

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.

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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, Laiacina, 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

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

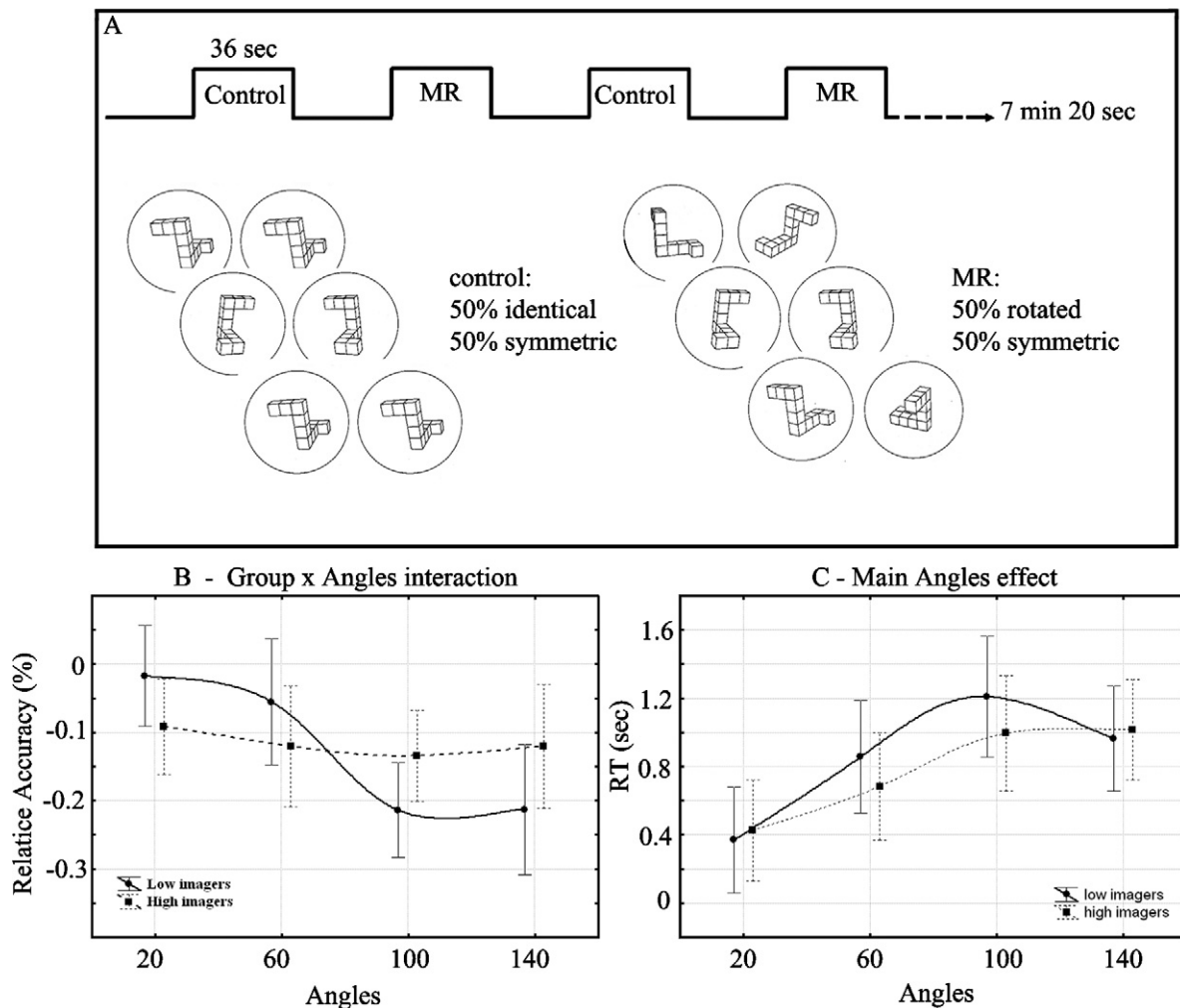


Fig. 1. Illustration of the fMRI paradigm (A) and corresponding behavioural performance: mean relative accuracy (panel B) and the mean relative correct response times (panel C) across angles of rotation for high and low imagery groups. Dashed lines represent 95% confidence intervals.

with one item rotated within three-dimensional space relative to the other. In half of the pairs, the objects were identical, in the other half the objects were mirror images of one another. The angle of rotation was 0°, 20°, 60°, 100° or 140°. For each pair the participant was asked to decide whether the two objects were the same or mirror images by pressing a button with the right index for same and a second button with the right middle finger for different. Stimuli were presented in blocks of 36 s (18 MRI volumes) alternating with rest periods. There were two sets of blocks for scanning, one set for mental rotation (20°, 60°, 100° or 140° conditions), and one set for control conditions (0° with identical objects and 0° with mirror images – Fig. 1A). The number of stimuli in each block was participant dependent, i.e. stimuli were displayed until response (or up to 8 s) and therefore the total number of stimuli varied from participant to participant, ranging from 119 to 276. However, the groups did not differ in the mean number of trials completed (low imagers 185.1 ± 47.4 trials; high imagers 192.9 ± 42.51 trials; $t(19) = 0.39$, $p = 0.69$).

2.4. Behavioural analyses and results

For each participant, a Median Absolute Deviation estimator based on correct RTs was used to remove outlier trials and the mean RT of correct responses and mean accuracy were subsequently computed. An initial analysis comparing the groups at 0°, showed that high and low imagers did not differ on accuracy or RT ($F < 1$ in both cases). We next examined accuracy and RT data for the other conditions (20°, 60°, 100° and 140°) correcting for intra-subject baseline. That is, we analysed the difference between participant performance at each of the rotation angles and participant performance at the baseline of 0°. This had the effect of removing the influence of inter-participant differences in baseline performance. The resulting relative accuracy and RT data are illustrated in Fig. 1B and C respectively. These were analysed using ANOVA with group (high/low imagers) and conditions (20°, 60°, 100° and 140°) as independent variables.

Relative RT analyses revealed the typical pattern of an increase of processing time with the rotation angle ($F(3,57) = 16.17$, $p < .0001$). Pairwise post-hoc comparisons using Newman–Keuls tests showed significant increases between 20° and 60° (+371 ms, $p < .001$), and from 60° to 100° (+332 ms, $p < .01$). No differences were observed between 100° and 140° (–110 ms, $p > .1$). There was no main group effect ($F(1,19) = .17$, $p > .1$) or interaction ($F(3,57) = .86$, $p > .1$). Analysis of relative accuracy showed a significant decrease with rotation angle ($F(3,57) = 8.27$, $p < .0002$), and the post-hoc comparisons showed a significant change between 60° and 100°. Notably, a significant interaction group by condition was observed ($F(3,57) = 5.1$, $p < .005$) such that only low imagers showed a decrease of relative performance between 60° and 100° (Newman–Keuls test –0.16%, $p < .005$) whereas high imagers showed no changes in their relative performance.

2.5. fMRI analysis

Preprocessing and statistical analyses were performed using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). For each participant, data were corrected for acquisition delay between slices, realigned to the first image of the first session, normalized onto the MNI template provided in SPM5 (resampling at 2 mm³ using a 4th degree spline interpolation) and smoothed with a 8 mm FWHM Gaussian kernel. Data at the first level of analysis were modelled as a block design with five regressors per session: control condition and a parametric regressor related to the number of trials per block in the control condition, mental rotation condition (all 20°, 60°, 100° and 140° pooled together) and a parametric regressor related to the number of trials per block, and the constant term. The six motion correction parameters were also entered as regressors across both sessions. Two contrasts per participant were then computed pooling the control condition regressor parameters and the mental rotation regressor parameters from each session. At the second level, an ANOVA on those contrasts with group (high vs. low imagers), condition (control vs. mental rotation), and interaction group by condition and

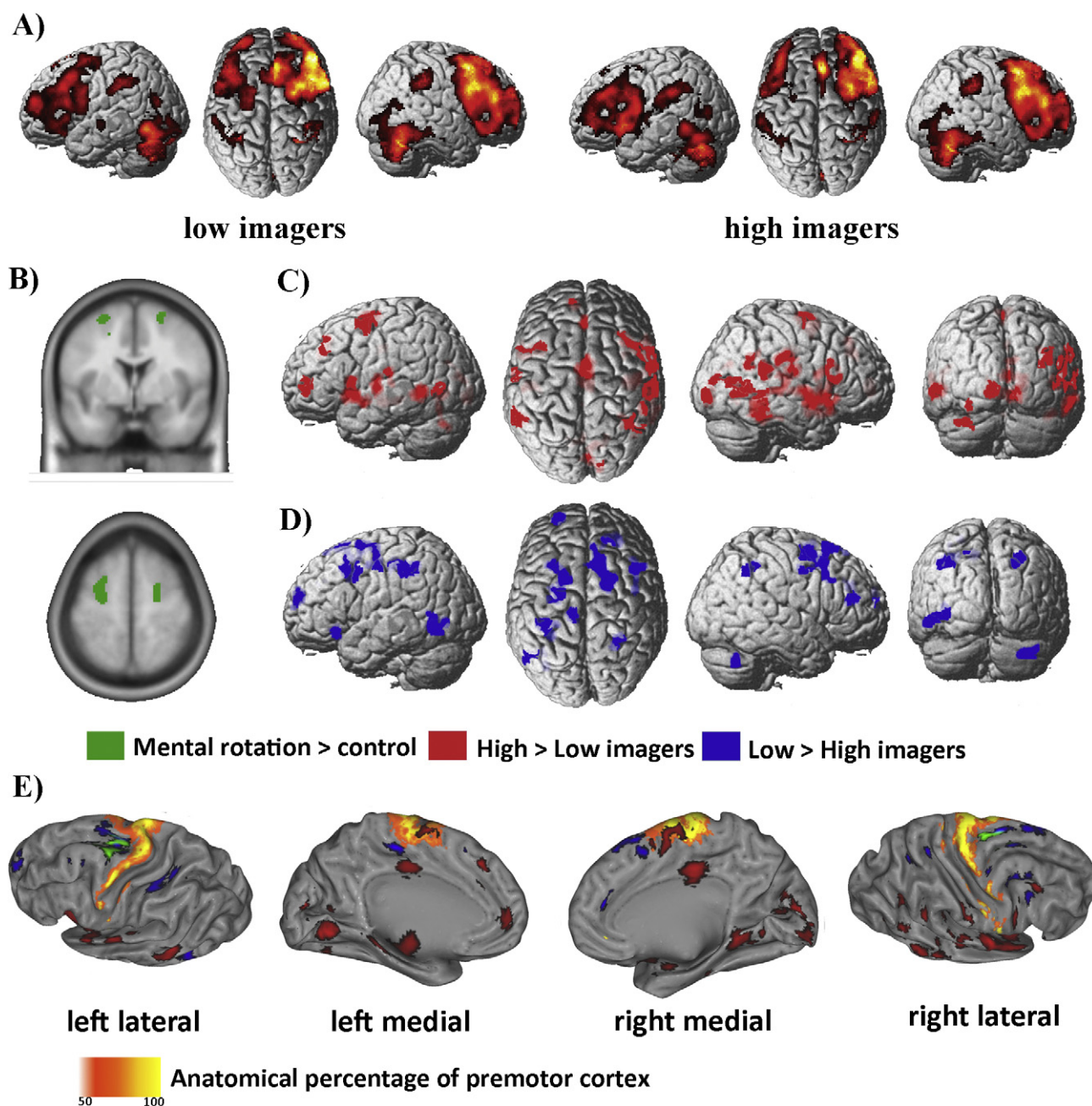


Fig. 2. Areas activated by a mental rotation task relative to rest in low and high imagers are displayed in A. In B, is illustrated the main effect of the task (mental rotation > control). In C and D, the main group effects are presented. In E, main effects are presented all together showing where task and group effects are located in relation to each other and in relation to the premotor cortex defined as a probabilistic location. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

participants as factors was set up. Importantly, because of a modulation by the number of trials was introduced at the first level of analysis, differences between groups cannot be explained by a difference in the total number of trials and/or motor responses. Results are reported at a threshold $\alpha = 5\%$ cluster-wise corrected for multiple comparisons using a false discovery rate (FDR) procedure (Chumbley & Friston, 2009). This first analysis allowed us to define six regions of interest (ROI) used to investigate a possible relationship between brain responses and experimental conditions.

In a second analysis, fMRI data from each participant were re-analysed using an event related model with seven regressors per session: all five original conditions (0° , 20° , 60° , 100° and 140°), an additional regressor coding for wrong answers and the constant term. Again, the six motion correction parameters were entered as regressors across both sessions. Beta parameters for each condition of interest from each ROI were extracted and the percentage of signal change computed. At this stage, a MANOVA with the group, hemispheres, ROI, and conditions was carried out on the relative BOLD percentage of signal change (i.e. the BOLD responses observed for 20° , 60° , 100° and 140° minus the BOLD response observed for the control condition). Similarly, correlation analyses were conducted for each ROI between

the relative BOLD response and the relative RTs and performances. p -values were obtained using a percentile bootstrap method and corrected for multiple comparisons (i.e. testing correlations on several ROIs). Note that in the first analysis, the design matrices coded the control and mental rotation blocks and, at the group level, group, condition, and interaction effects were tested. In the second analysis, events for control and all mental rotation trials were modelled and, at the group level, differences between BOLD responses per angle and correlations between the mental rotation trials (minus control) and behaviour were tested, i.e. tests were performed on different parameters than the one used to create the ROI, avoiding circularity and statistical power issues (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009).

2.6. fMRI results

Fig. 2 illustrates the patterns of activations from the planned contrast analyses. The ANOVA revealed a main group effect and a main task effect without interaction. Both groups activated a large network of areas including the ventral visual cortex, inferior parietal areas, secondary motor areas (premotor cortex

Table 1

Coordinates of the significant voxel clusters across contrasts. See text for explanation.

Contrast	T value	p value	k	Peak coordinate		
Mental rotation > control	5.39	<.001	278	–26	0	62
	3.96	.02	128	26	0	64
Control > mental rotation	5.27	.005	173	–6	–80	18
	5.08	.004	181	16	–78	22
	4.99	.034	113	58	–30	–8
High imagers > low imagers	9.31	<.001	627	–40	10	–4
	9.13	.001	238	42	–18	20
	8.62	.001	231	4	–86	12
	8.61	<.001	356	–10	–64	–4
	8.42	<.001	311	56	–28	30
	7.75	<.001	1219	60	0	–8
	7.60	<.001	416	60	–46	–16
	7.30	.001	245	26	14	–18
	7.08	<.001	346	0	–4	66
	6.95	<.001	257	6	–18	34
	6.89	.001	233	18	–42	–6
	6.88	.001	247	–52	–50	0
	6.79	<.001	396	–2	–22	–16
	6.33	.006	167	36	–54	22
Low imagers > high imagers	9.49	<.001	464	16	2	58
	5.06	.001	225	–20	10	44
	7.30	.007	158	40	–64	–36
	7.07	<.001	264	–32	–42	46
	4.76	<.001	267	–44	–56	–6
	4.62	.001	213	24	38	18
	5.76	.002	208	42	–6	44
	5.45	<.001	257	–20	6	68

p value are the FDR cluster corrected p values, k stands for the size of the clusters, the peak coordinate stands for the locus of highest T value within each cluster.

and supplementary motor area), the dorsolateral prefrontal cortex and insulae (Fig. 2A).

The main task effect revealed stronger activation for the mental rotation conditions than the control conditions over the supplementary motor area (SMA – Fig. 2B) whereas opposite effects (control conditions > mental rotation conditions) were observed over the visual cortex (right middle temporal gyrus and the left and right cuneus – see Table 1 for details).

The main group effect revealed that high imagers had stronger activations than low imagers over the left and right cingulate gyri, left and right superior frontal gyri, left and right anterior superior temporal gyri/insulae, left and right middle temporal gyri, right inferior frontal gyrus, right parahippocampal gyrus, right cuneus, left midbrain and left lingual gyrus (Fig. 2C). By contrast, low imagers showed stronger activations than high imagers over the right tuber (cerebellum), left middle occipital/inferior temporal gyri, left and right inferior parietal gyri, superior frontal gyri, and middle frontal gyri (Fig. 2D – see Table 1 for details).

2.7. Analysis of motor related activations

The mental rotation conditions elicited more activation than the control conditions in the left and right inferior SMA, and located above these clusters we also observed stronger activations for low imagers than high imagers. By contrast, premotor cortex (medially) was more activated in high imagers than the low imagers (Fig. 2E). The MANOVA conducted on the relative BOLD signal did not reveal any differences between groups, supporting the absence of an interaction in the whole brain analysis (i.e. difference between groups were in the overall level of activation). The only effects observed here on the relative BOLD signal were (i) a main ROI effect ($F(2,18) = 19.7, p < .0001$), (ii) a hemisphere \times ROI interaction ($F(2,18) = 8.25, p < .002$) and (iii) a hemisphere \times angle interaction ($F(3,17) = 3.36, p < .05$). This latter interaction is illustrated in Fig. 3. It showed that in the left hemispheric regions, the BOLD signal was significantly different between the 20° condition and the 60° and 100° conditions ($p_{\max} = .035$). In the right hemispheric regions, the BOLD signal was significantly different between the 20° condition and the 60° conditions ($p < .05$), and then between the 60° conditions and other conditions (for 100°, $p = .06$ and for 140°, $p < .03$). No significant correlations were observed between the relative BOLD signal and behavioural data.

3. Discussion

The behavioural data indicated that both high imagers and low imagers showed the typical increase in response time with increase

in angle of rotation in a mental rotation task. However, there was a clear contrast between groups in the accuracy data, with low imagers achieving poorer accuracy for the larger angles compared with the smaller angles of rotation. High imagers were consistently accurate for all angles of rotation. The response time data suggest that strategies used by both groups appear to involve some form of mental rotation, but the accuracy data suggest that the groups are using different mental rotation strategies, and that the strategy deployed by the low imagery group is prone to error.

One possible account for the group difference in accuracy could be that the task was more difficult for the low imagers than the high imagers. Difficulty is of course not easy to define, and a task may be difficult because participants are using a non-optimal strategy (for a discussion see Logie et al., 2004). However, overall task demand was equated across groups by allowing participants as long as they required to complete each trial. So the number of trials completed was determined by how long participants took to make their decision and produce a response. If the task had been differentially difficult for the low imagers, we would have expected this group to take longer to make their decisions and so to complete fewer trials than the high imager group. However, low imagers completed on average the same number of trials as high imagers and had similar mean response times. The difference appeared in the interaction for accuracy between group and angle of rotation, suggesting that whatever strategy was being deployed by the low imagers, it resulted in errors for the higher angles.

The activation patterns shown in both groups of participants (high and low imagers) confirmed that mental rotation as assessed by Shepard–Metzler figures include a discrete but distributed neural network which encompasses the ventral visual cortex, superior and inferior parietal areas, secondary motor areas (premotor cortex and supplementary motor area), the dorsolateral prefrontal cortex and the insulae (see Ecker, Brammer, & Williams, 2006; Milivojevic, Hamm, & Corballis, 2008; Zacks, 2008). Mental rotation experiments typically consider the role of motor related areas, and it has been hypothesized that these areas reflect motor simulation (Leek & Johnston, 2009; Zacks, 2008). More specifically, Leek and Johnston (2009) argue that the SMA involves the computation of spatial vector transformations, that is, the computation of mappings between spatial locations. This offers an explicit account for SMA involvement in tasks such as mental rotation, as well as in the planning and control of actions. However, a common confounding factor when analysing activity in motor related areas arises from the participant's manual responses. Here, although participants responded with a button press, the number of responses varied across participants, allowing us to regress out the motor component in each participant and therefore premotor and SMA activations reflected some aspect of the mental rotation independently of the motor response. Furthermore, (i) premotor and SMA cortices show stronger activity for mental rotation which involved mental rotation, object matching and decision making than for the control stimuli (0°) which involved only the latter two operations and (ii) analyses of responses to various angles show significant BOLD variations without correlating with behavioural performance. These two results thus confirm that the SMA and the premotor cortex are involved in computing rotations (maybe through motor simulation) but not in object matching and decision making.

From animal work (e.g. Mushiaki, Masahiko, & Tanji, 1991), clinical observations (e.g. Boccardi, Della Sala, Motto, & Spinnler, 2002), experimental studies (e.g. Cunnington, Bradshaw, & Iansek, 1996) and neuroimaging studies (e.g., Frith, Friston, Liddle, & Frackowiak, 1991; Toni, Schluter, Josephs, Friston, & Passingham, 1999) the accrued evidence suggests that the medial system, centred on the SMA, is responsible for internally-generated actions whereas the lateral system, centred on the pre-motor cortex is considered to be responsible for 'responsive movements', which are gen-

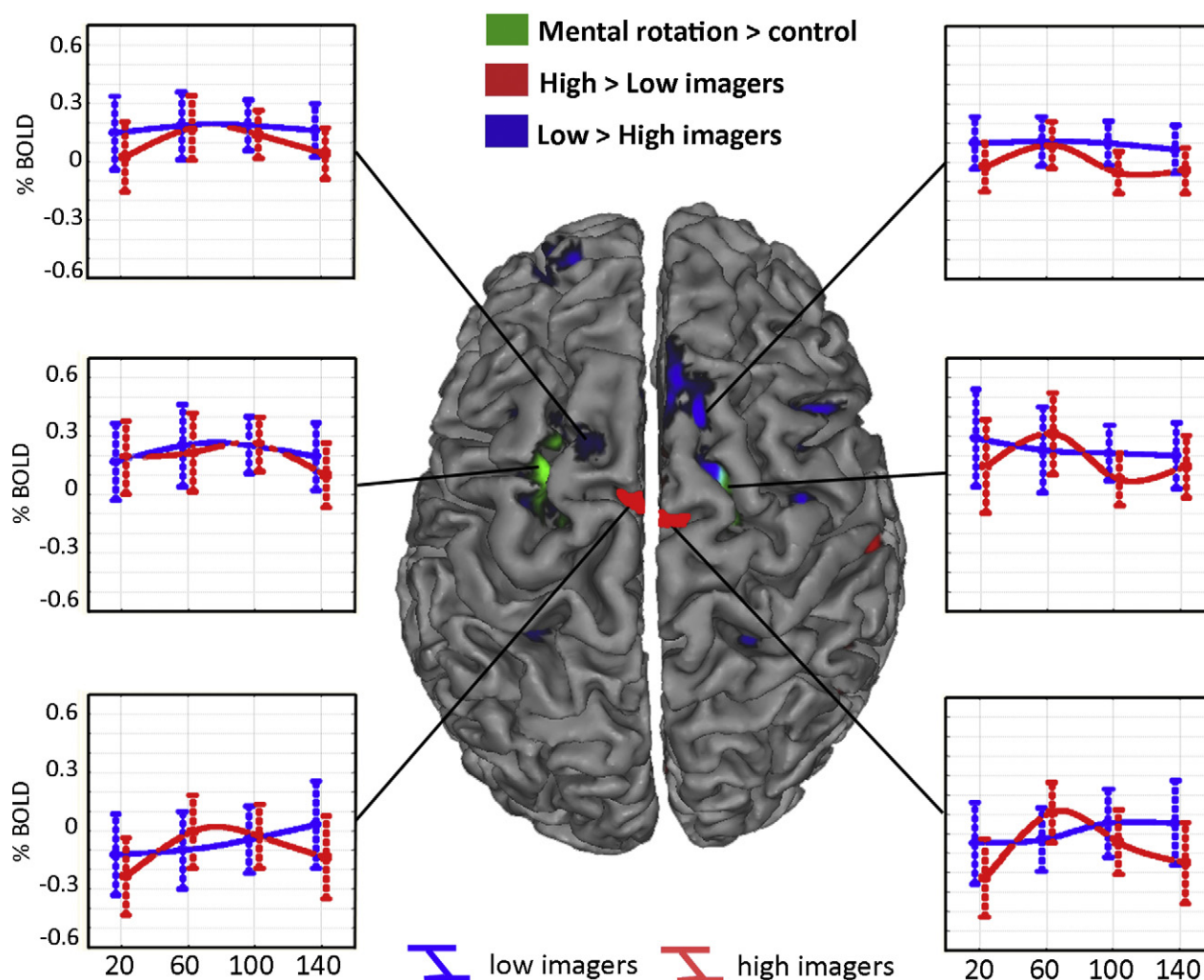


Fig. 3. Illustration of the pattern of activity (percentage of BOLD variation) for each rotation angle (20°, 60°, 100° and 140°) relative to the control conditions (0°) for low (blue) and high (red) imagers. Dashed lines represent 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

erated in response to external stimuli (Della Sala & Marchetti, 2005; Gazzaniga, Ivry, & Mangun, 1998, chap. 10; Goldberg, 1985; Passingham, 1993, chap. 7). In our own data over these motor areas, high imagers showed more activation than low imagers in their premotor cortex while low imagers showed greater activation in their SMA than did the high imagers. Therefore, the brain imaging as well as the behavioural data are consistent with the possible use of different strategies by different participants to comply with the demands of the rotation task. Other differences in activation patterns while performing mental rotation tasks have also been observed in previous studies. For instance, Ecker et al. (2006) noted changes in connectivity within the neuronal network thought to be involved in mental rotation according to the level of task demand. Gender differences in the cortical activation patterns have also been reported (Christova, Lewis, Tagaris, Ugurbil, & Georgopoulos, 2008; Jordan, Wustenberg, Heinze, Peters, & Jancke, 2002). Of special interest, Wraga, Shepard, Church, Inati, and Kosslyn (2005) showed that premotor cortex activity was related to object rotations while SMA activity was related to rotations of the self about an object. These are two acceptable strategies to perform our task which may reflect computational differences between our high and low imagers. Therefore, given the difference in the pattern of brain activation that we observed, one possible hypothesis is that the high imagers were performing the task by mentally simulating the

rotation of the object in view, whereas low imagers were using a more self-referential strategy to perform the task that was prone to error because it did not refer to an adequate mental representation of the precise visual details (i.e. depicted angle of rotation) of the external stimuli. This interpretation is also supported by the fact that high imagers showed stronger activity over the visual cortex (imagery of the object rotating) whereas low imagers showed stronger activity in the fronto-parietal network involved in visuo-spatial processing rather than rotation per se (Milivojevic et al., 2008). This further suggests that when low imagers report having poor experience of mental imagery they might be referring to the experience of having poor mental images of external objects, even if they can imagine their own actions.

As noted earlier, there is an ongoing debate between researchers who argue that mental imagery reflects functional operations in the brain (e.g. Kosslyn, 1994; Kosslyn, Thompson, & Ganis, 2006) and those who argue that all behavioural data indicating use of mental imagery could be interpreted as reflecting the operation of a propositional system for describing analogue information about the world (e.g. Pylyshyn, 1981, 2003). The combination of differences in the behavioural data (notably the error data) and in brain activation patterns linked systematically with groups of people who report differential use of visual imagery offers more objective evidence to suggest that the debate might be more about how a task is

performed by different people than about fundamentally different models of cognitive function.

These issues are also of very substantial practical relevance given recent debates on uses of fMRI other than diagnostic or scientific, for instance in courts of law (see e.g. debate <http://www.sinapse.ac.uk/media/events/ias.asp>). If an individual's activation pattern departs from that found for other individuals carrying out the same task, how can we be sure that the observed pattern is indeed abnormal, and not due to some peculiarity of the strategy used by the person under examination? In the case of mental rotation, our results suggest that a low imager performing a task that is assumed to involve visual imagery could show an activation pattern different from the "norms" collected on the general population, and still be "normal". Our results also add to the body of evidence that different individuals may use different combinations of cognitive functions (and therefore most likely show different brain activation patterns) to perform the same tasks.

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References

- Anderson, J. R. (1978). Arguments concerning representations for mental imagery. *Psychological Review*, 85, 249–277.
- Boccardi, E., Della Sala, S., Motto, C., & Spinnler, H. (2002). Utilisation behaviour consequent to bilateral SMA softening. *Cortex*, 38, 289–308.
- Chumbley, J., & Friston, K. J. (2009). False discovery rate revised: FDR and topological inference using Gaussian random fields. *Neuroimage*, 44, 62–70.
- Corballis, M. C. (1982). Mental rotation: Anatomy of a paradigm. In M. Potegal (Ed.), *Spatial abilities: Developmental and physiological foundations* (pp. 173–198). New York: Academic Press.
- Christova, P. S., Lewis, S. M., Tagaris, G. A., Ugurbil, K., & Georgopoulos, A. P. (2008). A voxel-by-voxel parametric fMRI study of motor mental rotation: Hemispheric specialization and gender differences in neural processing efficiency. *Exp. Brain Res.*, 189, 79–90.
- Cui, X., Jeter, C. B., Yang, D., Montague, P. R., & Eagleman, D. M. (2007). Vividness of mental imagery: Individual variability can be measured objectively. *Vision Research*, 47, 474–478.
- Cunnington, R., Bradshaw, J. L., & Iansek, R. (1996). The role of the supplementary motor area in the control of voluntary movement. *Human Movement Science*, 15, 627–647.
- Dean, G. M., & Morris, P. E. (2003). The relationship between self reports of imagery and spatial ability. *British Journal of Psychology*, 94, 245–273.
- Della Sala, S., & Marchetti, C. (2005). The Anarchic Hand syndrome. In H.-J. Freund, M. Jeannerod, M. Hallett, & R. Leiguarda (Eds.), *Higher-order motor disorders: From neuroanatomy and neurobiology to clinical neurology* (pp. 293–301). New York: Oxford University Press.
- Ecker, C., Brammer, M. J., & Williams, S. C. (2006). Combining path analysis with time-resolved functional magnetic resonance imaging: The neurocognitive network underlying mental rotation. *Journal of Cognitive Neuroscience*, 20, 1003–1020.
- Frith, C. D., Friston, K., Liddle, P. F., & Frackowiak, R. S. J. (1991). Willed action and the prefrontal cortex in man: A study with PET. In *Proceedings of the Royal Society, vol. B244* London, (pp. 241–246).
- Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (1998). *Cognitive neuroscience. The biology of the mind*. New York: Norton.
- Goldberg, G. (1985). Supplementary motor area structure and function: Review and hypothesis. *Behavioral and Brain Sciences*, 8, 567–616.
- Kosslyn, S. M. (1994). *Image and brain: The resolution of the imagery debate*. Cambridge: MIT Press.
- Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The case for mental imagery*. New York: Oxford University Press.
- Kriegeskorte, N., Simmons, W. K., Bellgowan, P. S. F., & Baker, C. I. (2009). Circular analysis in systems neuroscience: The danger of double dipping. *Nature Neuroscience*, 12, 535–540.
- Jordan, K., Wustenberg, T., Heinze, H. J., Peters, M., & Jancke, L. (2002). Women and men exhibit different cortical activation patterns during mental rotation tasks. *Neuropsychologia*, 40, 2397–2408.
- Leek, E. C., & Johnston, S. J. (2009). Functional specialization in the supplementary motor complex. *Nature Reviews Neuroscience*, 10, 78.
- Logie, R. H. (2011). The visual and the spatial of a multicomponent working memory. In A. Vandierendonck, & A. Szmalec (Eds.), *Spatial working memory* (pp. 19–45). Hove: Psychology Press.
- Logie, R. H. (in press). The functional organisation and the capacity limits of working memory. *Current Directions in Psychological Science*.
- Logie, R. H., Della Sala, S., Laiacona, M., Chalmers, P., & Wynn, V. (1996). Group aggregates and individual reliability: The case of verbal short-term memory. *Memory and Cognition*, 24, 305–321.
- Logie, R. H., Cocchini, G., Della Sala, S., & Baddeley, A. D. (2004). Is there a specific executive capacity for dual task co-ordination? Evidence from Alzheimer's Disease. *Neuropsychology*, 18, 504–513.
- Marks, D. F. (1973). Visual imagery differences in the recall of pictures. *British Journal of Psychology*, 64, 17–24.
- Marks, D. F. (1995). New directions for mental imagery research. *Journal of Mental Imagery*, 19, 153–167.
- McKelvie, S. J. (1995). The VVIQ as a psychometric test of individual differences in visual imagery vividness: A critical quantitative review and a plea for direction. *Journal of Mental Imagery*, 3–4, 1–106.
- Milivojevic, B., Hamm, J. P., & Corballis, M. C. (2008). Functional neuroanatomy of mental rotation. *Journal of Cognitive Neuroscience*, 21, 945–959.
- Mushiake, H., Masahiko, I., & Tanji, J. (1991). Neuronal activity in the primate premotor, supplementary, and precentral motor cortex during visually guided and internally determined sequential movements. *Journal of Neurophysiology*, 66, 705–718.
- Paivio, A. (1971). *Imagery and Verbal Processes*. New York: Holt, Rinehart and Winston.
- Passingham, R. (1993). *The frontal lobes and voluntary action*. New York: Oxford University Press.
- Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, 88, 16–45.
- Pylyshyn, Z. W. (2003). Return of the mental image: Are there really pictures in the brain? *Trends in Cognitive Sciences*, 7, 113–118.
- Richardson, J. T. E. (1999). *Imagery*. Hove: Psychology Press.
- Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge: MIT Press.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.
- Toni, I., Schluter, N., Josephs, O., Friston, K., & Passingham, R. E. (1999). Signal-, set- and movement-related activity in the human brain: An event-related fMRI study. *Cerebral Cortex*, 9, 35–49.
- Wexler, M., Kosslyn, S. M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition*, 68, 77–94.
- Wohlschläger, A., & Wohlschläger, A. (1998). Mental and manual rotation. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 397–412.
- Wraga, M., Shepard, J. M., Church, J. A., Inati, S., & Kosslyn, S. M. (2005). Imagined rotations of self versus objects: An fMRI study. *Neuropsychologia*, 43, 1351–1361.
- Zacks, J. M. (2008). Neuroimaging studies of mental rotation: A meta analysis and review. *Journal of Cognitive Neuroscience*, 20, 1–19.
- Zeman, A., Della Sala, S., Torrens, L., Gountouna, E., McGonigle, D., & Logie, R. H. (2010). Loss of imagery phenomenology with intact visual imagery performance. *Neuropsychologia*, 48, 145–155.