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Last updated
11 /4 / 2005



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Submit to: Neuropsychologia??

Functional specialization in human premotor cortex: Visuo-spatial transformation in pre-SMA during 2D image transformation

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RUNNING HEAD: PREMOTOR CORTEX AND IMAGE TRANSFORMATION

KEY WORDS: PREMOTOR CORTEX, PRE-SMA, MENTAL ROTATION, OBJECT RECOGNITION, VECTOR TRANSFORMATION

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Email: e.c.leek@bangor.ac.uk. The research reported in this paper was supported by project grant 5/S15963 from the Biotechnology and Biological Sciences Research Council (BBSRC), UK.

ABSTRACT

Premotor cortex has traditionally been associated with the planning and control of visually guided movements. Here we report converging evidence from psychometric, functional magnetic resonance imaging (fMRI) and eye tracking studies that provide further constraints on hypotheses about functional sub-divisions within the medial premotor area. A recognition memory paradigm was used to measure response times (RTs) to identify upright and misoriented novel objects from two stimulus sets. One stimulus set elicited a pattern of RTs consistent with the operation of an image transformation process during recognition. The other stimulus set showed an orientation-invariant RT pattern. A comparison of the patterns of cortical activation between conditions revealed a network of associated neural regions consistent with previous studies. This network included the left superior parietal (BA7) and dorsolateral prefrontal cortex (BA10/46), as well as bilateral superior parietal cortex (BA7) and fusiform gyri (BA19). The results also showed activation in the left anterior supplementary motor area (pre-SMA). These data suggest that pre-SMA also contributes to image transformation during recognition. It is proposed that the functional role of pre-SMA is to facilitate in the computation of vector transformations that can be used support different cognitive tasks including movement planning, visuo-motor control and image normalisation.

Word count: 200

There has been a longstanding association between the premotor cortex (BA6) and the planning, preparation and control of motor behaviour [5, 17, 42]. Recent evidence has also revealed apparent functional sub-divisions within this cortical area [1-6, 9].

Distinctions have been made between visuo-motor functions of the dorsal- (PMd) and ventral (PMv) lateral premotor cortex, as well as between distinct rostral and caudal areas of PMd and PMv [6]. It has been suggested that these lateral pre-motor areas contain two partially independent networks which both operate during the planning and control of prehensile movement [10-11]. Here we focus on the medial region of the premotor cortex – traditionally known as the supplementary motor area (SMA). There is now a growing body of evidence from both animal and human studies for a functional distinction between caudal (SMA-proper) and rostral medial areas (pre-SMA) [2, 5, 7-9, 13].

Anatomically, SMA-proper projects to PMd, primary motor cortex (M1) and the spinal cord [7, 12-14]. Pre-SMA has cortical connections with dorsolateral prefrontal cortex (DLPFC) and receives ventral pathway input via the anterior inferotemporal cortex (AIT) [13-15, 18]. The oculo-motor area of BA8 - the supplementary eye field (SEF) - is both lateral and rostral to pre-SMA [16]. While much is understood about the neural connectivity involving pre-SMA and SMA-proper, a precise functional characterization of these areas remains controversial [7]. It has been proposed that pre-SMA plays a role in the selection and preparation for specific movements [17]. However, while some studies have suggested a link between pre-SMA and the learning of sequential movement [19], it has recently been shown that pre-SMA can be active in tasks requiring visuo-motor associations irrespective of whether those tasks also involve sequential movements [20]. There are also other reasons to suppose that the functional role of medial premotor

areas, and pre-SMA in particular, is more computationally abstract than generally assumed [4]. Pre-SMA has cortical connections with dorsolateral prefrontal cortex (DLPFC) and receives ventral pathway input via the anterior inferotemporal cortex (AIT) [13-15, 18]. This anatomical connectivity is consistent with a role beyond movement preparation and planning.

Some evidence has shown that sensory-motor association in pre-SMA is both modality-, and effector-, independent, and not related to response selection or preparation during conditional motor behaviour [4, 21, 22]. Other data have shown that pre-SMA activation is also found in tasks requiring shifts of attention among visual features of objects [23, 24]. Of particular relevance to the current study are reports of medial premotor activation during tasks such as mental rotation that involve visuo-spatial transformation but no related motor response [25, 26, 28-31, 38, 41, 45]. These data motivate two theoretical issues. First, it remains unclear whether the observation of pre-SMA activation in classic mental rotation tasks reflects a more general role for medial premotor cortex in visuo-spatial transformation. Second, if this is the case then it becomes relevant to consider how such a functional role for pre-SMA in spatial normalisation can be integrated with other animal and human studies showing medial premotor involvement in motor behaviour [1-6, 9, 17, 44].

It is widely assumed that the spatial transformation component of classic mental rotation task performance is mediated by the parietal cortex [25, 33, 40] - activation in both the superior (SPL) and inferior (IPL) parietal areas in the region of the intra-parietal sulcus (IPS) have been frequently reported in studies of mental rotation and misoriented object recognition [25-38, 40]. Lesions of parietal cortex have also been associated with

deficits in misoriented object recognition in brain-damaged human subjects [42], and following transcranial magnetic stimulation (TMS) [43]. In this context, the potential contribution of medial premotor areas in the computation of visuo-spatial transformations is of considerable theoretical relevance. One limitation of current data on this issue is that premotor-related activation has typically been measured in tasks requiring mirror-image or recognition judgements about depth rotated forms [REFS]. Such manipulations confound image normalisation with effects related to perspective deformation and the occlusion of shape features [Vanrie]. In addition, it is unclear to what extent activation of medial premotor areas is related to differences in eye movement patterns between upright and rotated forms [Just and Carpenter, 1988]. This is particularly relevant given the anatomical proximity of rostral premotor areas to the frontal and supplementary eye fields [Paus], and the fact that many previous imaging studies have used the classic mental rotation task in which subjects make judgments about two simultaneously presented objects. The dual presentation of stimuli is likely to increase eye movements and the requirement for shifts of attention [Just and Carpenter, 1988] – both of which have previously been associated with parietal and frontal activation [Anderson et al., 1994; Corbetta et al., 1993].

The aim of the current study is to examine the generality of pre-SMA involvement in visuo-spatial image transformation using a recognition rather than classic mental rotation task. fMRI was used to measure BOLD-related cortical activation during the performance of a recognition memory task in which participants made recognition judgments about previously memorised novel shapes. The task was constructed to avoid the methodological limitations of some previous studies in order clarify the contribution

of pre-SMA to 2D image transformation. First, a sequential presentation paradigm was used that eliminates the additional eye movement and attentional demands of simultaneous stimulus presentation. Second, we also recorded eye movements to assess the potential contribution of saccade frequency to the observed patterns of cortical activation for orientation-dependent and orientation-invariant stimulus sets. Third, the use of novel object stimuli allowed us to control participants' prior experience with the stimulus set. Fourth, we manipulated only the 2D image plane orientation of the stimuli. Unlike depth rotation, image plane rotation permits behavioural measures of orientation-dependent performance costs without confounding problems of perspective deformation and feature occlusion.

METHODS

Behavioural task and fMRI study

Participants

Participants were 12 right-handed volunteers, 5 male and 7 female (mean age 25.8 ± 3.75 years). All had normal or corrected-to-normal eyesight¹. All participants reported no prior history of developmental or acquired cognitive disability.

Materials

¹ The protocols for all experiments reported in this paper were approved by the Ethics Committees of the School of Psychology, University of Wales, Bangor (UK) and Department of Biomedical Engineering, University of Manchester (UK) in accordance with the ethical standards laid down in the Declaration of Helsinki (1964). Informed consent was obtained from all participants prior to testing.

Stimuli were based on those used by Tarr and Pinker [48] – see Fig. 1. Set A consisted of seven asymmetrical novel shapes. Set B consisted of seven symmetrical objects that previously showed an orientation-invariant pattern. Stimuli were scaled to fit within an 8x8 cm frame, subtending X.XX degrees of viewing angle in the scanner. Stimulus presentation was controlled by E-Prime software version 1.1 (Psychology Software Tools, Inc. Pittsburgh, USA.) running on a Pentium 4 laptop computer. Subject responses inside the scanner were obtained through fibre-optic switches (Curdes, www.curdes.com).

Insert Figure 1 about here

Design & Procedure

A three-factor (Object set X Block X Stimulus orientation) repeated measures design was used. The experiment consisted of separate training and test phases. The training phase was performed outside the scanner prior to the start of the experiment. In the training phase participants memorised one shape from each stimulus set. They were asked to copy and redraw a stimulus from one of the novel object sets until this could be accomplished without error. During this phase the stimuli were always presented at the same single ‘upright’ orientation. At the ‘upright’ orientation the principal axis of each stimulus was aligned vertically with respect to the participants midline (in the drawing phase), or with the projected image (in subsequent phases of the experiment). The participants then completed a short computerised training task. On each trial a single stimulus was presented at its upright orientation. The participants had to indicate whether or not the

stimulus was the target object. There were a minimum of 12 target-present trials, and 6 distracter trials, maintaining a consistent 2:1 ratio in the practice and testing phases of the experiment. However, these trials continued until the subject reached a criterion level of accuracy of 80% correct. Once subjects had reached the criterion accuracy level they proceeded to the test phase of the experiment. Participants always completed the learning phase with a target stimulus from the Set B block, prior to completing the learning and test phases with stimuli from Set A. In the test phase, subjects first encountered sub-blocks of Set B stimuli, prior to being tested on Set A stimuli.

In the test phase participants completed four trial blocks whilst being scanned. Trial blocks had an interleaved structure consisting of 8 sub-blocks, 2 sub-blocks of Set B stimuli were followed by 2 sub-blocks of Set A stimuli. The first sub-block in each case consisted of 12 stimulus presentations at the 'upright' 0° orientation (target-non target ratio 2:1), while the second block consisted of stimuli rotated (60° or 120°) in the fronto-parallel plane. The test sub-blocks contained targets and distracters from only one of the two stimulus sets. In total, each block consisted of 96 trials, 48 from the Set A stimulus set and 48 from the Set B stimulus set.

Participants were laid in the scanner with a bird-cage head coil, with an integrated mirror, fitted over their head. The stimuli were back-projected onto a screen which the subjects viewed using the mirror fixed to the head coil. Each trial began with a 500 msec fixation (+) prompt appearing in the centre of the screen. The fixation was replaced by either a target or distracter stimulus shown at one of the tested stimulus orientations (ISI = 250 msec). The task was to indicate by switch-press (target, non-target) whether or not the stimulus was a previously memorised target object. The stimulus remained on the

screen until the participant responded, or the reaction time (RT) exceeded 3500 msec. Trial order was randomised within sub-blocks. Target present responses were always made with the dominant (right) hand. The experiment lasted approximately 40 minutes.

Image Acquisition

Imaging was performed on a Philips 1.5T Magnetic Resonance Imaging scanner. For each subject a total of 272 volumes were acquired, each consisting of 40 slices using a single-shot echo planar imaging sequence (TR=3.15 secs, TE=40ms, 224mm FOV, 64 x 64 matrix, 3.5mm slice thickness).

Image analysis

Image co-registration and reslicing was performed using TINA image analysis software (www.tina-vision.net, University of Manchester). Data Analysis was performed using SPM99b (<http://www.fil.ion.ucl.ac.uk>). The fMRI images were spatially normalised and transformed into a common coordinate system (MNI space, Montreal Neurological Institute). The data was smoothed using a 10mm 3D Gaussian kernel. Significant levels of activation for each subject were identified using the General Linear Model approach (Friston et al., 1985), the on-off cycle was modelled using a box-car convolved with the haemodynamic response function. Population level effects were assessed using a random effects procedure, where each individual subjects' t-map was used as a single entry in the second level analysis. The statistical height threshold use in the analysis was set to $p < 0.001$ providing a minimum cluster size of 15 suprathreshold voxels. The fMRI data from one participant was excluded due to reconstruction errors.

Eye Tracking Study

Participants

Participants were 12 right-handed volunteers, 5 male and 7 female (mean age 28.8 ± 4.9 years). All had normal or corrected-to-normal eyesight. None of the participants had taken part in the scanning study. All participants reported no prior history of developmental or acquired cognitive disability.

Materials

The stimuli were the same as those used in the fMRI experiment. The eye tracker was a Tobii ET-17 system (www.tobii.se) with a recording frequency 30Hz. The stimuli were presented using Tobii presentation software on a 1024 x 768 resolution monitor. Stimuli subtended 12.86 degrees of visual angle from a viewing distance of 36 cm.

Design & Procedure

A two-factor (Object set X Stimulus orientation) repeated measures design was used. The experiment consisted of separate training and test phases. The training phase was the same as for the fMRI experiment. The experimental phase consisted of two separate blocks of trials, one for the Set A stimuli and one for the Set B stimuli, both were identical save for the difference in Object set. In all cases, the Set B stimuli were performed first. Each block of trials consisted of 60 presentations of stimuli, 30 targets and 30 distracters, in both cases the proportion of stimuli at the three Stimulus orientation conditions was the same, i.e. 10 each at 0, ± 60 and ± 120 degrees. Each trial consisted of a fixation cross presented in the centre of the screen for 1 second, followed by a 1 second

ISI and presentation of the stimulus object until a key was pressed. Participants were instructed to respond by pressing the 'k' key with their right hand if the presented stimulus was their target, or the 'd' key, with their left hand, if it was not.

RESULTS

Behavioural data

All analyses were performed on RTs for correct responses in the test blocks of the experiment. RT and error data were collapsed across symmetrical orientations (i.e., $\pm 60^\circ$, $\pm 120^\circ$). RTs greater or less than three SDs from the mean in each condition were eliminated. Since target stimuli had been viewed more frequently at the zero degree upright orientation (learning plus test phases), analyses of orientation effects were conducted only across the range of stimulus orientations where frequency of presentation had been held constant (i.e. $\pm 60^\circ$ & $\pm 120^\circ$ degrees). Figures 2(a) and 2(b) show the mean RTs across blocks and the 60° and 120° conditions for the Set A and Set B stimuli.

 INSERT FIGURES 2(a) & 2(b) ABOUT HERE

A 3 (Stimulus set) x 4 (Block) x 3 (Orientation) repeated measures ANOVA showed significant main effects of Stimulus set, $F(1, 11) = 14.86$, $p < .005$; Block $F(3, 33) = 7.41$, $p < .05$; and an interaction between Stimulus set and Orientation, $F(1, 11) = 20.07$, $p < .001$. One way ANOVAs across orientations (RTs collapsed across blocks) showed a significant effects for the Set A stimuli, $F(1, 11) = 13.11$, $p < .005$; but not for Set B ($F(1, 11) = .268$, n.s.). This confirms that the theoretically relevant pattern of behavioural data – showing contrasting orientation-dependent and orientation-invariant

recognition latencies for the Set A and Set B stimuli – were found in the task performed by subjects in the scanner.

Overall error rates were very low, no condition in any block showed greater than a 5% error rate. ANOVA on error rates showed no significant differences for either Set A or Set B stimuli across blocks or stimulus orientations.

Imaging data

The aim of the analysis was to determine regions of cortical activation associated with upright vs. rotated objects for both Set A (orientation-dependent) and Set B (orientation-invariant) stimulus sets. Task performance for both Set A and Set B stimuli is assumed to involve several common functional processes. These include image registration, the encoding of feature locations, determination of object orientation, visual short term memory, and matching perceptual and long-term memory shape representations. We assume from the behavioural data that the image normalisation component is only involved during the recognition of rotated Set A stimuli. To determine areas of cortical activation associated with this component, two principal contrasts were performed on the imaging data. Set A (upright vs. rotated) and Set B (upright vs. rotated). For Set A, this contrast is assumed to highlight areas involved in image normalisation. For Set B, the same contrast should not, since, by hypothesis, spatial normalisation was not employed during the recognition of these forms. Areas of activation associated with other functional processes during recognition may be assumed to result in similar patterns of activation for upright and rotated forms for both Set A and Set B. An additional contrast was also performed between Set A (upright) vs. Set B (upright) conditions – see Table 1.

This was a control measure assessing for activation differences to differences in stimulus geometry (e.g., symmetry) and complexity.

Regions of significant activation for both the Set A (upright vs. rotated) and Set B (upright vs. rotated), as well as the control Set A (upright) vs. Set B (upright) contrasts are shown in Table 1. For each area the corresponding Talairach coordinates are shown for the central voxel in each cluster, along with k (cluster size).

 INSERT TABLE 1 ABOUT HERE

Set B (upright vs. rotated) – Orientation-invariant recognition

The contrast of Set B (rotated – unrotated) resulted in activation of a single cluster of voxels in the left hemisphere. The active cluster covered an area that included parts of the inferior occipital gyrus, middle occipital and the fusiform gyri.

Set A (upright vs. rotated) – Orientation-dependent recognition

Image normalisation of Set A stimuli resulted in predominantly right hemisphere activation. Significant voxel clusters were found bilaterally in middle and inferior occipital gyri and in the inferior temporal (BA19) and fusiform gyri. The inferior parietal cortex (BA40) was active bilaterally, while superior parietal lobe (BA7) showed left hemisphere activation only. In the frontal cortex, activation was also found in the dorsolateral (BA46/9) and ventrolateral prefrontal areas (BA10). Of key interest in the current study is the large significant voxel cluster in the anterior medial pre-motor area within BA6, and extending anteriorly into BA8. The caudal region of this cluster lies

within pre-SMA [5, 8]. Figure 3(a) shows the pre-SMA activation superimposed on a XXX standard brain template [STEVE – SAY WHAT STANDARD TEMPLATE WAS USED – MNI, SUBJECT]. Figure 3(b) shows the associated percentage signal change (PSC) for this cluster for the Set A (upright vs. rotated) and Set B (upright vs. rotated) contrasts.

 INSERT FIGURE 3(a) and 3(b) ABOUT HERE

Analysis of the PSC data confirmed that for the pre-SMA cluster percentage signal change was significant for the Set A (upright vs. rotated) contrast, $t(10) = 3.44$, $p < 0.005$; but not for the Set B (upright vs. rotated) contrast ($t(10) = -0.17$, n.s.). This analysis shows that the activation of pre-SMA seems to be determined by additional processing related to the identification of misoriented stimuli from Set A, rather than to some other process, for example, related to object orientation per se.

Control contrast: Set A (upright) vs. Set B (upright).

The control contrast was designed to assess activation that is due solely to differences in stimulus geometry and complexity. The contrast showed two areas of significant activation: one in the right hemisphere cerebellum and a large voxel cluster in the posterior parietal cortex involving the left SPL (BA7) and bilaterally in the IPL (BA40). This activation may be related to the encoding of feature locations in the objects resulting from differences in stimulus complexity – consistent with data from other imaging studies associating parietal cortex and feature encoding [REFS].

These analyses show that orientation-dependent time costs in recognition can be associated with cortical activation specifically in the pre-SMA. This activation cannot be explained by differences in stimulus geometry and complexity. However, this activation could be related to eye movements, rather than image normalisation. This possibility is raised by the anatomical proximity of pre-SMA to the oculomotor areas including the frontal eye field (FEF) [49] and supplementary eye field (SEF) – although the focus of the SEF is typically defined as being both more lateral and anterior to pre-SMA [16]. Data from the eye tracking study should be relevant to this question.

Eye tracking data

All analyses were performed on saccade frequency for correct responses in the test blocks. Data were collapsed across symmetrical orientations (i.e., $\pm 60^\circ$, $\pm 120^\circ$). Saccade frequency was defined by interruptions to eye movements (i.e., fixations) lasting less than 15 ms and remaining within a radius of 50 pixels. Figure 4 shows the mean saccade frequency as a function of stimulus set and orientation.

 INSERT FIGURE 4 ABOUT HERE

A 2 (Stimulus set) x 3 (Orientation) ANOVA was showed a main effect of stimulus orientation, $F(2, 18) = 5.812$, $p < 0.05$; but no effect of stimulus set ($F(1, 9) = 0.103$, n.s.) or interaction ($F(2, 18) = 3.117$, n.s.). Critically, for Set A there is no evidence that participants make more saccades for upright versus rotated stimuli. This suggests that

saccade patterns cannot account for the activation found in pre-SMA during 2D image transformation of Set A stimuli.

GENERAL DISCUSSION

The goals of this study were to provide further evidence about the potential role of pre-SMA in visuo-spatial image transformation under conditions that eliminate methodological limitations of some previous studies. The key finding was the observation of a cluster of activation in pre-SMA associated with image transformation of orientation-dependent novel shapes. Unlike several previous studies this demonstrates anterior medial premotor involvement in image transformation in a task that avoids confounds associated with depth rotation such as perspective deformation and feature occlusion. The task used here also involved a recognition judgment based on a single image presentation, rather than simultaneous or sequential matching of rotated or mirror-reversed shapes. This manipulation reduced eye movements and the need for shifts of attention. In addition, pre-SMA activation was found using within-object contrasts in the image analysis between upright and rotated forms. These contrasts provide purer measure of activation associated specifically with the image normalisation component of task performance. The current findings converge with other recent data showing pre-SMA activation in a task of mental rotation (rather than recognition) using sequential presentation of 2D novel objects [REF]. The control contrast between upright object sets eliminated activation associated solely with differences in stimulus geometry and complexity. Of significance also was the data from the eye movement study. This did not

reveal any differences in mean saccade frequency between upright and rotated objects using the same paradigm used in the scanner. These data suggest that differences in eye movement patterns cannot account for the pre-SMA activation. The lack of difference in saccade frequency between upright and rotated forms contrasts with some data from a previous study showing increasing saccade frequency as a function of angular disparity in mental rotation [Just and Carpenter]. In that study saccade patterns were examined for displays containing two simultaneously presented 3D cube shapes in a classic mental paradigm. In contrast, the current study only a single stimulus was presented on each trial, and a recognition memory paradigm was used. This important difference may underlie the different patterns of results found. Most notably, our data show that increases in saccade frequency do not correlate with angular disparity in the recognition of 2D rotated objects. With simultaneous displays in classic mental rotation tasks saccade frequency is likely to be related to feature-by-feature cross-checking between the two displays. It is also relevant to note that the location of the large medial voxel cluster was outside of the range of coordinates detailed by Paus [REF] for the FEFs, while the SEF is assumed to be located more laterally [REF].

The role of pre-SMA in visuo-spatial transformation

As noted earlier, pre-SMA activation has been associated with tasks requiring sequential movement learning [19], and visuo-motor association [20]. Other evidence suggests that sensory-motor association in pre-SMA is both modality-, and effector-independent, and not related to response selection or preparation during conditional motor behaviour [4, 21, 22]. Interestingly, there is also data that pre-SMA is involved in

tasks requiring shifts of attention among visual features of objects [23, 24]. These later findings suggest a functional link with the current results showing pre-SMA activation in 2D image normalisation. Together, they support a view of pre-SMA function beyond the planning and control of visually-guided behaviour. Image transformation tasks share an important computational similarity with other tasks implicating pre-SMA. We speculate that pre-SMA may be functionally involved in the computation of abstract vector transformations such as those that been associated with neuronal population vector transformations underlying the planning and on-line control of visually-guided movement [Georgopoulos et al., Pellizer, REFS]. This potential functional link between visuo-spatial transformation, and motor behaviour, is also supported by psychometric showing interference between the performance of mental and manual rotation tasks [46, 47]. The hypothesis that the computations performed by pre-SMA contributes to a variety of cognitive tasks requiring spatial vector transformation is also consistent with other evidence showing that activation in the area is modality-independent [4, 21].

Finally, in addition to the pre-SMA activation, we also found evidence that medial premotor cortex participates in a network of cortical areas involved in visuo-spatial transformation. Like other studies, we found evidence for activation in DLPFC (BA46), inferior (BA40) and superior parietal (BA7) cortex [REFS]. Consistent with the task of recognition we also found bilateral activation in IT around the fusiform gyri (BA19). It is likely that pre-SMA's role in visuo-spatial transformation during recognition involves interaction with stored object-specific knowledge. Such interaction may be mediated by apparent cortical connections between pre-SMA and AIT [14]. Evidence from other studies has linked DLPFC with visual working memory [Passingham, 1993; Rowe et al.,

2000). This raises the possibility that DLPFC may contribute to visuo-spatial transformation by maintaining outputs of vector transformations computed in pre-SMA².

Summary

This paper reports converging data from studies of psychometrics, functional magnetic resonance imaging (fMRI) and eye tracking that provide further evidence about functional sub-divisions within the medial pre-motor area. A recognition memory paradigm was used to measure response times (RTs) to identify upright and misoriented novel objects. The behavioural results were consistent with previous reports showing a contrast between orientation-dependent and orientation-invariant performance depending on the stimulus set used. Correlations between behavioural task and and BOLD data showed evidence of activation in pre-SMA associated with 2D image normalisation. Data from an the eye movement study using the same task provided no evidence that activation in pre-SMA could be accounted for by differences in mean saccade frequency for upright and rotated forms. We suggest that pre-SMA may be involved in the computation of abstract vector transformations underlying spatial normalisation in a variety of cognitive tasks including image alignment and the planning and control of visually-guided movement.

² It is important to note that we do not claim here to have elucidated the neural correlates of object constancy in visual recognition. The aim of this study was to examine the potential role of medial premotor cortex in visuo-spatial transformation – and not object constancy. Although we used a recognition task, this was done solely to provide a controlled manipulation of 2D image normalisation under conditions that reduce confounds in previous studies. For the most part, object constancy in visual recognition involves overcoming changes in object viewpoint (i.e., across depth rotation). The results of the current study may not be relevant to this issue. Indeed, it is not obvious that perspective deformation, foreshortening and feature occlusion could be overcome, during normal object recognition, using an image transformation process of the kind studied here. Furthermore, several recent imaging studies have shown dissociations between the recognition of depth rotation objects, and mental rotation [Vanrie et al., 2002; Jordan et al., 2001; Gauthier et al., 2002].

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TABLES

TABLE 2: Significant areas of activation in cerebral cortex for the conditions Set A (rotated – unrotated), Set B (rotated – unrotated) & Set A (rotated) – Set B (rotated). In each case the voxel with the highest t value in the cluster is reported along with the number of voxels (k) in the cluster. Neuroanatomical landmarks, found within the active cluster, are followed by the specific cortical region in brackets. Talairach coordinates show the centre of the cluster, in millimetres, from the anterior commissure. GFs/m = superior/middle frontal gyrus; GOm/i = middle/inferior occipital gyrus; FG = fusiform gyrus; LPs/i = superior/inferior parietal lobule; GTi = inferior temporal gyrus; BA = Brodmann area.

Task condition A (rotated – unrotated)

		<i>x</i>	<i>y</i>	<i>z</i>	<i>k</i>
<i>(mm)</i>					
<hr/>					
<i>Left hemisphere regions</i>					
GFm/GFs	(BA10/46)	-40	54	10	107
	(BA9)	-42	34	30	25
	(BA6/8)	-10	34	56	122
LPs	(BA7)	-24	-64	50	21
LPs/LPi	(BA40/7)	-38	-54	52	54
GOi/FG	(BA19)	-38	-84	-8	74

Right hemisphere regions

LPi	(BA40)	44	-46	56	59
GOm/GTi/FG	(BA18/19)	46	-72	10	163

Task condition B (rotated – unrotated)

		<i>x</i>	<i>y</i>	<i>z</i>	<i>k</i>
<i>(mm)</i>					
<hr/>					
<i>Left hemisphere regions</i>					
GOm/FG	(BA19)	-34	-78	-16	52

Task Condition A (unrotated) – B (unrotated)

		<i>x</i>	<i>y</i>	<i>z</i>	<i>k</i>
<i>(mm)</i>					
<hr/>					
<i>Left Hemisphere regions</i>					
LPi/LPs	(BA7/40)	-26	-76	40	384
Cerebellum		-6	-76	-32	29
<i>Right Hemisphere Regions</i>					
LPi	(BA40)	44	-50	54	38

FIGURE CAPTIONS

FIGURE 1. (A) Orientation-dependent and (B) orientation-invariant stimulus shapes. After Tarr & Pinker (1990).

FIGURE 2. Response-times from the behavioural study for the Set A stimuli as function of orientation for all blocks.

FIGURE 3. Response-times from the behavioural study for the Set B stimuli as function of orientation for all blocks

FIGURE 4. Slopes of the line fits to the RT data for the $\pm 60^\circ$ and $\pm 120^\circ$ for each block for both the Set A and Set B stimuli.

FIGURE 5. Activation in the Set B (rotated – unrotated) condition. The activation is superimposed on a standard MNI anatomical image.

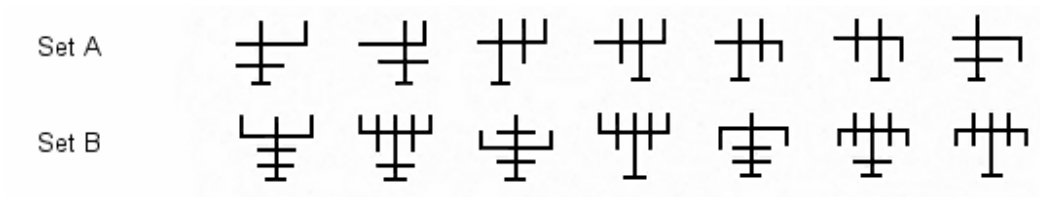
FIGURE 6. Activations in the Set A (rotated – unrotated) condition. The activations are superimposed on a standard MNI anatomical image; a) Medial BA6 (SMA) b) BA10.

FIGURE 7. Activations in the Set A (rotated) – Set B (rotated) condition. The activations are superimposed on a standard MNI anatomical image; a) Lateral BA6 (SMA) b) SPL.

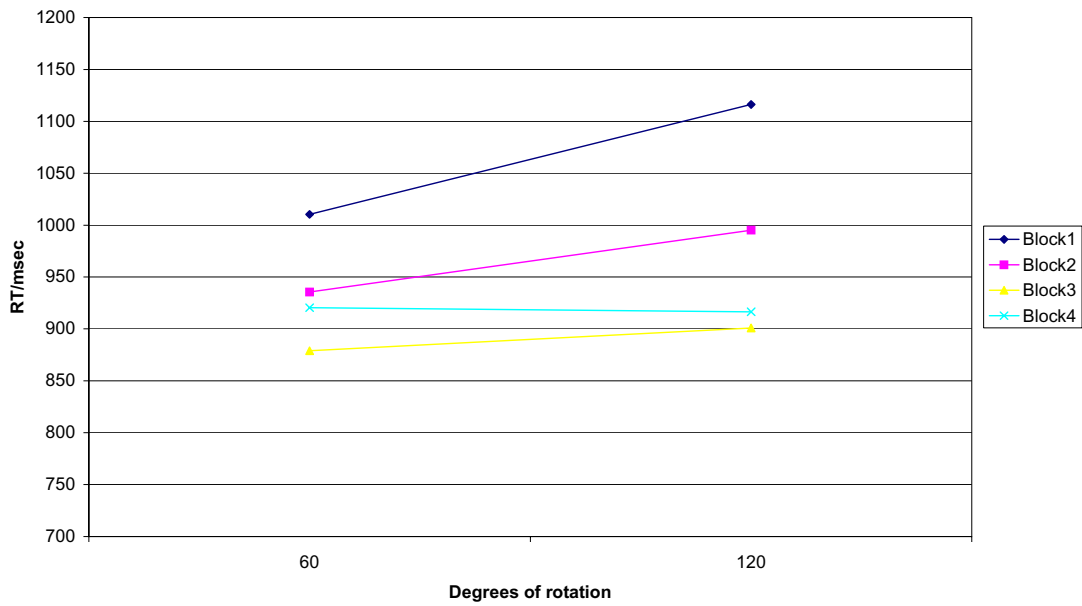
FIGURE 8. Percentage signal change in the cluster of pixels seen in Medial BA6 for the conditions AR-AU and BR –BU

FIGURE 9. Percentage signal change in the cluster of pixels seen in Lateral BA6 for the conditions AR-AU, BR-BU, AR-BR & AU-BU.

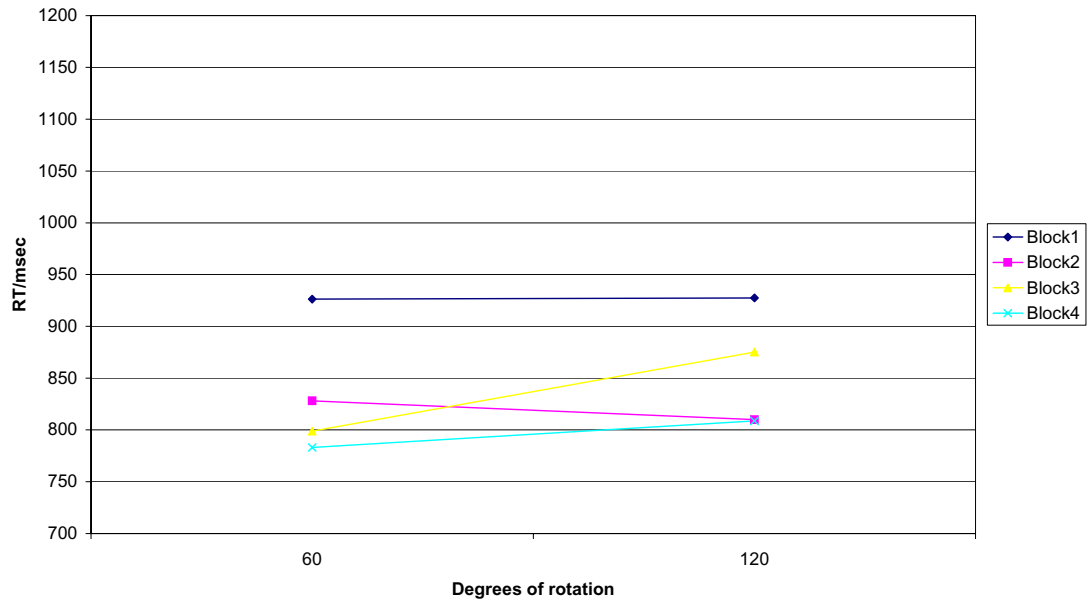
FIGURE 10. Mean saccades along with the standard error for each stimulus orientation condition for each stimulus set in the eye tracking study.



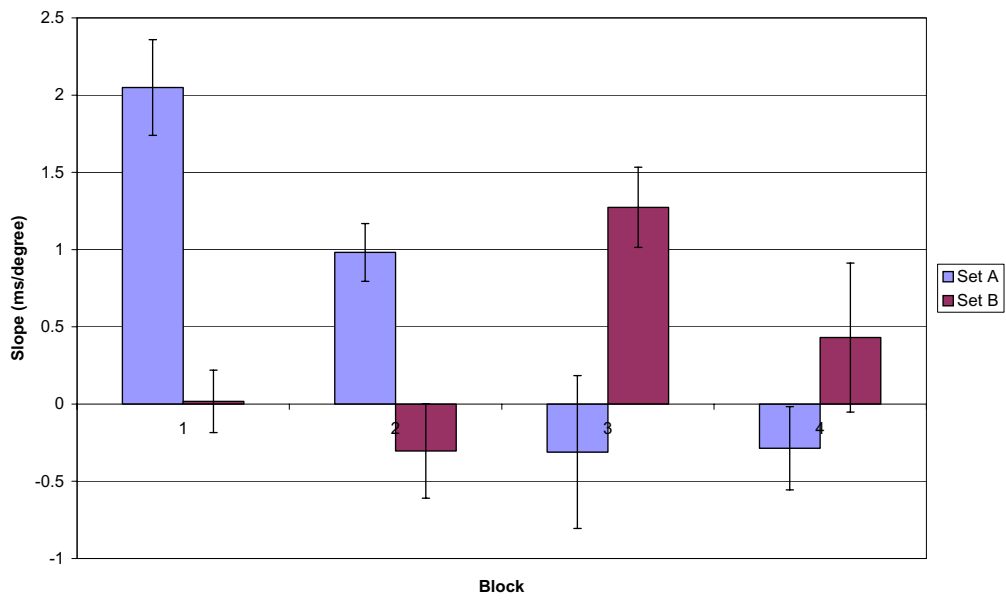
E.C. Leek - Figure 1



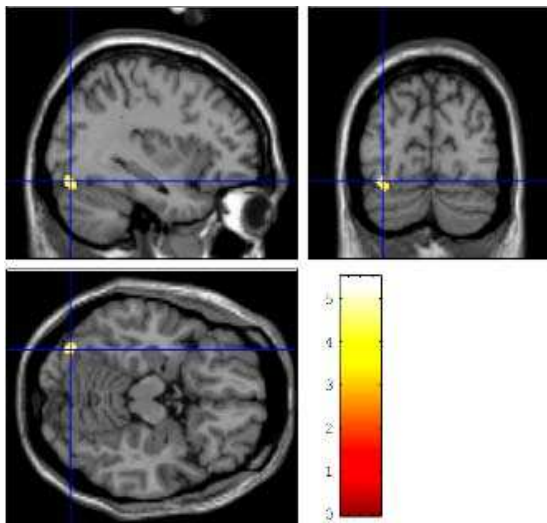
E.C. Leek – Figure 2



E.C. Leek – Figure 3

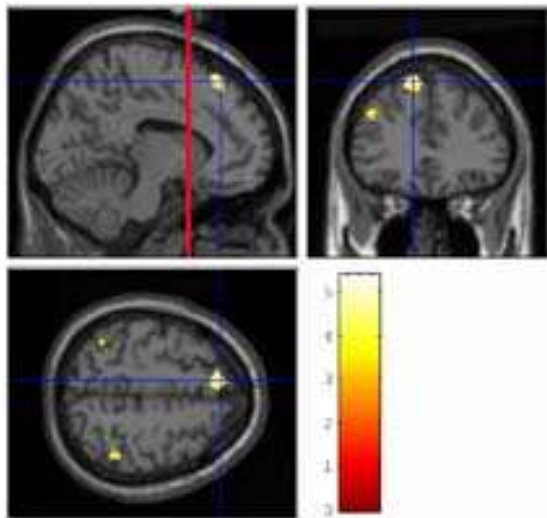


E.C. Leek – Figure 4

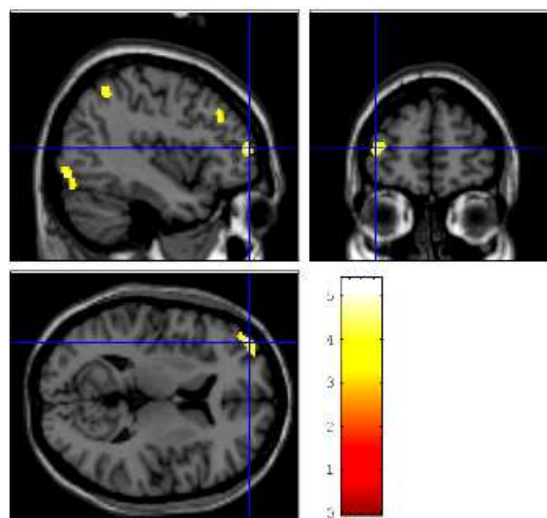


E.C. Leek – Figure 5

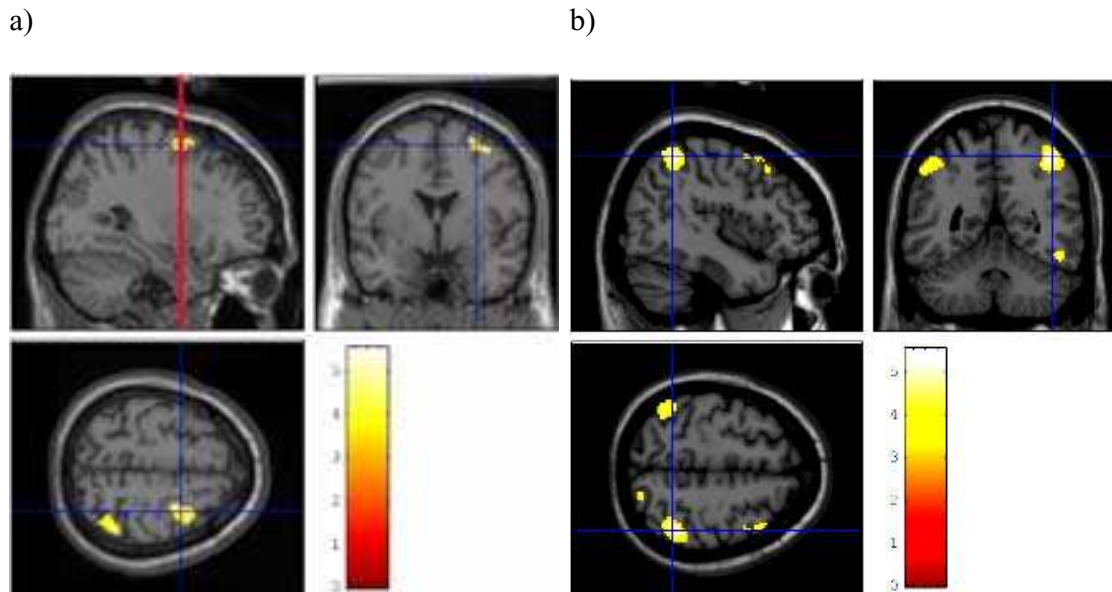
a)



b)



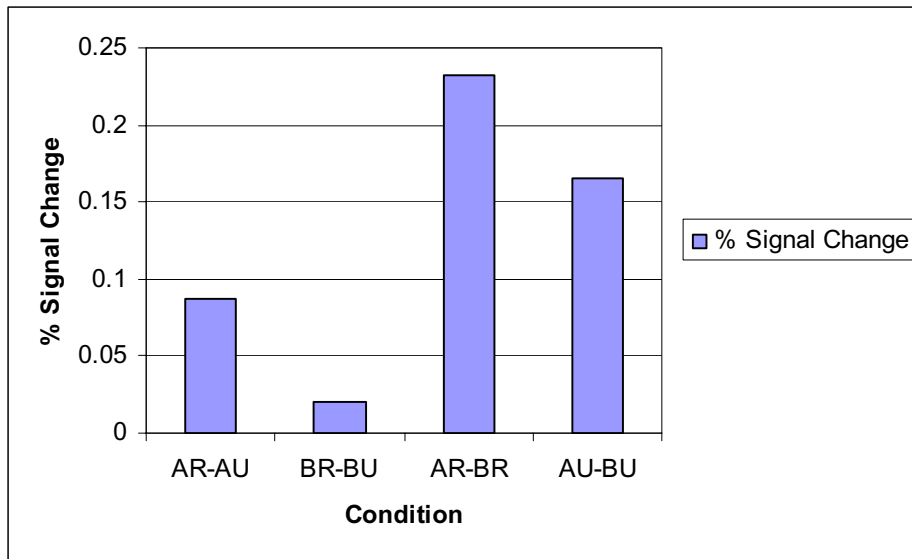
E.C. Leek – Figure 6



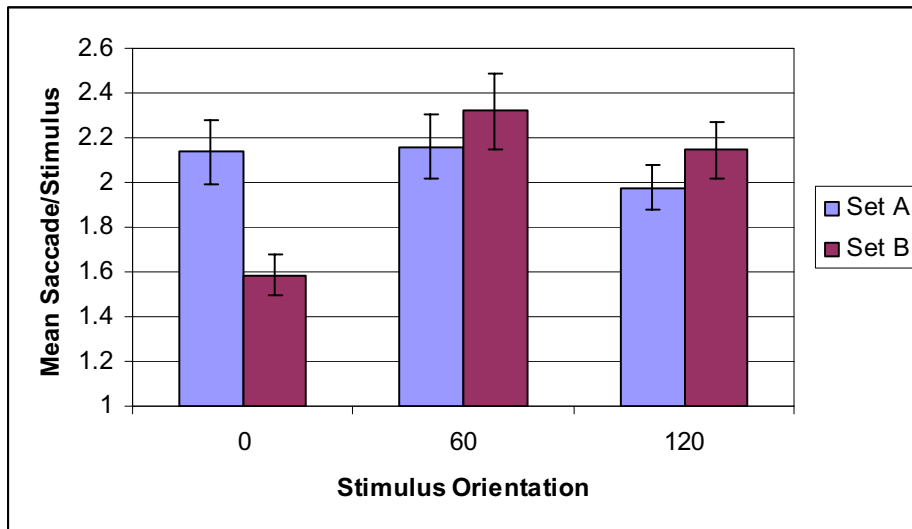
E.C. Leek – Figure 7



E.C. Leek – Figure 8



E.C. Leek – Figure 9



E.C. Leek - Figure 10

Mental Rotation studies showing PMC

- [25] Cohen et al (1996)
- [26] Richter et al (2000)
- [27] Tagaris et al (1997)
- [28] Tagaris et al (1998)
- [29] Kosslyn et al (1998)
- [30] Johnston et al (2003)
- [31] Vinghoets et al (2001)

Object Recognition Studies showing PMC

- [32] Gauthier et al (2002)
- [33] Sugio et al (1999) Lateral PMC
- [38] Kosslyn et al (1994)

Mental rotation Studies not showing PMC involvement

- [34] Alivisatos et al (1997)
- [35] Harris et al (2000)
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- [41] Lamm – Mental rotation, premotor, event related

[42] Warrington study

[43] Chauvel et al 1996

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[46] Wohlschlager

[47] Wohlschlager