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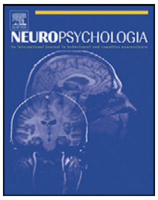

Low and high imagers activate networks differentially in mental rotation

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ABSTRACT

Whether mental visual images play a functional role in cognition or that propositional knowledge is sufficient for supporting performance in imagery tasks is a long-standing debate. It cannot be resolved using behavioural data alone, nor by brain imaging data alone; for example, across fMRI studies mental rotation has been shown to involve virtually all areas of the brain. Alternatively participants might adopt different cognitive strategies. We report behavioural and fMRI data for mental rotation from individuals reporting vivid or poor mental imagery. Groups differed in errors but not response times, and differed in brain activation patterns, suggesting that the groups performed the same task in different ways.

1. Introduction

There is a long-standing debate as to whether mental visual images play a functional role in cognition: one view suggests that propositional knowledge is sufficient for supporting performance in imagery tasks and that mental imagery is an epi-phenomenon (e.g. Pylyshyn, 1981, 2003), the other that imagery plays a key functional role (e.g. Kosslyn, Thompson, & Ganis, 2006; Paivio, 1971). An alternative possibility (Logie, 2011, in press; Zeman et al., 2010) is that a range of cognitive strategies might be available to participants in these tasks, or that individuals differ in their capacity for, or experience of visual images. For example, some participants might use mental imagery to perform tasks that are assumed to require mental imagery, but others might use a propositional strategy for the same task. Both strategies might be available to most healthy adults, and both strategies might generate the typical pattern of results indicating spatiotopic representations either as analog images or as spatial descriptions.

One of the most widely used behavioural paradigms for assessing mental imagery is mental rotation. Typically, the participant is asked to compare a pair of depicted objects rotated in 3-D space relative to one another and to determine whether they depict the same object but in different orientations. The task generates an extremely robust set of behavioural findings, with the time taken to respond to each stimulus pair increasing with the angle of rotation between them (e.g. Corballis, 1982; Shepard & Cooper, 1982; Shepard and Metzler, 1971). This result has been interpreted as suggesting a dynamic imagery process that is similar to the process of physically rotating real objects. When participants are asked to generate a physical hand or arm movement that is compatible with the direction of the mental rotation, then response time is reduced, but when the physical movement is incompatible with the assumed mental rotation then response times are slower (Wexler, Kosslyn, & Berthoz, 1998; Wohlschläger & Wohlschläger, 1998). However, there remains uncertainty as to whether the experience of mental imagery is essential for the typical data patterns in mental rotation experiments.

One means to resolve the general debate about the functional role of visual images and more specifically about the role of mental imagery in mental rotation tasks is to use neuroimaging as a source of converging evidence. That is, assuming we know which brain networks are involved in motor control and mental simulation of motor actions in the implementation of spatial maps and/or the experience of dynamic visual images, then we can investigate which of these areas are activated in mental rotation tasks. This would allow us to conclude which cognitive functions are involved in mental rotation. Numerous studies have examined brain activation with a wide range of mental rotation tasks (reviewed in Zacks, 2008). Unfortunately, as Zacks points out, virtually every area of the brain has been implicated in mental rotation. This variability across studies has been explained in terms of the specific mental rotation tasks employed and the control conditions for the fMRI contrasts. One further possibility is that different participants in the different experiments were performing the same tasks using different cog-

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nitive strategies. These could have arisen from subtle differences in the experimental instructions, or in the selection of participants.

Anderson (1978) noted the logical possibility that for the same set of stimulus inputs and the same set of response outputs, there could be a multitude of intermediate cognitive steps that could be different across different individuals. A corollary of this is that the same task could be performed in different ways by different individuals and the response patterns might be the same or different, but those response patterns would not necessarily allow us to draw conclusions about the nature of the intermediate steps. Logie, Della Sala, Laiacona, Chalmers, and Wynn (1996) showed that in a set of widely used verbal short-term memory paradigms, distinct subgroups of healthy participants spontaneously adopted different strategies and these resulted in different patterns of behavioural results from the established pattern in the literature and from the majority of their 252 participants. This was despite the fact that all participants could perform the task within the normal range. So, healthy adults may have a range of cognitive functions available, but different cognitive functions may be more or less efficient in different individuals, and individuals may deploy different combinations of those functions for performing the same task, and may even generate similar patterns of behavioural data in doing so (for a recent discussion see Logie, in press). Therefore, aggregate data across a group of participants in any one experiment may result in misleading conclusions as to the nature of the underlying cognition that generated those data patterns. In relation to the current topic, it has long been known that people vary in the extent to which they report using mental imagery (e.g. Marks, 1973, 1995), although these subjective reports do not always correlate with performance on mental imagery tasks (e.g. Dean & Morris, 2003; McKelvie, 1995). This suggests that either people have poor insight into their mental operations when rating them on mental imagery scales, or that people with poor mental imagery can perform mental imagery tasks, but by using some alternative, non-imagery strategy.

In a more recent study on visual imagery, Zeman et al. (2010) described a single case of an individual, MX, who reported suddenly losing the ability to generate visual images having experienced very vivid visual imagery throughout his life. He performed normally on a wide range of mental imagery and other cognitive tasks. A structural MRI revealed no obvious abnormalities. In fMRI his activation pattern in a perception task was identical to that of age and occupation matched controls. However, in a condition requiring generation of mental images, the activation patterns for MX and the controls were strikingly different. The neuroimaging findings were consistent with the idea that people might use different cognitive strategies, as reflected by the different activation patterns, to perform the same task. This was in the absence of any clear behavioural signatures of these differences in the vast majority of the tests used. The one exception was mental rotation, which he could perform with a high level of accuracy, but without showing the typical relationship between angle of rotation and response times. Specifically, there was no change in his response times across the angles between 20° and 160°. When debriefed, MX maintained that he was performing the task by visual perceptual comparisons between specific elements of the two depicted figures.

The results from MX together with the studies described earlier hint at the hypothesis that participants may use different strategies, capitalising on different brain networks to perform the same mental imagery task. However, MX is a single case study with an acquired impairment of visual imagery and the previously reported studies on healthy adults reviewed by Zacks (2008) do not provide a direct test of this hypothesis. In particular, studies of mental rotation in fMRI tend to treat all participants as a homogeneous group, without considering possible differences in how different individuals perform the task. We investigated this hypothesis directly in the study reported here. Our approach involved first exploring the extent to which healthy young adults report using mental imagery in their daily life. We then selected individuals who reported having little or no experience of imagery, and others who reported experiencing very vivid mental images, and asked these two groups (low imagery-high imagery) to perform a mental imagery task in an fMRI study. We chose mental rotation as the imagery task in part because it was the one task performed differently by MX in the Zeman et al. (2010) study, but also because there is a very large literature on the task both in behavioural (see review in Richardson, 1999) and in neuroimaging studies (Zacks, 2008). We aim to address the apparent inconsistency between self-reported experience of mental imagery and actual performance by exploring the brain activation patterns of self-reported high and low imagers while they are performing a mental imagery task. If indeed low imagers and high imagers are achieving the same behavioural performance using different underlying strategies, we would expect these differences to be reflected in the associated brain activation. If this is observed, then it would suggest that differences in brain activation patterns found across some previous studies for very similar mental imagery tasks might be explained in terms of averaging across individuals who are performing the same task in different ways. In turn, this would offer an argument suggesting that mental imagery tasks can be supported by different neuroanatomical networks in different individuals.

In sum, one of our aims was to contribute to the debate about whether the experience of mental imagery is necessary or functional in performing imagery tasks. A second aim was to investigate whether there are differential brain activation patterns in different individuals for the same task in an attempt to gain new insight into the debate about which brain areas support mental rotation (Zacks, 2008).

2. Method

2.1. Participants

Twenty-one right handed healthy participants with normal vision aged between 20 and 35 years took part in this study. They were selected from 486 participants who had completed the Vividness of Visual Imagery Questionnaire (VVIQ – Marks, 1973, 1995). Although the VVIQ tends not to correlate with a range of objective tests of mental imagery (Dean & Morris, 2003; McKelvie, 1995), patient MX (Zeman et al., 2010) scored very poorly on this test, and it appears to be a reliable measure of subjective experience of imagery. In addition, Cui, Jeter, Yang, Montague, and Eagleman (2007) have shown that individual variation on the VVIQ correlates with individual variation in activation of primary visual cortex while participants are performing an imagery task in fMRI. Participants for inclusion comprised 11 high imagery individuals (8 females) who had VVIQ scores greater than 4 (mean 4.37, SD 0.31) and 10 low imagery individuals (6 females) who had VVIQ scores lower than 3 (mean 2.48, SD 0.49).

2.2. MRI parameters

All participants were scanned at the University of Edinburgh Brain Research Imaging Centre (http://www.sbirc.ed.ac.uk/) on the same 1.5 T GE Signa MRI scanner. After sagittal localization images, 27 contiguous axial GE-EPI images were obtained parallel to the intercommissural plane ($T2^*$-weighted single-shot EPI, TR = 2 s, TE = 40 ms, flip angle = 90°, slice thickness 1.2 mm, FOV = 240 mm, matrix 64×64).

Stimuli were presented following a block design alternating periods of mental rotation, control condition and rest (see below Experiment) during two sessions of 7 min 20 (four dummy volumes followed by 216 volumes). In addition to the EPI data, a high resolution T1 3D-IRP (inversion recovery pulse) was obtained (slice thickness 1.2 mm, FOV 24, matrix 192×192) at the end of the scanning session.

2.3. Behavioural task and procedure

The mental rotation task used materials originally developed by Shepard and Metzler (1971). These involve pictures of 3-D objects comprising 10 cubes joined in different configurations.[1] Pairs of objects were presented on a computer screen

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[1] Materials were obtained in digitized form from: http://titan.cog.brown.edu:8080/TarrLab/stimuli/novel-objects/shepard.zip/view.