region which included the superior parietal lobule (BA 5 and 7), the posterior supramarginal gyrus (BA 40) and the angular gyrus (BA 39) (Carpenter et al., 1999), thus, specific differentiation of parietal subregions was not possible. Further, neither of the previous studies was able to show a functional specialisation of the parietal regions.

Of significant interest is whether parietal regions can be differentially associated with the components of the mental rotation process, particularly the object recognition and rotation components which may have differential angle dependence. The present study was undertaken to investigate whether differential activation occurs in parietal lobe regions and whether functional subspecialisation of these regions can be determined using increasing angle of rotation. We expect the superior and inferior parietal lobules to show differential involvement based on the model of mental rotation. Specifically, we expect the superior parietal lobule to have a greater increase in BOLD signal in response to increasing angle of rotation. The study sample comprised females with an average age of 55 years, as this study was part of a larger study examining cognitive function in post-menopausal women. These women were all in a similar hormonal state and thus provide a homogenous sample. Importantly, post-menopausal women have not yet been investigated in mental rotation research. We used an alphanumeric mental rotation task and examined parametric brain activation associated with increasing angle of rotation. Further, we examined the BOLD signal time courses of the activated regions of interest as a function of angle of rotation.

2. Method

2.1. Participants

Ten right-handed, healthy, English speaking women participated in this study, with a mean age of 55.4 ± 4.0 years (range: 47–60 years). Women were post-menopausal as indicated by natural menopause (greater than 12 months of amenorrhea) or surgical menopause (hysterectomy and bilateral oophorectomy) (Bell, Lijovic, Fradkin, & Davis, 2008). One participant was excluded due to an abnormality noted in the neuroradiological report. The remaining nine participants were free of any neurological or psychiatric conditions. The study was approved by Monash University Standing Committee on Ethics in Research Involving Humans and the Alfred Hospital Ethics Committee (Melbourne, Australia) and all participants gave written informed consent.

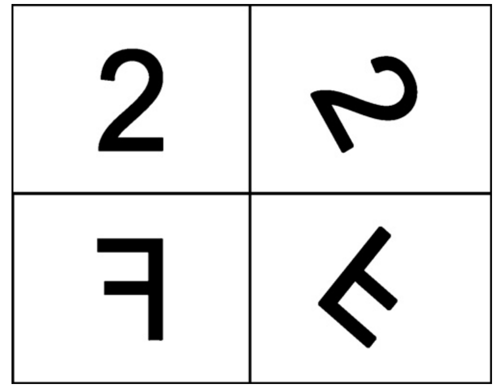

Fig. 1. Examples of stimuli used in the mental rotation task. Top panels show the number '2' in the correct orientation at zero (left) and 60° (right) rotation. Bottom panels show the letter 'F' in the mirror-reverse orientation at zero (left) and 220° (right) rotation.

2.2. Mental rotation

The mental rotation task was based on a previous study (Podzebenko et al., 2002) and consisted of 6 two-dimensional alphanumeric characters (F, G, R, 2, 4, 5) presented in their normal or mirror-reverse orientation. The characters were displayed in their upright position or at varying angles of rotation, ranging from 0° to 320° (Fig. 1). The five experimental conditions included a baseline, a zero rotation condition and three rotation conditions based on increasing angle of rotation. There were seven available rotation angles that we divided into three groups of average rotation angle of 50°, 100° and 150°. The rotation conditions were: (i) stimuli not rotated (0°, zero), (ii) 50° average rotation (included stimuli rotated 40/320° and 60/300°), (iii) 100° average rotation (included stimuli rotated 80/280°, 100/260° and 120/240°) and (iv) 150° average rotation (included stimuli rotated 140/220° and 160/200°). For rotated stimuli, participants were asked to determine stimulus orientation and responded by pressing a button placed in their right hand for 'correct' orientation or using their left-hand button for 'mirror-reverse' orientation. In the baseline condition, six consecutive presentations of an arrow pointing to the left (←) or right (→) required participants to respond with the hand corresponding with the arrow direction. Stimuli were presented using Presentation software (v12, Neurobehavioral Systems, CA, USA) on a laptop. Responses were automatically recorded by the Presentation software, for subsequent reaction time and accuracy analysis. Prior to scanning, participants underwent a practice of the mental rotation task outside of the scanner.

The five conditions were presented in a block design over two runs (8 min 24 s each). A total of 24 blocks were presented pseudo-randomly per run: six baseline, six 0° rotation and four 50°, four 100° and four 150° rotation blocks. Each block duration was 21 s and consisted of 6 trials of 3500 ms per trial. Each stimulus was presented in black Arial font on a white screen (3000 ms), followed by a blank white screen (100 ms), fixation point ('+', 300 ms) and another blank white screen (100 ms). In each run, there were a total of 108 alphanumeric stimuli, consisting of 18 trials of each of the 6 characters. The sequence of stimuli within each run was consistent between all participants; however the order in which the runs were presented differed between participants.

2.3. Functional MRI data acquisition

Images were acquired using a 3 T scanner (Siemens, Erlangen, Germany) at the Royal Children's Hospital (Melbourne, Australia). Whilst in the scanner, participants lay supine with their head supported in a volume coil, with foam padding used to reduce motion. Task stimuli were projected onto a 1.2 m × 1 m ground screen placed at the end of the scanner table and participants viewed this from an angled mirror mounted above their head. Headphones were used to reduce the discomfort of scanner noise and to allow communication. T2*-weighted functional images were acquired using a gradient-echo, echo-planar imaging (EPI) pulse sequence (TR = 3000 ms, TE = 40 ms, flip angle = 90°, matrix 128 × 128, FOV = 220 mm). Thirty-seven contiguous 3.5 mm transverse slices were taken (in-plane resolution 1.7 mm × 1.7 mm). The field of view was aligned parallel with the commissural line and included the full dorsal extent of the brain. A total of 168 whole-brain volumes were acquired during the rotation task. High resolution T1-weighted structural MRI images were also recorded for each participant (TR = 1900 ms, TE = 2.2 ms, matrix 256 × 256, 1 mm slice thickness, FOV = 256 mm).