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Dissecting hemisphere-specific contributions to visual spatial imagery using parametric brain mapping

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ABSTRACT

In the current study we aimed to empirically test previously proposed accounts of a division of labour between the left and right posterior parietal cortices during visuospatial mental imagery. The representation of mental images in the brain has been a topic of debate for several decades. Although the posterior parietal cortex is involved bilaterally, previous studies have postulated that hemispheric specialisation might result in a division of labour between the left and right parietal cortices. In the current fMRI study, we used an elaborated version of a behaviourally-controlled spatial imagery paradigm, the mental clock task, which involves mental image generation and a subsequent spatial comparison between two angles. By systematically varying the difference between the two angles that are mentally compared, we induced a symbolic distance effect: smaller differences between the two angles result in higher task difficulty. We employed parametrically weighed brain imaging to reveal brain areas showing a graded activation pattern in accordance with the induced distance effect. The parametric difficulty manipulation influenced behavioural data and brain activation patterns in a similar matter. Moreover, since this difficulty manipulation only starts to play a role from the angle comparison phase onwards, it allows for a top-down dissociation between the initial mental image formation, and the subsequent angle comparison phase of the spatial imagery task. Employing parametrically weighed fMRI analysis enabled us to top-down disentangle brain activation related to mental image formation, and activation reflecting spatial angle comparison. The results provide first empirical evidence for the repeatedly proposed division of labour between the left and right posterior parietal cortices during spatial imagery.

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Introduction

Mental visual imagery, or our ability to generate, inspect, evaluate, and manipulate, visual images in the absence of physical stimulation, describes a multi-facetted set of cognitive processes that at least mediate, if not constitute several core functions of human cognition including object recognition (Riesenhuber and Poggio, 2000), spatial orientation (Goldstein, 2002), attention (Kanwisher and Wojciulik, 2000), and memory (Cohen et al., 1996). Mental imagination may even be considered to be the key function underlying any abstract reasoning or thinking in general (Kosslyn et al., 1995a), because objects in visual imagery can be manipulated much like actual objects, which can help one to reason about the consequences of the corresponding physical manipulation (Kosslyn et al., 1998).

The representation of mental images in the human brain has been a topic of debate for several decades. Whereas the pictorial or analogue view claims that mental images are subject to analogue, spatial

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representations similar to those observed in visual perception, and are thus in fact picture-like representations that share all features of a real picture perceived by the eyes (James, 1890; Kosslyn, 1980; Kosslyn and Ochsner, 1994; Paivio, 1971), the propositional view regards mental images as a collection of language-based abstract propositions describing features and relative properties of the image derived from memory (Anderson and Bower, 1973; Pylyshyn, 1973). The advent of brain imaging techniques such as PET or fMRI led to a renewed interest in the nature and neural correlates of mental imagery. Results from neuroimaging studies seem to converge to the conclusion that most of the neural correlates that underlie perception also form the neural basis of mental imagery (Ganis et al., 2004; Kosslyn et al., 1997, 2001, 2006). Brain imaging studies investigating mental imagery have commonly revealed a widespread frontoparietal network of brain areas including the dorsolateral prefrontal cortex (DLPFC), supplementary motor area (SMA), posterior parietal cortex (PPC) and, depending on whether the imagery task requires the inspection of fine-grained images, early visual cortex (EVC) (Thompson and Kosslyn, 2000).

Although the network activated during mental imagery is largely bilateral, functional specialisation has been proposed for the left versus the right parietal cortex, especially regarding imagery tasks requiring mental spatial transformations. Evidence has been found for the





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existence of two types of spatial representations, with respective hemispheric specialisations: categorical spatial processing would be subserved by the left PPC, while coordinate spatial processing would be supported by the right PPC (Kosslyn et al., 1989, 1995b; Palermo et al., 2008; Trojano et al., 2002). This is in line with evidence that the right parietal cortex is generally more involved in spatial processing, such as spatial attention (e.g. Hilgetag et al., 2001) and numerical information such as magnitude, duration, size and distance (e.g. Cohen Kadosh et al., 2007; Walsh, 2003).

One well-known example of a spatial mental imagery task entailing coordinate spatial processing is the mental clock task (MCT; Paivio, 1978; Trojano et al., 2000) that involves the schematic generation of a mental image and a subsequent spatial judgment of two angles. Two clock times are presented auditorily, and the participant is asked to report which of the two times represents a greater angle between the respective clock hands. In order to answer this question, participants are generally expected to generate mental images of the two clocks (Paivio, 1978), compare the angles between the large and small clock hands, decide which one is larger, and indicate the result by pressing the corresponding button. A trial of the MCT typically requires several seconds of processing, and produces controllable, metric behavioural output, making it a suitable task for investigating the cortical processes involved in spatial mental imagery. It has been confirmed that the mental representations constructed from verbal descriptions incorporate metric information, and that visual images constructed from descriptive texts have genuine analogue properties (Denis, 2008).

In a previous fMRI investigation, the MCT was shown to involve bilateral posterior parietal cortex (PPC) (Trojano et al., 2000). In an extended investigation of this task, Formisano et al. (2002) disclosed a more widespread bilateral network of brain areas involved, including the auditory and motor areas, PPC, dorsolateral prefrontal cortex (DLPFC) and supplementary motor area (SMA). By visualising how blood oxygen level dependent (BOLD) activation progressed through the cortex from the onset of the auditory stimulus until the final behavioural response of each experimental trial, Formisano and colleagues were able to infer the different temporal stages during which these areas contributed to task execution, revealing activation spreading from the auditory cortex, through the DLPFC and SMA, to the PPC, and finally reaching the motor cortex. Whereas the auditory and motor cortex activations could be directly retraced to the initial auditory stimulus and the final button press, respectively, the DLPFC, SMA and PPC seemed to be involved in the intermediate stages of the task: mental imagery of the two clocks, and subsequently the spatial comparison of the two angles

While the DLPFC and SMA seemed to be largely co-activated during a longer period of time, a hemispheric asymmetry was observed in the parietal cortex: the left PPC seemed to be activated earlier in the process than part of the right PPC, indicating a functional distinction between the two parietal cortices. Subsequent correlational analyses implied that whereas the left PPC is proposedly involved more during the mental imagery stage of the task, the profile of the right PPC fits best with the subsequent spatial angle comparison stage of the MCT. This account of a division of labour between the left PPC and the right PPC was further strengthened by transcranial magnetic stimulation (TMS) studies using the same behavioural paradigm (Sack et al., 2002, 2005). Sack et al. (2002) demonstrated that after temporarily disrupting the left or right PPC with repetitive TMS (rTMS), only right parietal disruption resulted in a significant task execution impairment. This led to the hypothesis that the right parietal lobe might be able to compensate for a temporary suppression of the left, but not vice versa, in line with theories and lesion studies concerning spatial hemineglect. This postulation was addressed in a follow-up study (Sack et al., 2005), in which the right PPC was probed with event-related TMS, while the left PPC was either functioning normally or temporarily impaired by rTMS. Results showed that if the left PPC was unavailable, the right PPC was able to compensate for this functional loss – in addition to carrying out its own task, most likely spatial angle comparison – by taking on the function previously carried out by the left PPC – most likely, mental image generation. While these studies collectively suggest that the left PPC and the right PPC fulfil at least partly different tasks during spatial mental imagery, the actual involvement of both hemispheric counterparts in this process still remains speculative.

One particularly interesting aspect of the MCT that was not employed in the aforementioned studies is that task difficulty can be systematically manipulated by varying the amount of difference between the angles formed by the two subsequently presented clock times in each trial. When comparing two simple physical stimuli on a metric dimension, such as the length of two parallel lines, the time required for comparison varies inversely with the distance between their referents on the judged dimension (Moyer and Bayer, 1976; Moyer and Landauer, 1967). This symbolic distance effect (SDE) is also of relevance when comparing non-physical stimuli recalled from longterm memory (Paivio, 1975), abstract, symbolic numerical representations (Moyer and Landauer, 1967) and, indeed, also when mental images are generated after processing a verbal description (Denis, 2008). In the current study, this phenomenon was exploited to disentangle the various steps involved in the spatial mental imagery process, aiming to visualise the previously proposed hemispheric specialisation in the PPC.

When comparing clock times represented by more similar angles (hence, a smaller difference or symbolic distance between the two angles), participants respond relatively slower and/or less accurate (Paivio, 1978). We hypothesised that since the distance between the two angles is of no relevance during the mental image formation of the two clocks, it only starts to play a role after the mental images have been formed, and are ready for spatial comparison. We used functional brain imaging to reproduce the previously described frontoparietal network involved in spatial mental imagery. Moreover, by employing parametrically weighed BOLD mapping we were able to top-down separate non-parametric pre-comparison activation from parametrically varying post-comparison activation, thereby revealing different brain activation topologies related to different stages of the MCT. Parametric brain imaging has previously only been employed to investigate motor cortex involvement during mental rotation (Lange et al., 2005; Richter et al., 2000; Seurinck et al., 2011). We expected increased processing demands to result in a difficultyrelated modulation of BOLD-response. Moreover, we hypothesised that these parametric variations would be present especially in those brain regions preferentially occupied with the spatial comparison of the angles, which based on previous evidence, would most likely be the right PPC.

Thus, parametric modelling of MCT-related brain activation was hypothesised to reveal new empirical evidence concerning the underlying neural processes involved in spatial mental imagery. Although Formisano et al. (2002) and Sack et al. (2002, 2005) already proposed a hemispheric asymmetry with regard to parietal involvement during spatial imagery, the evidence presented for such a division of labour was so far based on indirect, observational inferences concerning temporal aspects of brain activation. In the current study, combining the distance effect in mental imagery with concurrent parametric brain imaging allowed us to dissociate between the image formation and spatial angle comparison stages of the spatial mental imagery process from a top-down perspective (Fig. 1). While the spatial relation between the two angles would not be of any influence yet during the mental imagery phase, a smaller difference was hypothesised to result in increased task difficulty from the spatial comparison phase onwards. Based on the previously discussed existing evidence, this parametric modulation related to angle comparison would be expected to emerge more strongly in the right PPC than in its left-hemispheric counterpart. This would provide new direct evidence for a parietal hemispheric specialisation in spatial mental imagery.

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