NeuroImage

www.elsevier.com/locate/ynimg
NeuroImage 36 (2007) 955 – 968

Visuospatial working memory and changes of the point of view in 3D space

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Received 14 September 2006; revised 9 March 2007; accepted 12 March 2007

We used functional magnetic resonance imaging to explore the brain mechanisms of changing point of view (PoV) in a visuospatial memory task in 3D space. Eye movements were monitored and BOLD signal changes were measured while subjects were presented with 3D images of a virtual environment. Subjects were required to encode the position of a lamp in the environment and, after changing the PoV (angular difference varied from 0° to 180° in 45° steps), to decide whether the lamp position had been changed too or not.

Performance data and a scan-path analysis based on eye movement support the use of landmarks in the environment for coding lamp position and increasing spatial updating costs with increasing changes of PoV indicating allocentric coding strategies during all conditions (0°- to 180°-condition).

Subtraction analysis using SPM revealed that a parieto–temporo–frontal network including left medial temporal areas was activated during this 3D visuospatial task, independent of angular difference. The activity of the left parahippocampal area and the left lingual gyrus (but not the hippocampus) correlated with increasing changes of the PoV between encoding and retrieval, emphasizing their specific role in spatial scene memory and allocentric coding. The results suggest that these areas are involved in a continuous matching process between internal representations of the environment and the external status quo. In addition, hippocampal activation correlated with performance was found indicating successful recall of spatial information. Finally, in a prefrontal area comprising, the so-called "deep" frontal eye field, activation was correlated with the amount of saccadic eye movements confirming its role in oculomotor processes.

Keywords: Spatial memory; Point of view; Egocentric and allocentric coding; Eye movements

Introduction

The ability of humans to orient in the environment from different points of view (PoV) is based on the use of spatial reference systems. Generally, two distinct spatial reference frames enable subjects to memorize the locations of objects in this environment: egocentric and allocentric (Howard, 1982). Egocentric frames encode spatial locations with reference to the viewer's perspective of the world (e.g. head-centered or body-centered coordinates) whereas allocentric frames encode spatial locations with respect to a viewer-independent object-to-object reference system (Vogeley and Fink, 2003). Both of these systems could be used to update object locations across different PoVs (Simons and Wang, 1998; Wraga et al., 1999).

Psychophysical studies have shown that allocentric- or egocentric-based mental transformations lead to different chronometry and response patterns. This indicates that these two processes are dissociable. Using an object centered (allocentric) frame of reference in order to explore mentally a given environment is more time-consuming than using a viewer-centered (egocentric) frame of reference (Amorim and Stucchi, 1997). In addition, in studies investigating allocentric coding (e.g. by changing the PoV during an object location memory task) subject's reaction times vary linearly with the angular difference between the views (Amorim, 2003; Diwadkar and McNamara, 1997; King et al., 2002). In contrast, for egocentric coding of body parts or body

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doi:10.1016/j.neuroimage.2007.03.050

postures, the reaction times depend on biomechanical constraints reflecting the real movements (Amorim et al., in press; Parsons, 1994; Zacks and Tversky, 2000).

Lesion studies support the notion of dissociable neural systems underlying the different spatial transformations. While allocentric coding appears to be dependent on the hippocampal formation (Holdstock et al., 2000; Incisa della Rocchetta et al., 2004; King et al., 2002), the posterior parietal cortex seems to be important for performing egocentric coding (Fink et al., 2003; Pizzamiglio et al., 2000; Vallar et al., 1999). Patients with lesions of the posterior parietal cortex are impaired in visuomotor coordination (optic ataxia: Perenin and Vighetto, 1988) or show spatial hemineglect (Vallar et al.,1999). These are both deficits which could be related to impaired egocentric coding (Bisiach, 1997; Vallar et al., 1997).

From an object location memory study with Jon, a patient with focal bilateral hippocampal pathology (Vargha-Khadem et al., 1997), King et al. (2002) conclude that (i) “although egocentric memory is sufficient for the same point of view task, allocentric processing also makes an important additional contribution when long lists are used…” and (ii) “when the viewpoint is shifted within a rich 3-D environment, hippocampal-dependent allocentric mechanisms are crucial as soon as there is more than one location to remember”. Based on these results it could be hypothesized that spatial tasks from a fixed point of view can be solved by using pure egocentric representations of the distances and directions of objects, but spatial memory tasks involving manipulation of the subject’s PoV require a PoV independent representation of object locations.

Several functional imaging studies support the involvement of parietal areas during the egocentric coding of space (Bonda et al., 1995; Galati et al., 2000; Vallar et al., 1999; Vogeley and Fink, 2003). In a PET study investigating the neural correlates of mental transformations of the body-in-space by using a hand rotation paradigm, Bonda et al. (1995) showed bilateral involvement of the superior parietal lobule, the premotor cortex, the cingulate motor areas and the anterodorsal part of the insula. Vallar et al. (1999) also demonstrated an activation of posterior parietal and premotor areas by instructing subjects to localize stimuli with respect to the body mid-sagittal plane.

The neural basis of allocentric/object-based spatial coding has been investigated by several functional imaging studies predominantly using mental rotation tasks (Alivisatos and Petrides, 1997; Barnes et al., 2000; Bonda et al., 1996; Carpenter et al., 1999; Cohen et al., 1996; Harris et al., 2000; Tagaris et al., 1997; Vingerhoets et al., 2001; Zacks et al., 2002). Interestingly, several of these studies reveal similar activation patterns as for egocentric coding tasks. Studies using alphanumerical stimulus material predominantly demonstrated parietal activations (Alivisatos and Petrides, 1997; Harris et al., 2000), studies introducing 3D-objects as stimulus material found additional activation of occipito-temporal areas including the fusiform gyrus (Barnes et al., 2000; Carpenter et al., 1999; Vingerhoets et al., 2001; Zacks et al., 2002). An activation of hippocampal structures was not seen in any of these studies. Only more complex allocentric coding tasks including allocentric coding of topographical space revealed an involvement of the hippocampal formation: either the posterior parahippocampal cortex (Aguirre et al., 1996; Aguirre and D’Esposito, 1997; Ghaem et al., 1997; Gron et al., 2000; Maguire et al., 1997, 1998; Mellet et al., 2000) or the hippocampus proper (Aguirre et al., 1996; Gron et al., 2000; Mellet et al., 2000).

Summarizing the results of these functional imaging studies, it seems that different systems participate in spatial transformation either during mental rotation or topographical orientation: posterior parietal areas (the intraparietal sulcus and the superior parietal lobule) are responsible for visuospatial transformations mainly related to egocentric coding, whereas areas in the ventromedial occipito-temporal cortex (fusiform, lingual and posterior parahippocampal cortex) could be associated with allocentric environment-centered or object-centered coding. However, (parahippocampal or) hippocampal activation was only demonstrated in studies requiring the processing of topographical information.

Similar results were shown by the few functional imaging studies directly comparing the brain systems for egocentric and allocentric spatial coding (Committeri et al., 2004; Fink et al., 2003; Galati et al., 2000; Zacks et al., 2002). Zacks et al. (2002) investigated brain activity during spatial judgements (viewer-centered egocentric body laterality vs. object-centered allocentric body rotation) using pictures of human bodies. They demonstrated that areas in the right parietal cortex and occipito-temporal areas were differentially involved in object-based spatial transformations. Using a line bisection task, Galati et al. (2000) demonstrated a bilateral fronto-parietal network involved in egocentric processing and a right lateralized subset of these regions activated during object-based processing. Only Committeri et al. (2004) investigated egocentric and allocentric coding in a realistic environment and found the parahippocampal cortex significantly more activated during the (allocentric) environment-centered coding than during (egocentric) viewer-centered coding. While all these studies tried to separate brain areas involved in egocentric or allocentric coding, Fink et al. (2003) showed that the interaction between ego- and allocentric reference frames takes place in a parieto-premotor network. Since the parietal lobes host common neural mechanisms for object-based and space-based attention and the respective reference frames (Fink et al., 1997), they are well equipped for the interaction between ego- and allocentric reference frames.

By simulating neuropsychological tests manipulating viewpoint changes, the present study tries to further separate the brain areas involved in spatial coding processes. First, the study addresses the question of which brain areas are involved when subjects store and remember the location of an object from different PoVs in general. More specifically the aim of the study is to identify which areas are influenced by increasing the angular difference between encoding and retrieval view. Taken the results of neuropsychological studies demonstrating a correlation between the amount of changing the PoV and reaction times, it was hypothesized that during tasks solved by allocentric processes two steps were included: first, updating changes in the observer’s position and second, orientation with respect to a constant external reference frame.

A virtual environment was used to investigate visuospatial memory in three-dimensional (3D) space employing fMRI and a spatial task adapted from Amorim (2003). By systematically changing the PoV during the memory task, subjects permanently updated spatial information related to internal spatial reference systems in a parametric way. In addition, performance and eye movements were monitored during all tasks. These behavioral data may help to understand subject’s strategy to solve the task. Moreover hippocampal involvement may be demonstrated only by correlating hippocampal activation with performance measures.

In the same-view condition, the object location could be remembered relative to the virtual environment (allocentric memory), or to the subject, or the frame of the video display unit, or the perceptual features of the display as seen from that view (egocentric or iconic memory). In the shifted-view condition, using any of the latter forms of memory would leave the subject severely disadvantaged compared with using allocentric memory.

First, we hypothesized that a fronto–parieto–temporal network generally supports spatial memory as demonstrated in several studies before (Aguirre et al., 1998; Burgess et al., 2001; Committeri et al., 2004). Secondly, we hypothesized that with increasing change of the PoV, subjects were forced to use allocentric coding strategies triggering activation of the medial temporal lobe structures. Furthermore, based on previous studies (Hartley et al., 2003; Iaria et al., 2003; Maguire et al., 1998; Wolbers and Buchel, 2005) we expected that the activity in the hippocampus would positively correlate with performance measures. Finally, we aimed at showing a correlation of the amount of saccadic eye movements with the neural activity in the frontal eye fields.

Material and methods

Subjects

Thirteen young healthy right-handed volunteers (11 male, 2 female; mean age 30±2 years) took part in the study which was approved by the local ethical committee of the Heinrich-Heine University. All subjects gave informed, written consent for participation in the study.

Virtual environment

A first-person perspective virtual environment was designed using 3Dstudio MAX® (Autodesk®,www.autodesk.com) and Character Studio®: a computer model based on the interior view of the roof garden of the Villa Savoye designed by Le Corbusier. The room contained a table, a ramp, two areas with plantings and a small basin (Fig. 1). A lamp could be added on the floor of the room, at different locations, to test memory.

Stimuli

During fMRI sessions, subjects were presented with snapshots of the virtual environment (of about 18×14° of visual angle) from eight different points of view. These positions are arranged on a circle around the center of the room at a distance of 45° (Fig. 1A). That means that the point of view could be varied from 0 to 180° in steps of 45°. During the experimental memory task (not during the baseline task) in each snapshot, the lamp was also visible in the environment in one of eight different places (Fig. 1B).

Stimuli were generated by a PC located outside the MR room, running the ERTS software (BeriSoft Cooperation, Germany). Stimuli were projected on a back projection screen using a LCD video projector. Participants viewed the stimuli through mirror glasses.

Experimental task

Subjects were presented with an image from one of the eight different views and had to encode the position of the lamp. After 5 s a second image from the same or another PoV was shown and subjects were asked to decide whether the position of the lamp had been changed or not. Subjects responded by pressing a button with

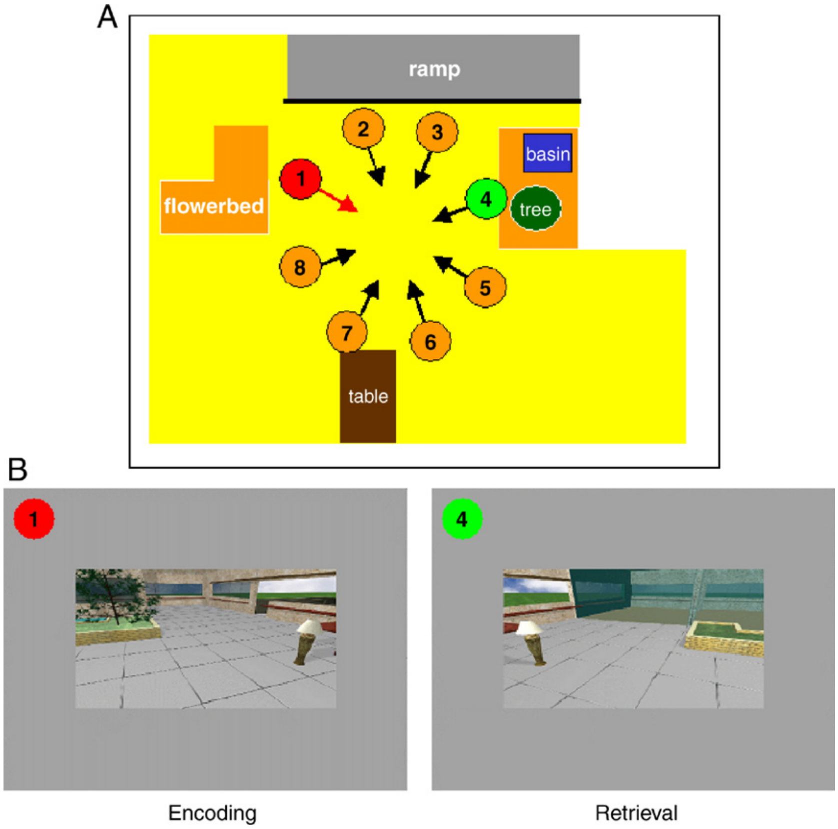

Fig. 1. Virtual environment and examples of stimuli. (A) A sketch of the virtual environment including the different points of view from which snapshots of the environment were presented. (B) Two examples of snapshots used during the spatial task (Change of the point of view from 1 to 4=135°).

their left hand if the lamp position had been changed and with their right hand if the lamp position had not been changed. The subject's PoV was parametrically changed by 0, 45, 90, 135 and 180° between the "encoding" and the "retrieval" image (0°-condition, 45°-condition, 90°-condition, 135°-condition and 180°-condition). During each block of experimental spatial task trials, subjects were presented with three image pairs using the same angle for changing the PoV. For each angle, 6 blocks were presented. In one block the position of the lamp never changed, in one block the position of the lamp always changed, in two blocks the position of the lamp changed in one image pair only and, finally, in two blocks the position of the lamp changed in two of the three image pairs. That means that the number of changes in the lamp position and, therefore, the "Yes/No" responses given by the right and the left hand, respectively, were balanced across blocks.

Before fMRI scanning, subjects were familiarized with the experimental procedures and tasks. Furthermore, subjects were presented with a 5 min video clip of the complex virtual environment on a 17-inch PC monitor. It was emphasized that subjects realized the ordering of images as pairs of an encoding and retrieval image. During scanning only the high-level baseline (table task) was indicated by a sign to clearly separate it from the experimental spatial task, whereas subjects got no information about the angular change of PoV to ensure that subjects increasingly utilized their visuospatial working memory and to prevent any form of "out of body" priming (Amorim, 2003).

Baseline task

The table task (TT) served as a high-level baseline task. In the table task, the same virtual environment as for the experimental spatial memory task was presented with the only difference that no lamp was present. The task of the subjects was to indicate whether (right hand button response) or not (left hand button response) the table was present in the image. During one block of the table task, subjects were presented with four different images, each lasting 5 s. The table task was designed to be as similar as possible to the experimental memory task, but the table task contained no demands on visuospatial working memory. Therefore, the contrast experimental task vs. table task should specifically yield the neural activations associated with visuospatial working memory.

To further explore the neural activations associated with the perception of the complex virtual environment, a low-level baseline task was introduced, in which the subjects were presented with a blank screen without any special instructions, but to look at the screen. The subtraction of this low-level baseline task from the experimental task and the high-level baseline task should reveal the neural areas processing the complex virtual environment with or without visual-spatial working memory demands, respectively.

Finally, a second low-level baseline task (fixation) was introduced to facilitate the analyses of the neural activations associated with the control of eye movements and to control the quality of the on-line eye movement measurements by monitoring the gaze position in respect to the position of the fixation point.

Experimental protocol

The fMRI paradigm consisted of a total of 314 scans per experimental run: three dummy acquisitions were followed by 31 repetitions of a baseline period of 20s (high- or low-level baseline) alternating with 30 repetitions of activation period of 30 s in a pseudo-random order. For each angle 6 blocks were presented. For example, this led to the following scanning sequence: 3 dummy acquisitions – low-level baseline (fixation) – 0°-condition - high-level baseline (table task) – 180°-condition - low-level baseline (fixation) – 135°-condition - low-level baseline (blank screen) – 0°-condition and so on. Subjects performed two experimental runs.

Functional MRI

Functional MR imaging was performed on a 1.5 T MRI system (Siemens Magnetom Vision, Erlangen, FRG), equipped with EPI capabilities and a transmit/receive head coil. The subjects were positioned in the scanner with the head immobilized using foam support cushions. Sequences with the following parameters were employed: gradient echo EPI; repetition time (TR) = 5 s; echo time (TE) = 66 ms; field-of-view (FOV) = 200 mm; flip angle (θ) = 90°; matrix size = 64×64 giving an in-plane pixel size of 3.13×3.13 mm^2. Using a mid-sagittal scout image, 26–32 axial slices (4 mm thickness and 0.4 mm inter-slice gap, number of slices depended on the geometry of the subject's brain) were oriented along the anterior-posterior commissure (AC–PC) line. In addition, high-resolution anatomical images of the brain were obtained by using the 3D MP-RAGE sequence (rapid acquisition gradient echo) with the following sequence parameters: TR = 11.4 ms; TE = 4.4 ms; θ = 15°; FOV = 200 mm; matrix size = 200×256; 128 sagittal slices with a thickness of 1.33 mm.

Data analysis

Data analysis was performed on SPARC 20 workstations (SUN Microsystems computers) using MATLAB (The MathWorks Inc., Natick, MA, USA) and the SPM99 software (Statistical Parametric Mapping software, SPM; Wellcome Department of Cognitive Neurology, London, UK; http://www.fil.ion.ncl.ac.uk). SPM99 was used for image preprocessing and to create statistical maps of significant relative regional BOLD response changes (Friston, 2002). After realignment of the functional images and coregistration with anatomical MR, images were normalized to a standard anatomical space based on a representative brain from the Montreal Neurological Institute series (MNI brain). Finally, the images were smoothed with an isotropic Gaussian kernel of 8 mm full-width half-maximum.

Group analysis was based on a random-effect approach (Friston et al., 1999; Holmes and Friston, 1998). First, the time series of functional MR images obtained from each participant were analyzed separately. The effects of the experimental paradigm were estimated on a voxel-by-voxel basis by modeling the experimental blocks (separately for each baseline and each angular condition) as box-car functions convolved with a hemodynamic response function in the context of the general linear model (Friston et al., 1994; Worsley et al., 1992). Low-frequency changes over time were filtered out using a high-pass filter with a cut-off frequency of 1/180 Hz. For each subject, design matrices were defined with eight separate conditions (low-level baseline [blank screen] / low-level baseline [fixation] / table task [high-level baseline] / 0°-condition / 45°-condition / 90°-condition / 135°-condition and 180°-condition). Then, a contrast representing the difference between all experimental conditions and the high-level baseline (0°-condition + 45°-condition + 90°-condition + 135°-condition + 180°-condition relative to table task) was calculated at the subject level first. In addition, contrasts representing the difference between each experimental condition and the high-level baseline (table task) were calculated at the subject level. The table task was used as high-level-baseline condition because this task was as close as possible to the experimental memory task, but minimized visuospatial memory demands.

For the random effects group analysis, the contrast images representing the difference between all experimental conditions and the high-level baselines from each subject's individual analyses were entered into a second level analysis using one-sample *t*-tests. Furthermore, two parametric analyses were performed. The first analysis used the 5 contrast images each representing the difference between a PoV condition (i.e. 0°, 45°, 90°, 135° or 180°) and the high-level baseline (table task) from all 13 subjects (i.e. 65 images total) and (i) the angular difference between encoding and retrieval PoV as a covariate of interest, and (ii) performance as a covariate of no interest. The second analysis included the 10 subjects whose eye movement data could be acquired (50 images total); (i) the relative number of saccadic eye movements was used as a covariate of interest and the angular difference between encoding and retrieval PoV as well as performance were used as covariates of no interest, (ii) the performance was used as covariate of interest and the angular difference between encoding and retrieval PoV as well as eye movements were used as covariate of no interest.

The focus of the current study was to investigate the modulation of the known neural systems involved in the processing of 3D spatial information by the differential use of ego- and allocentric strategies triggered by increasing PoV changes. Thus, activations were considered significant if they (at least) survived correction at the cluster level ($p<0.05$), corrected for clusters representing the known 3D processing areas, clusters were defined using the WFU pickatlas (Maldjian et al., 2003) using a height threshold of $p<0.001$, uncorrected at the voxel level ($Z=3.09$) (Worsley et al., 1996). Furthermore, region-of-interest (ROI) analyses were performed (small volume correction with spherical search volumes of 16 mm diameter) for anatomically defined small structures, e.g. hippocampus (Friston, 1997). Coordinates to define the ROIs for the frontal eye fields, the lingual and the parahippocampal gyrus and the hippocampus were retrieved from previous studies investigating spatial coding processes or eye movements (Committeri et al., 2004; Iaria et al., 2003; Grosbras et al., 2001).

Other (non-predicted) activations (outside the predefined clusters or ROIs) were observed but are only reported if they were significant at $p<0.05$, corrected for multiple comparisons at the voxel level.

The anatomical location of the peaks within areas of activation was confirmed by inspection of the activation maps overlaid on MNI-normalized structural MRI images.

Eye movement monitoring

Eye movements were monitored using an Applied Science Laboratories Model (ASL, Waltham, MA) adapted to the MR environment. The accuracy of the ASL system is nominally less than 1° of visual angle. The subject's eye was imaged via a mirror designed to allow unobtrusive viewing of the eye by the camera and an unimpeded view of the behavioral stimuli by the subject. Focusing the camera on the eye took 5 to 10 min. Calibration of the subject's point-of-gaze took approximately 5 min using the 9-point calibration routine built into the ASL software. Eye position was sampled at a rate of 60 Hz. Due to technical problems, only the eye movement data of 10 subjects could be acquired.

Eye movement analysis

Horizontal and vertical saccades were defined as eye movements with an initial velocity >20°/s (Zuber et al., 1965) and were categorized as relevant if they had an amplitude >3°; the remaining small saccades were interpreted as correction saccades. Artifacts such as drifts or blinks were identified by visual analysis and removed. The experimenter verified all saccade selections. The number of saccades and the total distance calculated were used as parameters to characterize the eye movements between different conditions. In addition, scan-paths were visualized on scene by ILAB (Gitelman 2002; http://www.brain.northwestern.edu/ilab), see Fig. 3. For both parameters (number of saccades and total distance) a one-way within-subjects ANOVA was used to test for differences between the high-level baseline (table task) and the activation tasks (0°-condition, 45°-condition, 90°-condition, 135°-condition and 180°-condition).

Results

Performance

The percentages of correct judgements of lamp position changes during the activation task and of the presence of the table during the high-level baseline task and reaction times referring to correct responses are presented in Table 1. A repeated measures ANOVA on ranks indicated that there were significant differences ($p<0.001$) between the task performance and the relative change of the PoV for baseline condition vs. all spatial condition ($p<0.05$) and for 0°-condition vs. 90°-condition ($p<0.05$) as well as 0°- vs. 180°-condition ($p<0.05$). The performance of the baseline condition was more accurate than the performance of all spatial conditions and the performance of the 0°-condition was again more accurate than the 90°-condition and the 180°-condition, respectively. For reaction times, a one-way repeated measures ANOVA analysis indicated that there were significant differences ($F(5,12)=69.65$; $p<0.001$) between different changes of points of view. A pairwise multiple comparison (post hoc Tukey Test) showed significant differences ($p<0.05$) between reaction times for baseline condition vs. all spatial conditions ($p<0.001$) and for the 0°-condition vs. all other conditions (0°-condition vs. 45°-condition, $p<0.001$; 0°-condition vs. 90°-condition, $p<0.001$; 0°-condition vs. 135°-condition,

Table 1
Behavioral data and eye movement data (mean±standard deviation)

Task	Performance (% correct answers)	Reaction time (ms)	Number of saccades	Total distance (degree)
High-level baseline (table task)	99%±2	1219 ms±213 ms	7.4±1.8	128.2±15.6
0° task	97%±6	1487 ms±305 ms	9.1±2.0	141.7±20.8
45° task	93%±8	1760 ms±352 ms	9.9±1.8	145.7±16.2
90° task	89%±10	1817 ms±307 ms	9.8±2.1	144.5±20.9
135° task	90%±10	1935 ms±329 ms	9.7±1.7	148.4±16.7
180° task	90%±8	1928 ms±313 ms	10.9±1.6	154.0±13.8

Behavioral data and results of eye movement analysis. Performance (% correct answers) and reaction time (ms), number of saccadic eye movements and total distance (in degree) are listed for the control task and spatial tasks separately (mean±standard deviation).

$p<0.001$ and 0°-condition vs. 180°-condition, $p<0.001$), for the 45°-condition vs. 135°- ($p<0.05$) and 180°-condition ($p<0.001$) and for the 90°- vs. 180°-condition ($p<0.05$). The reaction times for the baseline condition were faster than for all spatial conditions and these for the 0°-condition were faster than for all the other spatial conditions, the reaction times for the 45°-condition were faster than for the 135°- and 180°-condition and the reaction times for the 90°-condition were faster than for 180°-condition. Although there are linear trends for both performance and reaction time across the different spatial conditions, these were statistical significant for reaction times ($r^2=0.87$, $p=0.02$) only.

Testing for within-block learning effects concerning the reaction times for the different spatial conditions separately revealed no statistical significant changes of reaction times within blocks. For the 0°-condition and the 90°-condition, reaction times tendentially decreased from image pair one to image pair three, but for the other three conditions, reaction time increased within the block. Testing between-block learning effects for the different spatial conditions also failed to reveal any statistical significant changes.

After scanning subjects were interviewed about encoding strategies. Three of them had difficulties to define their strategy, the others had encoded the lamp's position either in relation to other objects (6 subjects) and/or in relation to the tilted floor (9 subjects). One subject used also the shadow of the lamp to solve the task.

Eye movements

Eye movements were characterized using two quantitative parameters: the number of saccades and total distance of the scan-path (cumulative saccadic amplitude). Table 1 shows the mean number of saccades and the total distance for the 10 subjects in whom eye movements could be measured for the high-level baseline and each spatial task separately. The number of saccades was seen to increase according to the angular difference between encoding and retrieval PoV (Table 1). A one-way repeated measures ANOVA analysis indicated that there were significant differences ($F(5,9)=19.03$; $p<0.001$) in the number of saccades during the high-level baseline and the experimental conditions. A pairwise multiple comparison revealed significant differences ($p<0.05$) between saccadic eye movements for the baseline condition vs. 0°-/45°-/90°-/135°- and 180°-condition (baseline vs. 0°-condition, $p<0.001$; baseline vs. 45°-condition, $p<0.001$; baseline vs. 90°-condition, $p<0.001$; baseline vs. 135°-condition, $p<0.001$ and baseline vs. 180°-condition, $p<0.001$) and for the 0°-condition vs. 180°-condition ($p<0.05$). The number of saccades was lower for the baseline condition than for all other conditions and the number of saccades for the 0°-condition was lower than for the 180°-condition. As shown for performance and reaction time, there was a linear trend for saccadic eye movements which increased between 0°- and 180°-condition. The correlation analysis revealed that this linear trend was not statistical significant ($r^2=0.685$, $p=0.084$). However, analysis of the saccades separated for coding and retrieval demonstrated a statistical significant correlation between angular difference and retrieval saccades ($r^2=0.80$, $p<0.05$), whereas the correlation between angular difference and encoding saccades ($r^2=0.16$, $p=0.5$) was not significant (Figs. 2A, B).

For total distance of scan-paths, the one-way repeated measures ANOVA analysis indicated that there were significant differences ($F(5,9)=13.1$, $p<0.001$) between the different conditions. The pairwise multiple comparison (post hoc Tukey Test) revealed significant differences ($p<0.05$) between scan-paths for table task condition vs. all other conditions (TT vs. 0°-condition, $p<0.017$; TT vs. 45°-condition, $p<0.001$; TT vs. 90°-condition, $p<0.001$, TT vs. 135°-condition, $p<0.001$, TT vs. 180°-condition, $p<0.001$), for 0°-condition vs. 180°-condition ($p=0.001$) and for 90°-condition vs. 180°- condition ($p<0.05$). Therefore, the scan-paths were shorter for the high-level baseline (table task) than for all other experimental conditions and shorter for 0°- and 90°- condition than for 180°-condition. The linear relationship was also significant ($r^2=0.90$, $p<0.05$).

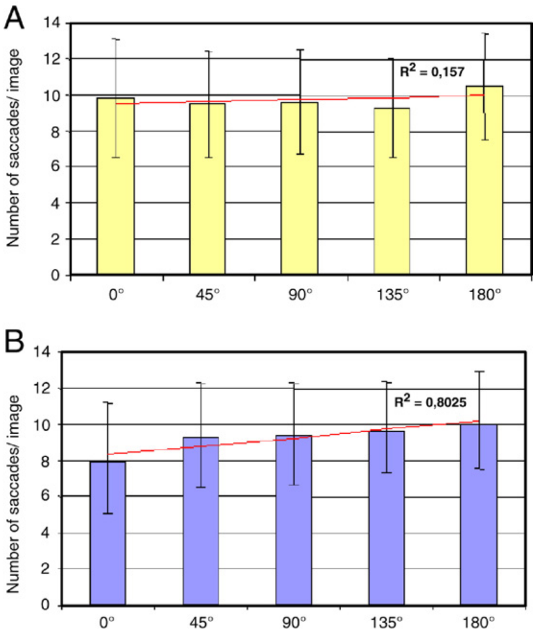

Fig. 2. The diagrams show the mean number of saccades for the activation tasks – separate for each angular difference between encoding and retrieval point of view – during encoding (A) and during retrieval (B). Analysis of saccades separated for encoding and retrieval demonstrated a significant correlation between angular difference and retrieval saccades ($r^2=0.80$, $p=0.04$). There was no correlation between angular difference and encoding saccades ($r^2=0.16$, $p=0.5$).

Secondly, qualitative assessment of the gaze trajectories in the environment was performed by visual inspection. Fig. 3 shows examples of the scan-path during encoding and retrieval lamp position changing PoV 0° or 180° for three subjects. Subjects adopted similar scan-paths and explored a similar area of the room shown in both conditions. For all memory conditions, subjects firstly fixate on a part of the lamp, mostly the base of the lamp, or in some cases also the lampshade, and then used landmarks in the environment to define its exact position by moving their eyes between the chosen landmark and the lamp. Landmarks could be the table-leg, the boundary of the flowerbed and the tree, the wall, the ramp or the pattern of the floor. Predominantly more than one landmark was used. It was not possible to define criteria for the chosen landmark, subjects did not always use the landmark next to the lamp nor did they use the same landmarks during encoding and retrieval of the lamp position. The study design, in principle, allowed a pure egocentric strategy to solve the task in the 0°-condition, but subjects seemed to use landmarks to define the lamp position in all conditions, i.e. suggesting the use of an allocentric strategy in all conditions.

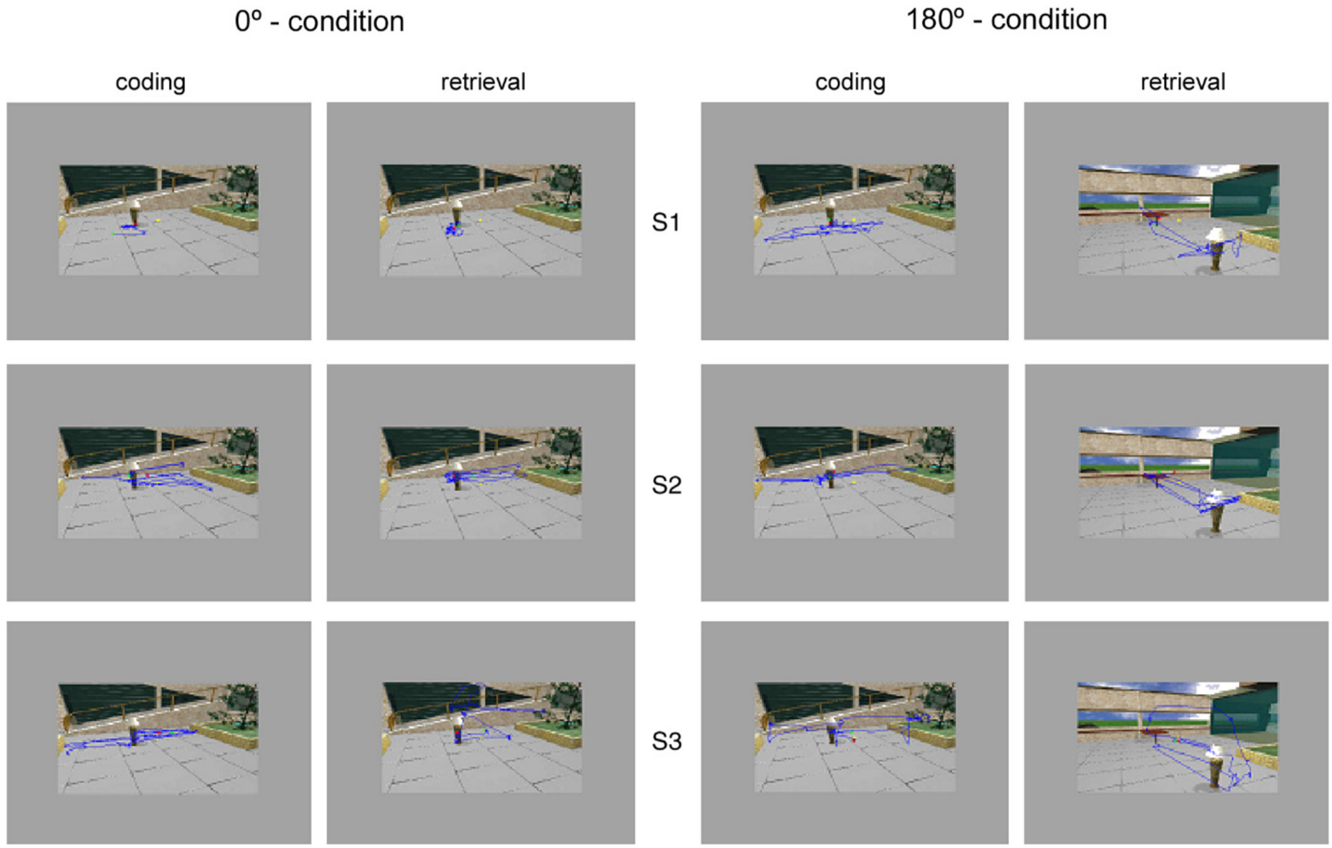

Fig. 3. Individual eye movement patterns (scan-paths) were projected on the explored scene. Examples are presented from three different subjects (S1–S3) for encoding (column 1/3) and retrieval (column 2/4) changing the point of view either 0° (column 1/2) or 180° (column 3/4) [green point = start, red point = end, yellow point = center of the image].

Neural activations

Categorical analysis

Neural activations associated with all experimental conditions (0°-, 45°-, 90°-, 135°- and 180°-conditions) vs. the high-level baseline.

The categorical random effects analysis identified a network consisting of parietal, occipito-temporal and frontal areas activated by all experimental spatial conditions as compared to the high-level baseline (Fig. 4). As listed in Table 2, the activated parietal regions included parts of the superior parietal lobule (adjacent to the intraparietal sulcus), bilaterally, extending ventrally into the inferior parietal lobe and medially to the parieto-occipital sulcus. Furthermore, the middle occipital gyrus was activated. In addition, a left-lateralized activation of the ventromedial temporal cortex was found. This activation included the fusiform gyrus, the lingual gyrus and the posterior part of the parahippocampal gyrus.

In the frontal lobe significant activations were detected in the inferior frontal gyrus, in the middle frontal gyrus (dorso-lateral prefrontal cortex, DLPFC) and in the superior frontal gyrus. The anterior cingulate cortex was also significantly activated. Activations in the superior prefrontal cortex were also found along the precentral gyrus near the junction of the precentral sulcus and superior frontal sulcus. Three distinct peaks were identified, one on the surface of the superior frontal gyrus extending rostrally in the superior frontal sulcus and the second in the deep portion of the precentral sulcus (called superior/medial frontal eye field). The third area was located in the inferior branch of the precentral sulcus close to its junction with the inferior frontal sulcus (the so-called inferior/lateral frontal eye field).

Parametric analyses

Parametric (multiregression) analyses were used to reveal areas whose activity significantly correlated with relative change of the PoV between encoding and retrieval of the lamp position, with performance or the amount of saccadic eye movements (Fig. 5, Table 3).

Activations in the left ventromedial occipital-temporal cortex were identified showing a positive correlation with changing the PoV. These activations included the parahippocampal area (−20/−48/−12, *Z*-value 3.78) and the left lingual gyrus (−12/−72/−4, *Z*-value 4.5) (Figs. 5A, B). No areas were identified showing a negative correlation with changing the PoV. Activity of the hippocampus bilaterally was found to demonstrate a positive correlation with performance (−32/−16/−20; *Z*-value 3.65 and 20/−20/−20; *Z*-value 3.77) (Fig. 5C).

Activation in the right prefrontal area representing superior FEF (28/4/52, *Z*-value 4.5) correlated with the relative number of saccadic eye movements. This activation extended rostrally along the superior frontal sulcus including two submaxima (28/12/56, *Z*-value 3.73 and 32/16/52, *Z*-value 3.69) (Fig. 5D).

Discussion

This study is the first demonstration of neural activity changes in left parahippocampal and lingual gyri in relation to parame-

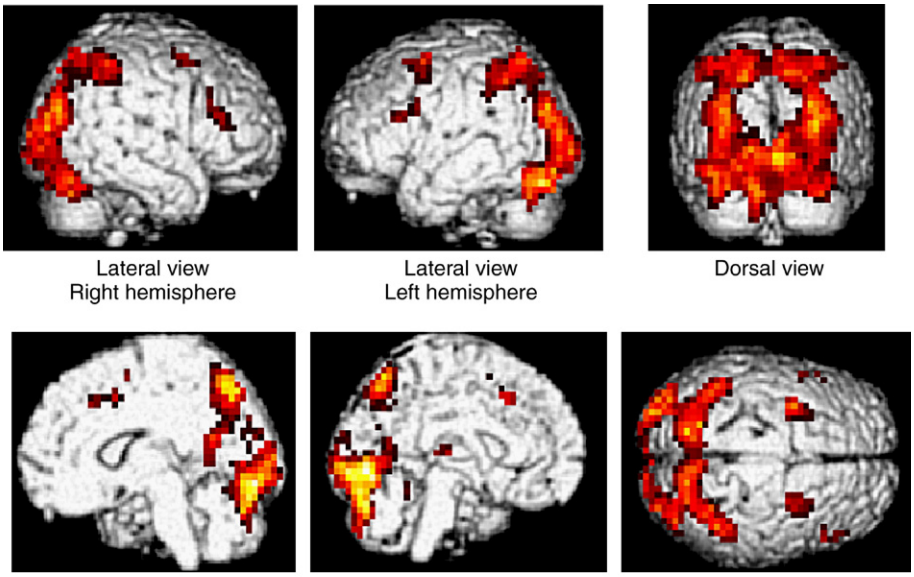

Fig. 4. Significant activations common to all activation tasks (0°-/45°-/90°-/135°-/180°-condition) vs. high-level baseline (table task) are shown on the rendered standard brain (random effect analysis, $p<0.05$, corrected for multiple comparisons at the cluster-level using a height threshold of $p<0.001$, uncorrected, at the voxel-level).

trically changing the perspective in a 3D visuospatial task involving detection of object–location. Furthermore, activation in a hippocampal area correlated with performance. In addition, activity of the superior "deep" FEF (Lobel et al., 2001) correlated with the amount of saccadic eye movements. While the categorical subtraction analysis confirmed the general involvement of a parieto–temporo–frontal network in the current task as identified for tasks of spatial coding or topographical learning (Aguirre et al., 1996; Aguirre and D'Esposito 1997; Burgess et al., 2001; Ghaem et al., 1997; Gron et al., 2000; Maguire et al., 1997, 1998; Mellet et al., 2000), the parametric analyses demonstrated a correlation of activation in the parahippocampal area and the lingual gyrus with the increasing change of PoV between encoding and retrieval indicating a specific role of both areas during allocentric coding strategies.

Behavioral data

Analysis of scan-paths as well as saccadic eye movements (saccades) may reveal information about coding strategies. Several

Table 2
Subtraction analysis of all experimental conditions (0°, 45°, 90°, 135° and 180°) vs. high-level baseline

Frontal cortex								
Inferior frontal gyrus	L	−48/8/28	$k=21$	$Z=3.85$				
Medial frontal gyrus	L	−48/24/24	$k=21$	$Z=3.6$	R	48/24/32	$k=26$	$Z=4.03$
	L	−28/16/56	$k=55$	$Z=3.75$	R	36/8/52	$k=61$	$Z=4.10$
Superior frontal gyrus	L	−32/4/56	$k=55$	$Z=4.84$	R	28/4/52	$k=61$	$Z=4.45$
Anterior cingulate cortex		0/16/44	$k=21$	$Z=3.57$				
Parietal cortex								
Precuneus	L	−12/−64/56	$k=2034$	$Z=4.79$	R	8/−68/56	$k=2034$	$Z=4.95$
Superior parietal cortex	L	−16/−68/44	$k=2034$	$Z=5.22$	R	20/−68/44	$k=2034$	$Z=5.17$
Inferior parietal cortex	L	−36/−52/44	$k=2034$	$Z=5.06$	R	44/−52/44	$k=2034$	$Z=4.78$
Parieto occipital sulcus	L	−16/−60/8	$k=2034$	$Z=4.47$	R	12/−52/12	$k=2034$	$Z=4.57$
Occipital cortex								
Middle occipital gyrus	L	−28/−72/28	$k=2034$	$Z=4.91$	R	32/−72/28	$k=2034$	$Z=6.12$
Temporal cortex								
Lingual gyrus	L	−12/−76/0	$k=2034$	$Z=5.68$				
Parahippocampus	L	−24/−52/−16	$k=2034$	$Z=5.16$				
Fusiform gyrus	L	−24/−72/−12	$k=2034$	$Z=5.12$				

Regions and main peaks of activation common to all activation conditions (0°-condition + 45°-condition + 90°-condition + 135°-condition + 180°-condition) with respect to the table task ($p<0.05$, corrected at the cluster-level using a height threshold of $p<0.001$, uncorrected, at the voxel-level). For each activated area, the coordinates of the maximally activated voxel in MNI space, k-values and Z-values are given.

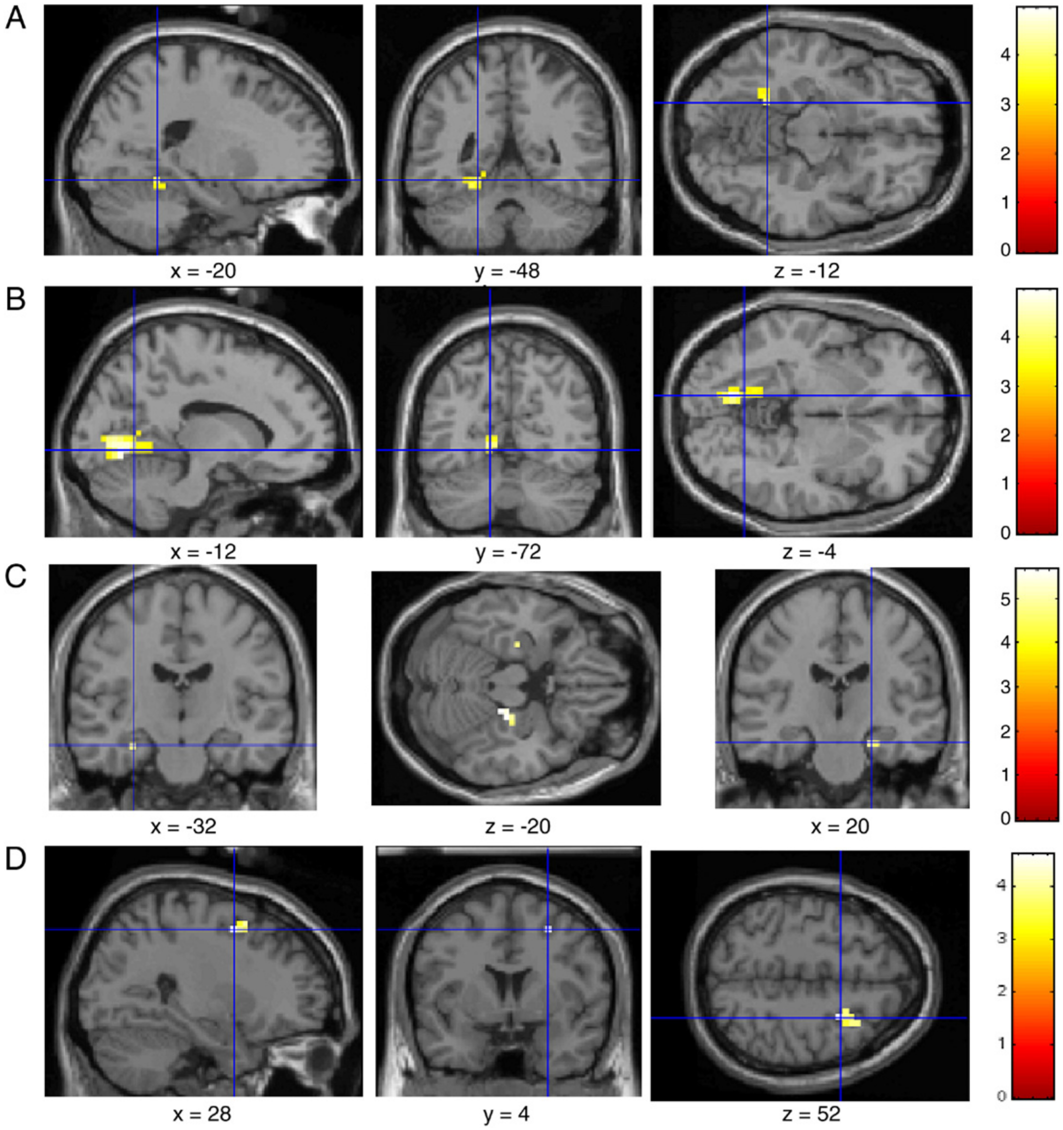

Fig. 5. Projections of the activation foci showing signal increases correlated with angular difference between the point of view during encoding and retrieval (A and B), with task performance (C) or with saccadic eye movements (D) either on sagittal, coronal and transversal slices (A, B and D) or on sagittal and coronal slices (C) of the standard brain: (A) left parahippocampal area (−20/−48/−12, *Z*-value 3.78), (B) left lingual gyrus (−12/−72/−4, *Z*-value 4.5), (C) left (−32/−16/−20, *Z*-value 3.65) and right (20/−20/−20, *Z*-value 3.77) hippocampus and (D) right superior frontal gyrus (28/4/52, *Z*-value 4.5).

studies recording eye movements during cognitive tasks have demonstrated an association of particular cognitive strategies with specific scan-paths (Carpenter and Just, 1983; Hayhoe et al., 1998; Land and Furneaux, 1997). The results indicate that scan-path is influenced by cognitive factors such as planning and sequencing, visuospatial attention and spatial working memory. In further experiments, interference between eye movements and spatial memory was demonstrated (Lawrence et al., 2004; Pearson and Sahraie, 2003).

During the exploration of the current virtual scene, subjects performed a number of saccades which significantly increased with changing the PoV between coding and retrieval. Although it is well known that cognitive factors related to instruction or scene complexity lead to an increased number of saccades during visual search, this particular modification of scan-path characteristics during perspective change has not been described before. A more detailed analysis separating the saccades during encoding and during retrieval demonstrated a stronger correlation between angular difference of the PoV and retrieval saccades than encoding saccades. Given the fact that subjects do not know the amount of PoV change during retrieval, it is not surprising that subjects use a constant strategy during encoding. After changing PoV, eye movements are used for spatial updating as well as for controlling the lamp position. However, the eye movement measurements could not disentangle these two processes during retrieval.

In our study, for all memory conditions subjects defined the lamp position by a number of saccadic eye movements between the lamp and landmarks in the environment. It was not possible to define criteria for the chosen specific landmark, subjects neither consistently used the landmark next to the lamp nor did they use the same landmarks during encoding and retrieval of the lamp position. The study design, in principle, allowed a pure egocentric strategy to solve the task in the 0°-condition, but subjects used landmarks to define the lamp position in all conditions, thus employing allo-

Table 3
Parametric analyses

Positive correlation with relative change of the point of view (PoV)				
Parahippocampal area	L	−20/−48/−12	k=73	Z=3.78
Lingual gyrus	L	−12/−72/−4	k=73	Z=4.5
Positive correlation with task performance				
Hippocampus	L	−32/−16/−20	k=3	Z=3.65
	R	20/−20/−20	k=7	Z=3.77
Positive correlation with the amount of saccadic eye movements				
Superior FEF	R	28/4/52	k=9	Z=4.5

Results of the parametric analyses. Given are the coordinates of the maximally activated voxel in MNI space, k-values and Z-values for the regions whose activity showed a positive correlation with relative change of the point of view (PoV), with task performance, or with the amount of saccadic eye movements.

centric strategies during all PoV changes. This finding is supported by the results of the postscanning debriefing of the subjects about their encoding strategies. Predominantly, subjects stated to have coded the lamp position in relation to landmarks in the 3D environment. That means allocentric strategies were involved in all spatial conditions including the 0°-condition.

With the increase of angular difference between encoding and retrieval PoV, performance decreased and reaction times increased. Such an increase of reaction times has been found in previous neuropsychological studies (Easton and Sholl, 1995; Zacks and Tversky, 2000). It was interpreted as the time needed to perform a mental transformation from the old to the new PoV reflecting an automatic updating of the internal map of the environment with the actual position. With increasing shifts in PoV, subjects need more time to mentally transform the encoding PoV to the retrieval PoV.

Taken together, behavioral results and eye movement analysis reveal allocentric coding strategies in all memory conditions independent of the shift in PoV. They are in line with the allocentric model of a combination of spatial reorientation processes continuously updating the subject's position and comparing actual lamp position with a constant external reference frame. As mentioned above, the behavioral data (performance, reaction time and eye movements) could not disentangle these processes. However, we hypothesize that spatial reorientation processes seem to have been more engaged with increasing angular difference between PoV resulting in an increase of reaction time and saccadic eye movements and in a decrease of performance. Based on the behavioral data, allocentric specific areas may be identified in which activation is modulated by angular difference in PoV. In accordance to other studies (e.g. Iaria et al., 2003; Wolbers and Buchel, 2005), hippocampal involvement may be demonstrated by showing a correlation of its activation with performance.

Neural activations

In fact, a parieto-frontal network extending to the ventromedial occipital-temporal cortex was revealed by the categorical comparison, reflecting involvement of this network in all conditions. A similar network was previously described for navigation tasks and topographical memory (Aguirre et al., 1996; Aguirre and D'Esposito 1997; Burgess et al., 2001; Ghaem et al., 1997; Maguire et al., 1997, 1998; Mellet et al., 2000). Surprisingly, there was no activation of the hippocampus proper.

Medial temporal lobe (parahippocampus vs. hippocampus)

In the current study, only the parahippocampus–not the hippocampus proper–was activated during the visuospatial memory tasks in 3D as demonstrated by the categorical analysis. Furthermore, the parametric analysis failed to show a significant correlation between increasing change of the PoV and hippocampal activation.

Parahippocampus

The current results indicate a special role of the parahippocampus in spatial memory. Recent lesion studies support this hypothesis (Barrash et al., 2000; Bohbot et al., 1998, 2000). Bohbot et al. (1998) showed that patients with a right parahippocampal lesion were impaired on a spatial memory task while subjects with hippocampal lesions were not. The authors suggest that the parahippocampus plays a major role during integration of scenes from multiple views (Bohbot et al., 2000) rather than a special role for object–location memory (Bohbot et al., 1998; Stepankova et al., 2004). This notion fits well with the concept of our study. Furthermore, Barrash et al. (2000) could demonstrate that parahippocampal lesions seem to be primarily responsible for topographical amnesia. Our results are also in line with the results of the few functional imaging studies specifically investigating the network related to allocentric coding (Committeri et al., 2004; Galati et al., 2000; Zacks et al., 2002). All of these studies found no significant activation of the hippocampus proper, but of the parahippocampus. For single subjects Galati et al. (2000) demonstrated that a right parahippocampal area was more activated when directly comparing an object-based and an egocentric task. Activation of a right parahippocampal area was also seen during an environment-centered object-coding in the study of Committeri et al. (2004). Epstein et al. (2003) demonstrated a stronger activation of the parahippocampus for identical than for changed viewpoints. They suggested that scene representations in the parahippocampus seem to be viewpoint specific and hypothesized that activity in the parahippocampus codes the relationship between the subject and the environment. This notion is consistent with the results of our parametric analysis which revealed a correlation of left parahippocampal activation with the increasing change of the PoV between encoding and retrieval, as with increasingly changing PoV the demand for updating one's position in the environment as a prerequisite for utilizing allocentric reference systems also increases. These results corroborate our hypothesis that increasing change of the PoV leads to increasing demands on allocentric coding strategies and accordingly on medial temporal structures supporting allocentric coding.

Interestingly, the left and not the right parahippocampus was activated in our study. In contrast, some previous lesion studies have found that the right parahippocampus and hippocampus were predominantly responsible for spatial memory (Bohbot et al., 1998, 2000, Feigenbaum and Morris, 2004). On the other hand, Bohbot et al. (2002) found subjects with left parahippocampus lesions more impaired during an object location task than subjects with right parahippocampal lesions and Barrash et al. (2000) demonstrated a serve impairment of topographical learning in patients with left parahippocampal damage. The involvement of the left parahippocampus in spatial memory is also underlined by several neuroimaging studies demonstrating bilateral parahippocampal activations during spatial memory tasks (Aguirre et al., 1996; Burgess et al., 2001; Gron et al., 2000).

In the rostral part of the lingual gyrus–an area known as the lingual landmark area (Aguirre and D'Esposito, 1999)–the level of activation also increased with increasing change of the PoV. Committeri et al. (2004) discussed that activation of this area reflects the matching processes between the environment seen from the actual PoV and stored environmental representations. While during the 0°-condition presented and stored environmental representations are identical, with increasingly changing the PoV a more intensive matching process will be required. After this basic step of topographical orientation further allocentric coding processes were used to solve the spatial task. However, the study design did not allow to further disentangle these two processes.

Hippocampus

In several lesion studies (Abrahams et al., 1997; King et al., 2002; Lambrey et al., 2003) manipulating the PoV within 3D space revealed an impairment of spatial memory in patients with hippocampal lesions. This was interpreted as a specific dependence of allocentric coding on the hippocampus. However, in the present study using a similar paradigm no significant hippocampal activation was found by categorical subtraction analysis. One explanation for the lack of hippocampal activation in the present study is that the task was not complex enough. Also Lambrey et al. (2003) discussed that similar tasks could be solved by simple object location memory even for greater differences between encoding and retrieval PoV. This is in line with the observation that also the performance of Jon, the patient with bilateral hippocampal lesions, was not impaired concerning object–location memory using only one item in the shifted-PoV condition (King et al., 2002). Furthermore, in earlier studies using object location tasks, hippocampal deficits were demonstrated only by using a significant delay between encoding and retrieval (Holdstock et al., 2000). This suggests that subjects may be able to compensate impaired hippocampal function by using parietal (egocentric) or parahippocampal (allocentric) coding strategies—but that this compensation degrades with time or the number of stored objects.

To understand the (differential) functional role of the parahippocampus and the hippocampus in spatial tasks and navigation, it is important to consider the nature of the adopted paradigms. Processing of spatial information in visual scenes (Epstein and Kanwisher, 1998) and the perception of buildings (Aguirre et al., 1998) exclusively activates the parahippocampus. In addition, the parahippocampus is involved in the identification of landmarks (Avila et al., 2006) and in the extraction of distances to landmarks (Burgess et al., 2001; Hartley et al., 2000; O'Keefe and Burgess, 1996). In contrast, the hippocampus is thought to be involved in way-finding (Ghaem et al., 1997; Maguire et al., 1996, 1997, 1998; Shelton and Gabrieli, 2002) and route memory (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Maguire et al., 1997). Wolbers and Buchel (2005) discuss a role of the hippocampus in integrating between local aspects of places and superordinate entities. Thus, these results provide evidence that parahippocampal areas are required for the more perceptual aspects of spatial processing and that the hippocampus seems to be necessary for more complex navigation (or longer storage of that information over time) which was – in fact – not demanded in the current study.

Another aspect of hippocampal activation has to be taken into account. Recent studies demonstrated that the hippocampus is involved in place learning allowing subjects to navigate. In these studies the hippocampal activation correlated with performance or learning effects (Hartley et al., 2003; Iaria et al., 2003; Maguire et al., 1998; Wolbers and Buchel, 2005). Hartley et al. (2003) and Iaria et al. (2003) found that stronger activation of the right hippocampus correlated with better performance. Wolbers and Buchel (2005) demonstrated a correlation between learning effects and left hippocampal activation. In line with these data, our parametric analysis revealed areas in the left and right hippocampus whose activity correlated with performance.

Parietal cortex

Categorical subtraction analysis revealed parietal cortical involvement – including areas in the superior parietal cortex, along the parieto-occipital and intraparietal sulci – during the current 3D-visuospatial memory task. These findings are consistent with the role of parietal regions in spatial localization (Galati et al., 2000, 2001; Vallar et al., 1999). In particular several functional imaging studies have demonstrated activations in posterior parietal regions associated with egocentric perspective transformations (Aguirre and D'Esposito, 1997; Bonda et al., 1996).

The current results also support recent models proposing a cooperation between egocentric and allocentric coding strategies to solve 3D-spatial tasks including navigation (Arbib, 1997; Burgess et al., 2002). Such a cooperation could also be proposed for our study: First, subjects encoded a lamp position by transforming the primary egocentrically processed visual input into view(er)-independent allocentric codes and, secondly, after changing PoV the allocentric information has to be translated again into parietal egocentric representations taking into account the new (retrieval) PoV.

Consistent with these results, Mellet et al. (2000) found the left dorsal precuneus activated during mental navigation in an environment learned from a route perspective in contrast to mental navigation learned from a survey perspective and discussed a contribution of this area in transformation of route coordinates into survey coordinates.

Activation of precuneus was also demonstrated when additional processing was required to compute new object-to-self relations after rotation (Vogeley and Fink, 2003). Finally, the relevance of parietal areas for mental transformation is supported by studies modulating task difficulty: Carpenter et al. (1999) identified parietal regions as most responsive to the manipulation of angular disparity between Shepard–Metzler stimulus pairs and in a PET study by Harris et al. (2000) changes in rCBF in a right parietal area along the intraparietal sulcus were correlated with the rotational demands of a task using alphanumerical stimuli.

Prefrontal cortex

The frontal network identified during the spatial coding task included areas in the superior frontal lobe, in the ventrolateral prefrontal and in the dorsolateral prefrontal cortex.

Prefrontal areas and eye movements

Categorical subtraction analysis consistently revealed distinct bilateral activations in and around the superior prefrontal sulcus. Single subject analysis revealed a similar activation pattern concerning these areas in nearly all subjects. The activated regions comprised the Frontal Eye Fields (FEF) involved in the execution of eye movements (Grosbras et al., 2001; Lobel et al., 2001; Paus, 1996; Petit et al., 1996, 1997). The FEF are involved in the control of all intentional saccades, including memory guided saccades and predictive saccades (Gaymard et al., 1999; Israel et al., 1995; Rivaud et al., 1994). Some eye movements, such as visually guided saccades (Gaymard et al., 1999; Rivaud et al., 1994) and smooth pursuit (Gaymard et al., 1999; Heide et al., 1996; Petit et al., 1997; Rivaud et al., 1994), appear to be controlled more specifically by the FEF. The frontal eye fields constitute, with the supplementary eye field (SEF), a network of regions that are activated in overt (Petit et al., 1993), covert (Lang et al., 1994) and memorized (Berthoz et al., 1992) saccades as well as during fixation.

In our study, visually and memory guided saccades had to be executed to solve the spatial memory task. The eye movement analysis demonstrated saccadic eye movements – numerically different between control and activation task – for each subject.

Classically two eye-movement-related regions can be separated for saccades called inferior/lateral and superior/medial FEF (Grosbras et al., 2001; Heide et al., 2001; Lobel et al., 2001; Luna et al., 1998). In our study these distinct areas were separated: one located in the deep portion of the precentral sulcus, near its junction with the superior frontal sulcus corresponding to the superior FEF (Grosbras et al., 2001; Lobel et al., 2001; Luna et al., 1998), the second located in the inferior branch of the precentral sulcus close to its junction with the inferior frontal sulcus related to the inferior FEF (Grosbras et al., 2001; Heide et al., 2001; Luna et al., 1998). In addition, an activation on the surface of the superior frontal gyrus near the junction of the precentral and superior frontal sulcus was found. The results of the parametric analysis demonstrated for the superior FEF and for the adjacent area around the superior frontal sulcus a correlation of activation with number of saccadic eye movements. Such a superior frontal activation was not described during the execution of eye movements (Grosbras et al., 2001; Lobel et al., 2001; Luna et al., 1998; Petit et al., 1996, 1997).

However, since the parametric regressors for eye movements are correlated with those for performance and for changing the PoV, we cannot exclude an additional influence of these factors on the activity of the superior FEF. In fact, several functional imaging studies found superior frontal activations close to the activations observed in the present study during spatial memory tasks (Courtney et al., 1998; Jonides et al., 1993; Petit et al., 1996). Mellet et al. (1996) found a bilateral superior frontal sulcus activation during mental construction of 3-D cube assemblies based on auditorily presented instructions. Committeri et al. (2004) demonstrated that this region in the superior frontal cortex appeared to be more involved in an environment-centered than in an object-centered spatial coding task. Nevertheless, our results indicate that activation in this superior frontal area *also* depends on eye movements.

Conclusion

A fronto–parieto–temporal network including the parahippocampal and lingual gyrus was activated in a three-dimensional visuospatial memory task. Eye movements indicated an object-to-environment (allocentric) coding strategy to locate the object from different PoV. The increase of reaction times with increasing perspective change supports the notion of a simultaneous updating of subject's position during the task pointing to parallel allocentric/egocentric strategies.

The activation of a parahippocampal but not a hippocampal area emphasizes the specific role of the parahippocampus during spatial coding. The correlation of activation in this area as well as in the left lingual area with increasing change of the point of view is likely to reflect continuous updating between internal maps and external representations of the environment as the basis for further allocentric coding processes. Thus, the present study extends the idea of cooperation between egocentric and allocentric coding systems to solve spatial tasks from different point of views by including a step of general orientation.

Acknowledgments

Grant: D. Schmidt was supported by a scholarship from the French Embassy Berlin. G.R.F. is supported by the Deutsche Forschungsgemeinschaft (DFG-KFO112).

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