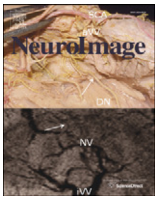
NeuroImage 60 (2012) 1630–1637

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Distinct neural networks underlie encoding of categorical versus coordinate spatial relations during active navigation

Oliver Baumann *, Edgar Chan, Jason B. Mattingley

The University of Queensland, Queensland Brain Institute & School of Psychology, St Lucia 4072, Australia

ARTICLE INFO

Article history:
Received 27 September 2011
Revised 14 January 2012
Accepted 17 January 2012
Available online 24 January 2012

Keywords:
Categorical
Coordinate
Spatial
Memory
Navigation

ABSTRACT

It has been proposed that spatial relations are encoded either *categorically*, such that the relative positions of objects are defined in prepositional terms; or in terms of visual *coordinates*, such that the precise distances between objects are represented. In humans, it has been assumed that a left hemisphere neural network subserves categorical representations, and that coordinate representations are right lateralised. However, evidence in support of this distinction has been garnered exclusively from tasks that involved static, two-dimensional (2D) arrays. We used functional magnetic resonance imaging (fMRI) to identify neural circuits underlying categorical and coordinate representations during active spatial navigation. Activity in the categorical condition was significantly greater in the parietal cortex, whereas the coordinate condition revealed greater activity in medial temporal cortex and dorsal striatum. In addition, activity in the categorical condition was greater in parietal cortex within the left hemisphere than within the right. Our findings are consistent with analogous studies in rodents, and support the suggestion of distinct neural circuits underlying categorical and coordinate representations during active spatial navigation. The findings also support the claim of a left hemispheric preponderance for the processing of categorical spatial relations.

Introduction

As humans navigate, they acquire knowledge about their environment, such as the spatial layout of landmarks. This information is encoded and stored in memory, allowing us to find our way back to a desired location within the same environment. Despite many decades of research, surprisingly little is known about the encoding of visual–spatial relationships during active exploration of novel environments. Much of the literature on human visual–spatial memory has been derived from tasks involving static, two-dimensional (2D) arrays (c.f. Jager and Postma, 2003). Relatively less attention has been paid to memory encoding of spatial relationships for dynamic, three-dimensional (3D) displays in which participants actively explore virtual environments that mimic conditions encountered in real-world navigation. By contrast, research on mnemonic mechanisms for the processing of spatial relationships in rodents has relied almost exclusively on tasks in which the animal must learn the layout of a maze or arena in 3D, based upon continually changing sensory inputs encountered during exploration (e.g. Goodrich-Hunsaker et al., 2005). Not surprisingly, therefore, the scope and predictions of models of spatial memory have been inconsistent across the human and rodent literature.

In humans, two distinct processes for encoding spatial relationships have been distinguished (Gallistel, 1990; Jager and Postma, 2003; Kosslyn, 1987). *Categorical* spatial relationships refer to equivalence classes of spatial positions relative to a perceptually distinguishable reference object (e.g., left/right, below/above, inside/outside). By contrast, *coordinate* spatial relationships refer to precise spatial locations, which can be expressed in terms of distances between objects (e.g., Object A is located 2.1 m from Object B). Reasonably compelling behavioural and neural evidence has been garnered in support of the distinction between categorical and coordinate spatial relationships. Particular importance has been attached to the suggestion that the left cerebral hemisphere subserves categorical processing, whereas the right hemisphere subserves coordinate processing (e.g. Jager and Postma, 2003; Palermo et al., 2008; Trojano et al., 2002). The proposed lateralization effect is most consistently found in the parietal cortex (c.f. Jager and Postma, 2003), but similar claims have been made for frontal areas (Slotnick and Moo, 2006; Van der Ham, et al., 2009). Kosslyn (1987; 1989) originally proposed that the left hemisphere advantage for categorical processing emerged from its preexisting dominance for language, particularly with respect to category formation, and that the right hemisphere advantage for coordinate processing is related to its fundamental role in spatial navigation. Crucially, however, the left hemisphere advantage for categorical

---

* Corresponding author. Fax: +61 7 3346 6301.
E-mail addresses: o.baumann@uq.edu.au, oliverbaumann@yahoo.de (O. Baumann).

1053-8119/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2012.01.089

processing has also been observed in monkeys (Jason et al., 1984; Vogels et al., 1994) and pigeons (Yamazaki et al., 2007), implying that the processing of categorical relations need not invariably arise from verbal codes (see also van der Ham and Postma, 2010 for complementary results in humans).

An alternative hypothesis suggests that the hemispheric asymmetry for categorical and coordinate spatial relations arises from a difference in the receptive field properties of the two hemispheres (Chabris and Kosslyn, 1998; Jacobs and Kosslyn, 1994; Kosslyn et al., 1992). According to this account, the right hemisphere has a bias towards encoding outputs from neurons with relatively large receptive fields, whereas the left is biased to neurons with relatively small receptive fields; the assumption is that these biases might in turn account for the hemispheric differences in categorical and coordinate representations, respectively. The receptive field hypothesis is broadly consistent with the observation that inputs from the magnocellular visual pathway are more pronounced in the right hemisphere, and that inputs from the parvocellular visual pathway are more pronounced on the left (Hellige and Cumberland, 2001; Kosslyn, et al., 1992; Roth and Hellige, 1998). These and similar findings have led some researchers (e.g., Vauclair et al., 2006) to suggest that the categorical versus coordinate distinction should be rephrased in terms of a distinction between perceptual processes operating at global and local spatial scales, respectively, whereas others (Laeng et al., 2011; Michimata et al., 2011) have proposed interactive effects of global and local attention on the processing of categorical and coordinate spatial relations.

Critically, the hypothesis of a hemispheric asymmetry for categorical versus coordinate spatial relations is based mainly upon findings from tasks in which participants are asked to encode and recall visual stimuli within static, 2D displays. For example, in seminal work by Kosslyn et al. (1989) participants judged whether a dot was on or off the contour of a line drawing of a blob (the categorical task) or whether or not a dot was within 2 mm of the contour (the metric task). Even though other studies have employed more realistic stimuli, such as meaningful objects (Saneyoshi et al., 2006) and natural scenes (van der Ham, et al., 2011), it remains unclear whether the categorical/coordinate distinction proposed for spatial memory also holds for spatial navigation, in which individuals must build up a representation of the external environment based upon continually changing visual inputs obtained from a first-person perspective. Indeed, recent brain imaging studies have found *bilateral* activity during both categorical and coordinate spatial processing tasks (e.g. Amorapanth et al., 2010; Martin et al., 2008), challenging the strict hemispheric dichotomy originally proposed for these two processes. This apparent inconsistency has given rise to an alternative model, known as the continuous spatial coding hypothesis (Martin et al., 2008; Van der Lubbe et al., 2006). According to this proposal, the same brain areas are involved in processing categorical and coordinate relations, with the balance being determined by other cognitive factors such as attention and executive control. Several lines of evidence contradict the idea of continuous spatial coding (Kosslyn et al., 1992; Slotnick et al., 2001), however, and this hypothesis has therefore been the subject of considerable debate (e.g. van der Ham et al., 2009).

In contrast to the behavioural and brain imaging studies of spatial learning in humans, the neural circuits underlying categorical and coordinate encoding in rodents have been investigated exclusively for active navigation in 3D environments (Goodrich-Hunsaker et al., 2005; Long and Kesner, 1998a, 1998b). Here, there is an emerging consensus in favour of structural specialisation for categorical and coordinate representations in the rodent brain, but no hemispheric asymmetry. Thus, for example, it has been shown that rats with hippocampal lesions display deficits in coordinate spatial learning tasks, but behave normally in categorical tasks. On the other hand, rats with parietal lesions show significant impairments in categorical spatial memory but not in coordinate tasks. Thus, whereas rodent research clearly supports a structural specialisation (hippocampus vs. parietal cortex) for coordinate and categorical representations, the human literature has tended to suggest a hemispheric specialisation (left vs. right).

As suggested earlier, one possible explanation for the apparent discrepancy between human and rodent models of spatial relations is that the relevant human studies have employed static 2D stimulus arrays, whereas the rodent studies have used 3D mazes and arenas that the animal must learn through active exploration. This account is supported by previous studies in humans that have identified differences in behaviour and brain activation for spatial environments encoded from a 2D, overhead perspective versus a 3D, ground-level perspective (Mellet et al., 2000; Shelton and Gabrieli, 2002). Moreover, it has been suggested that active exploration leads to the formation of more flexible (Sun et al., 2004) and robust (Christou and Bülthoff, 1999) spatial representations than passive exploration. To date, however, no study has investigated the neural circuits responsible for encoding coordinate and categorical spatial relations under conditions in which participants explore a novel 3D virtual arena, analogous to those employed in rodent research.

Here we used event-related fMRI and a novel virtual navigation task to isolate differences in the neural activity patterns underlying the formation of navigation-based categorical and coordinate spatial representations. Participants were required to actively navigate a virtual arena and to encode either the distance of a target object relative to a reference landmark (coordinate task), or the target object's relative position defined with respect to the reference landmark (categorical task). We limited the memory load to one item in both conditions to minimise differences in task difficulty and to avoid taxing general cognitive resources too heavily (Collette and Van Der Linden, 2002; Morris and Jones, 1990). Consistent with the structural specialisation hypothesis, derived from rodent studies, we predicted more robust parietal activity during the encoding of categorical spatial relations than during the encoding of coordinate relations. By contrast, we predicted stronger hippocampal activity in the coordinate task than the categorical task, consistent with the suggestion that the human hippocampus represents distance information during active spatial navigation (Morgan et al., 2011).

Material and methods

Participants

Fourteen right-handed, healthy volunteers (7 males, mean age 21.5 years, SD = 2.0) with normal or corrected-to-normal vision gave written, informed consent to participate in the study, which was approved by The University of Queensland Ethics Committee.

Task and stimuli

We used the Blender open source 3D content creation suite (The Blender Foundation, Amsterdam, The Netherlands) to create a virtual environment and administer the navigation task. Participants moved through the virtual arena by means of a joystick held in their right hand. The arena consisted of an infinite plane with a pebble-like texture covering the ground to enhance its 3D quality (Fig. 1a). It contained two visual objects, with one serving as a landmark and the other as a target. The landmark was a cylinder with a virtual height of 2.2 m and a diameter of 1 m. The landmark was rendered in four different colours (red, blue, green, yellow), with each colour occupying exactly one quarter of its circumference, effectively dividing the arena into four quadrants (see Fig. 1b). The target was a yellow pyramid with a virtual height and width of 50 cm. The pyramid had a virtual 'light beacon', which projected vertically from the apex, to allow its position to be determined when occluded by the landmark.

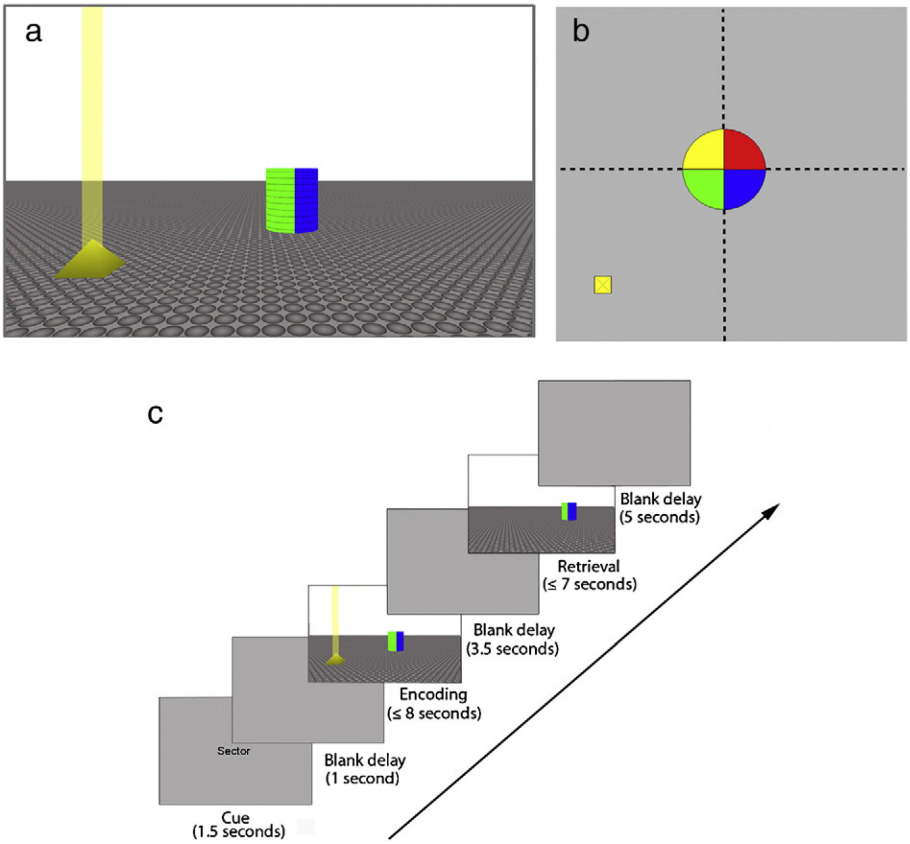


Fig. 1. Schematic of the virtual environment used in the navigation task. (a) Example display of the virtual environment during the encoding phase of an experimental trial. The green and blue side of the reference landmark is shown. The target is shown in yellow, with a virtual light beacon projecting vertically from its apex. (b) A schematic, top–down view on the virtual environment, illustrating the role of the colour-coded reference landmark (the dashed lines were not visible in the actual experiment). (c) Sequence of events in a typical experimental trial. Participants entered the environment and navigated to the target before pressing a button on the joystick to indicate when they had reached its location. The encoding phase was followed by a short delay period (3.5 s). In the subsequent retrieval phase, participants always re-entered the arena from a different location than in the encoding phase (shifted by 90°, 180° or 270°, with equal probability). They were required to navigate to a position that corresponded either with the remembered *distance* (coordinate condition) or *quadrant* (categorical condition) of the target, which was now absent from the display, and to indicate via the joystick when they had arrived there. The next trial commenced after a further delay of 5 s.

In the *categorical condition*, participants were instructed to remember the quadrant in which the target object was located, as defined by the colour-code of the central landmark. (In Fig. 1b, the target is located within the green quadrant.) In the *coordinate condition*, participants were instructed to remember the distance between the target object and the landmark, irrespective of the quadrant in which the target appeared. On each trial, participants were instructed to navigate to the target and press a button on the joystick to indicate when they had arrived there. Participants were trained to complete the initial *encoding phase* within a time limit of 8 s. The encoding phase was followed by a short delay period (3.5 s) in which the display remained blank. In the subsequent *retrieval phase*, participants re-entered the arena from a location that was always different from that used in the encoding phase (shifted by 90°, 180° or 270°, with equal probability). During retrieval, the landmark appeared in its original location, but the target pyramid was now absent. In the categorical condition participants were required to navigate back to the remembered quadrant of the target's location, ignoring their distance from the central landmark, and to press a button on the joystick when they arrived there. In the coordinate condition participants were required to navigate back to the remembered distance of the target from the landmark, irrespective of the quadrant, and to press a button on the joystick when they arrived there.

The retrieval phase had a time limit of 7 s, and was included so that we could measure performance as a function of the two task conditions. Note that we did not compare neural activity arising from the retrieval phase of the task, since our pilot work revealed that participants' virtual movement patterns were different during the categorical and coordinate conditions. Following completion of the retrieval phase, the display remained blank for 5 s before participants commenced the next trial. Fig. 1c shows the sequence of events in a typical trial.

The locations of the landmark and target object within the arena were altered on every trial, to ensure that a completely new spatial layout had to be learned on each occasion. The study consisted of 60 categorical trials and 60 coordinate trials, which were randomly intermingled in five separate runs of equal length. Participants received a cue prior to each trial to indicate whether they were to perform the categorical or coordinate task.

In the categorical condition we counted categorical errors – defined as trials in which the target quadrant selected by the participants did not match the actual target quadrant in which it appeared during the encoding phase – to provide an index of performance. In the coordinate condition we recorded participants' absolute metric error, in virtual meters, for judging the distance between the landmark and the remembered location of the target. We also recorded other behavioural variables related to participants' movements within the virtual environment, including the speed and duration of their movements, and the unsigned rotation (defined as the cumulative sum of the participants' angular motion within the virtual environment).

MRI acquisition

Brain images were acquired on a 3 T MR scanner (Trio; Siemens, Erlangen, Germany) with a 32-channel head coil. For the functional data 33 axial slices (slice thickness, 4 mm) were acquired in an interleaved order, using a gradient echo echo-planar T2*-sensitive sequence (repetition time, 2.21 s; echo time, 30 ms; flip angle, 90°; matrix, 64×64; field of view, 210×210 mm; voxel size, 3.3×3.3×4.0 mm). On average 222 (SD = 22) volumes per session were acquired for each participant. A liquid crystal display projector back-projected the virtual environment onto a screen positioned at the head end of the scanner gantry. Participants lay on their backs within the bore of the magnet and viewed the stimuli via a mirror that reflected the images displayed on the screen.

Image processing and statistical analysis of fMRI data

Image processing and statistical analyses were performed using SPM5 (Wellcome Department of Imaging Neuroscience, UCL, London, UK). Functional data volumes were slice-time corrected and realigned to the first volume. A T2*-weighted mean image of the unsmoothed images was co-registered with the corresponding anatomical T1-weighted image from the same individual. The individual T1-image was used to derive the transformation parameters for the stereotaxic space using the SPM5 template (Montreal Neurological Institute (MNI) Template), which was then applied to the individual co-registered EPI images. Images were then smoothed with an 8-mm full-width half maximum (FWHM) isotropic Gaussian kernel. Encoding and retrieval periods for the categorical trials and the coordinate trials were modelled separately as boxcar functions convolved with a hemodynamic response function (HRF), with predicted responses always covering the entire period. Specific effects were tested with appropriate linear contrasts of the parameter estimates, and the corresponding contrast images were subsequently entered into a random effects analysis. Main effects of object–location encoding in the two conditions were assessed with single-sample t-tests.

Results

Behavioural data

Fig. 2 shows the average duration, movement speed and extent of rotational movement for the encoding and retrieval phases of the categorical and coordinate conditions. In the encoding phase there were no significant differences between the categorical and coordinate conditions for all three behavioural parameters (paired *t*-test, $p > 0.05$). By contrast, and as expected, in the retrieval phase duration and rotational movement were significantly greater in the categorical condition than in the coordinate condition (paired *t*-test, $p < 0.001$). None of these behavioural variables correlated significantly with absolute metric errors or categorical errors ($p > 0.05$), nor was there any significant correlation between accuracy in locating the target and trial number ($p > 0.05$), indicating that behavioural performance remained consistent over the course of the experiment. In the categorical condition, participants navigated to an incorrect quadrant on 4.28% (SE = 0.67) of trials. In the coordinate condition, the average metric error was 1.2 virtual meters (SE = 0.1).

Brain imaging data

Brain imaging data were analysed separately for the encoding phase of the categorical and coordinate navigation tasks. We performed exploratory whole-brain analyses to identify regions that were differentially activated during the two conditions. In addition, consistent with recent literature in the field (Baumann et al., 2010; Doeller et al., 2008; Epstein et al., 2007; Wolbers, et al., 2007), we sought to increase the sensitivity of our analyses for a set of selected areas of the brain known to be involved in spatial learning and navigation. These were the hippocampus (e.g. Doeller et al., 2008; Ekstrom and Bookheimer, 2007; Wolbers et al., 2007), the parahippocampus (e.g. Ekstrom and Bookheimer, 2007; Epstein et al., 2007; Janzen and van Tourennout, 2004), the striatum (e.g. Bohbot et al., 2004; Doeller et al., 2008), and the inferior and superior parietal lobule (c.f. Jager and Postma, 2003). All regions of interest (ROIs) were defined separately for the left and right hemispheres using the AAL atlas (Tzourio-Mazoyer et al., 2002). Brain regions were counted as active if they surpassed a statistical threshold of $p = 0.05$ (corrected for multiple comparisons), on either a voxel- or cluster-level (height threshold $p = 0.005$).

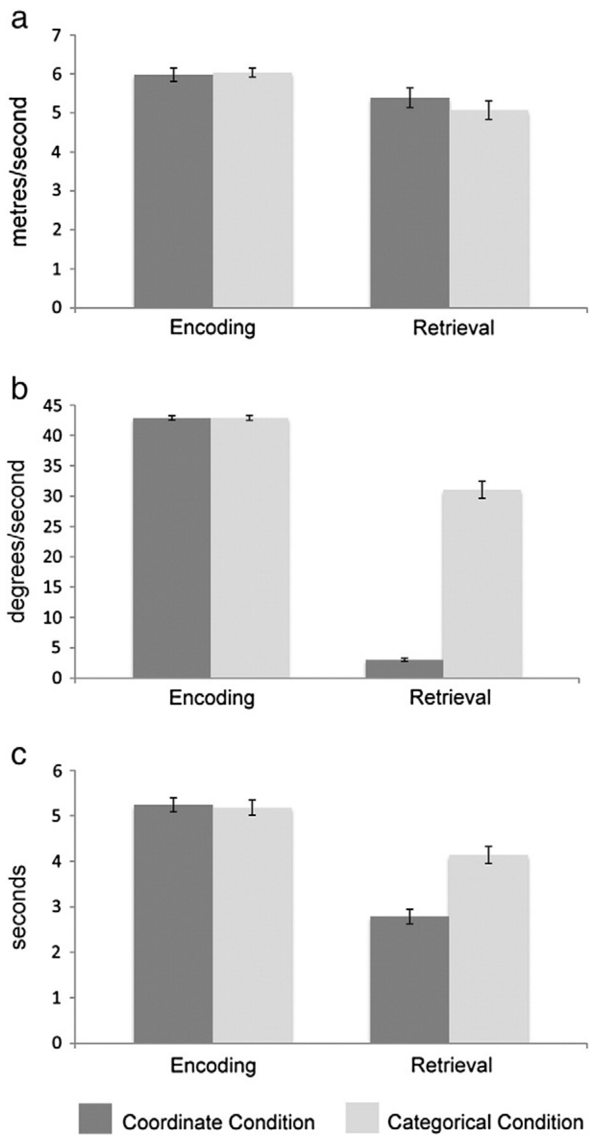


Fig. 2. Mean behavioural performance (±1 standard error) during encoding and retrieval phases of the navigation task, plotted separately for the coordinate and categorical conditions. (a) Speed. (b) Unsigned rotation. (c) Duration.

Comparing categorical and coordinate encoding of object locations

We aimed to identify differentially activated brain regions by contrasting encoding-related activity during the categorical condition with activity during the coordinate condition. As mentioned previously, we did not compare activity during the retrieval phase of the task, since differences in duration and in activity related to the participants' movements in the virtual environment might confound the results. There were no statistically significant differences in the behavioural parameters for the coordinate and categorical conditions during the *encoding phase*, which means that any effects on neural activity during this phase can be attributed unambiguously to differences in the neural substrates of spatial encoding. At a whole brain level, we identified four regions that responded more strongly during categorical encoding than during coordinate encoding (see Table 1a and Fig. 3). These were the right inferior parietal lobule and supramarginal gyrus (BA 40; 410 voxels), the left inferior and superior parietal lobule (BA 40 and 7; 1123 voxels), the left middle temporal gyrus (BA 21 and 22; 412 voxels), and the precuneus bilaterally (areas BA 7 and 31; 1501 voxels). In line with the hemispheric specialisation hypothesis, the extent of neural activity was more pronounced in the left hemisphere. Within the targeted ROIs, we did not detect any further statistically significant activation.

Using the complementary contrast, comparing BOLD activity for trials in which participants were engaged in coordinate encoding with the analogous categorical condition, we found significant activation (based on the whole-brain analysis; see Table 1b and Fig. 4) within the right dorsal striatum (637 voxels), parahippocampal gyrus and hippocampus (461 voxels). Using the ROI approach, we detected additional activation clusters in the left dorsal striatum (92 and 36 voxels) and hippocampus (49 voxels). In accord with the hemispheric specialisation hypotheses, the extent of neural activity was clearly more pronounced in the right hemisphere. However, the findings of stronger medial temporal activity in the coordinate condition and stronger parietal activity in the categorical condition clearly support the structural specialisation hypothesis.

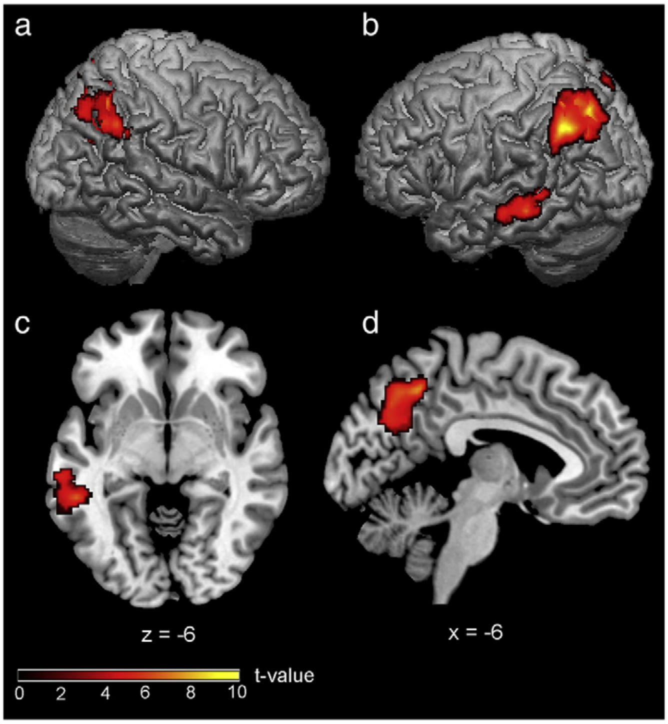


Fig. 3. MR brain slices and three-dimensional rendered MR images showing mean BOLD activity from the analysis of categorical minus coordinate conditions. Activation maps are overlaid onto a rendered MNI-normalised template. (a) Right posterior parietal cortex. (b) Left posterior parietal cortex and middle temporal gyrus. (c) Left middle temporal gyrus (d) Medial parietal cortex (precuneus).

Discussion

The primary aim of the present study was to determine whether distinct neural substrates are responsible for the encoding of categorical and coordinate aspects of spatial environments. Motivated by the apparent discrepancy between human and rodent models of spatial memory, we focused on the specific hypothesis that coordinate and categorical encoding during active navigation are supported by structural specialisation (hippocampus vs. parietal cortex), in addition to some evidence for hemispheric specialisation (left hemisphere vs. right hemisphere). Previous research investigating active navigation in humans has shown that particular neural networks in the parietal cortex, medial temporal area and striatal cortex underpin the encoding and retrieval of spatial environments (Baumann, et al., 2010). However, it has remained unclear whether any of these brain regions is differentially engaged for coordinate versus categorical encoding of spatial relationships.

We found that categorical encoding of object locations led to significantly stronger activity bilaterally in lateral and medial parietal cortex, as well as in the left middle temporal gyrus. In contrast, coordinate encoding led to significantly stronger activity in the right hippocampus, parahippocampus and dorsal striatum, and to a lesser degree in the homologous left-hemispheric structures.

Our results are in clear support of the “structural specialisation” hypothesis, initially derived from rodent research, which proposes that the hippocampal formation is crucial for encoding coordinate information, whereas the parietal cortex is crucial for encoding categorical spatial information (DeCoteau, et al., 1998; Goodrich-Hunsaker et al., 2005; Long and Kesner, 1998a, 1998b). Our findings are also in line with findings from previous human imaging studies, including our own, which have shown that the hippocampus is involved in the encoding of distance information during active navigation (Morgan et al., 2011), and whenever spatial associations need to be formed in a way that allows metric accuracy during navigation (Baumann, et al., 2010). Unlike these earlier studies, however, we ensured that our protocol was effective in teasing apart any unique contributions from coordinate and categorical space representations. Our study extends current knowledge by showing that medial temporal lobe structures (i.e., the hippocampus and the parahippocampal gyrus) underlie the formation of *metrically precise* spatial representations of object locations in 3D environments.

The categorical vs. coordinate distinction in spatial memory has been criticised on the basis that in many experimental paradigms the two conditions have not been well matched in terms of task difficulty (Martin et al., 2008; Van der Lubbe et al., 2006). We aimed to minimise this potential problem by matching the memory load across the two conditions. We also employed an easy spatial memory task, in which only one target object had to be remembered to dissociate the effects of categorical and coordinate encoding without drawing too heavily on general cognitive resources. Unfortunately, by their very nature, categorical and coordinate tasks will always differ in terms of the cues that might prove useful in completing the task. A

Table 1a

Summary of fMRI findings for the contrast of categorical > coordinate conditions during the encoding phase.

Region	Hemisphere	Brodmann area	MNI coordinates X	Y	Z	T-values/z-values of maxima (cluster size in number of voxels)
Whole brain						
Inferior parietal lobule/superior parietal lobule	L	40/7	−32	−58	40	8.50/4.87 (1123)
Precuneus	L + R	7/31/	2	−68	38	7.45/4.57 (1501)
Middle temporal gyrus	L	21/22	−54	−40	−6	5.72/3.98 (412)
Inferior parietal lobule/supramarginal gyrus	R	40	40	−52	36	5.18/3.75 (410)

Table 1b
Summary of fMRI findings for the contrast of the coordinate > categorical conditions during the encoding phase.

Region	Hemisphere	Brodmann area	MNI coordinates			T-values/z-values of maxima (cluster size in number of voxels)
			X	Y	Z	
Whole brain						
Dorsal striatum	R	–	34	0	4	10.51/5.33 (637)
Parahippocampus/hippocampus	R	–	24	−44	−6	7.83/4.68 (461)
ROI						
Dorsal striatum	L	–	−24	−10	12	6.32/4.20 (92)
Hippocampus	L	–	−20	−32	−2	5.33/3.81 (49)
Dorsal striatum	L	–	−20	−12	22	5.32/3.81 (36)

Spatial coordinates, anatomical locations and cluster-size of the local maxima in the group analysis, showing significant activations ($p \leq 0.05$, corrected for multiple comparisons) for the contrast (a) categorical minus coordinate, and (b) coordinate minus categorical. Abbreviations: L = left hemisphere, R = right hemisphere.

simple comparison of error rates across conditions is unlikely to provide a particularly useful or sensitive index of "difficulty", however one chooses to define that concept. Nevertheless, the fact that we did not observe any difference between conditions in frontal brain activity, which has been taken as a marker of cognitive and attentional demands (e.g. Barch et al., 1997), suggests that the level of difficulty was similar for both conditions. Furthermore, the particular brain areas we found to be associated with coordinate and categorical encoding, and the absence of differential activity in visual and language areas, weigh against the likelihood that participants merely engaged in distinct visual or verbal encoding strategies.

Our study is the first to identify parts of the human parietal cortex as the neural structures underlying categorical encoding during active navigation. Several previous neuroimaging studies reported bilateral posterior and medial parietal cortex activity during short-term memory maintenance of spatial information (for a meta-analysis, see Wager and Smith, 2003). In particular, certain regions of the parietal cortex have previously been found to underlie the learning of static 2D, categorical spatial relationships. For example, a recent fMRI study (Amorapanth et al., 2010) observed that directing attention to categorical spatial relations, as opposed to the identity of objects, resulted in greater activity in superior and inferior parietal cortices. Moreover, early clinical reports associated bilateral parietal cortex lesions with difficulties in learning categorical spatial relationships (e.g., Robertson et al., 1997).

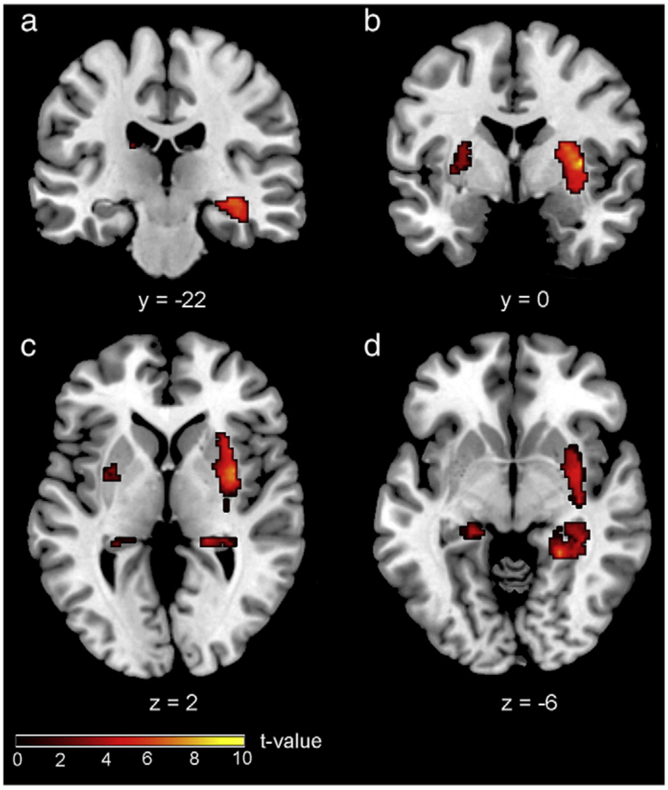


Fig. 4. MR brain slices showing mean BOLD activity from the analysis of coordinate minus categorical conditions. (a) Right hippocampus. (b) Left and right dorsal striatum. (c) Bilateral hippocampus and dorsal striatum. (d) Bilateral hippocampus, right parahippocampus and right dorsal striatum.

We found that activity during the categorical condition was greater in parietal cortex within the left hemisphere than within the right. This left hemisphere bias in parietal cortex is consistent with the claim that, in humans, the left hemisphere preferentially processes categorical spatial relations (Jager and Postma, 2003; Kosslyn et al., 1989; Van der Ham et al., 2009). Our findings extend current knowledge by demonstrating that posterior and medial parietal regions are engaged during the encoding of categorical properties within dynamic, 3D environments.

In addition to the robust parietal activity observed in the categorical condition, we also uncovered a strong response in the left middle temporal gyrus. The middle temporal region is thought to be crucial for the storage of semantic information associated with biological and non-biological objects, and neurons in this area are recruited during semantic association tasks involving pictures of objects (Adams and Janata, 2002; Martin et al., 1995) or visual scenes (Damasio et al., 2001). We speculate that activity in the middle temporal gyrus reflects semantic encoding processes, which are likely to arise when participants memorise categorical aspects of a novel spatial environment. Our findings therefore provide indirect support for the claim that memory for categorical relationships is akin to a declarative representation of spatial knowledge (Kosslyn et al., 1989).

Encoding during the coordinate condition yielded robust activity within the dorsal striatum. Previously we had shown that the striatum is important not only for spatial navigation in general, but also for metric accuracy in locating a target object during active navigation (Baumann et al., 2010). It is now widely accepted that the dorsal striatum is crucially involved in non-declarative or procedural memory processes (e.g., McDonald and White, 1994; Poldrack and Packard, 2003; Squire and Zola, 1996). We propose that the increased striatal activity during the coordinate condition of the present study indicates that landmark-based navigation requiring metrically precise responses might represent a non-declarative process, akin to skill learning (Yin and Knowlton, 2006).

Finally, positional and directional spatial information can be encoded either relative to a person's location and orientation (i.e., egocentrically) or relative to other objects, independent of the location or orientation of the observer (i.e., allocentrically; Burgess, 2006; Klatzky, 1998). It has been suggested that egocentric/allocentric and categorical/coordinate representations constitute different dimensions of spatial memory, which can nevertheless be fully combined (Jager and Postma, 2003; Ruotolo et al., 2011). This yields four possible combinations of spatial memory representation:

(a) egocentric-categorical (the target is in front of you); (b) egocentric-coordinate (the target is 1.25 m from yourself); (c) allocentric-categorical (the target is to the left of the landmark); (d) allocentric-coordinate (the target is 1.25 m from the landmark). Previous studies have indicated that the hippocampus underlies the encoding of allocentric spatial relations, and that the striatum underlies egocentric encoding (e.g., Doeller et al., 2008). Interestingly, we found that both these structures were more active during the coordinate condition, raising the question of the extent to which the hippocampus and striatum subserve divergent roles in the encoding of egocentric and allocentric spatial relations. Our task design does not permit us to draw conclusions about the relative extent to which the participants relied on egocentric versus allocentric frames of reference, and further studies will be necessary to answer this question.

In conclusion, we have shown for the first time that distinct neural circuits underlie categorical and coordinate representations of object locations during active spatial navigation. Crucially, our findings suggest that the neural networks that subserve categorical and coordinate encoding are different from those commonly reported in studies involving static, 2D stimulus arrays. Our findings are specific to processes involved in the initial encoding of categorical and coordinate representations. In future work it will be important to determine the networks that underlie the subsequent maintenance and retrieval of categorical and coordinate spatial relationships during active navigation.

Acknowledgments

This work was supported by an Australian Research Council (ARC) Thinking Systems Grant. We gratefully acknowledge the Thinking Systems Team for their support, and in particular Mark Wakabayashi and Robert Ninnes for programming the virtual environment used in the study.

References

Adams, R.B., Janata, P., 2002. A comparison of neural circuits underlying auditory and visual object categorization. NeuroImage 16, 361–377.

Amorapanth, P.X., Widick, P., Chatterjee, A., 2010. The neural basis for spatial relations. J. Cogn. Neurosci. 22, 1739–1753.

Barch, D.M., Braver, T.S., Nystrom, L.E., Forman, S.D., Noll, D.C., Cohen, J.D., 1997. Dissociating working memory from task difficulty in human prefrontal cortex. Neuropsychologia 35, 1373–1380.

Baumann, O., Chan, E., Mattingley, J.B., 2010. Dissociable neural circuits for encoding and retrieval of object locations during active navigation in humans. NeuroImage 49, 2816–2825.

Bohbot, V.D., Iaria, G., Petrides, M., 2004. Hippocampal function and spatial memory: evidence from functional neuroimaging in healthy participants and performance of patients with medial temporal lobe resections. Neuropsychology 18, 418–425.

Burgess, N., 2006. Spatial memory: how egocentric and allocentric combine. Trends Cogn. Sci. 10, 551–557.

Chabris, C.F., Kosslyn, S.M., 1998. How do the cerebral hemispheres contribute to encoding spatial relations. Curr. Dir. Psychol. Sci. 7, 8–14.

Christou, C.G., Bülthoff, H.H., 1999. View dependence in scene recognition after active learning. Mem. Cognit. 27, 996–1007.

Collette, F., Van der Linden, M., 2002. Brain imaging of the central executive component of working memory. Neurosci. Biobehav. Rev. 26, 105–125.

Damasio, H., Grabowski, T.J., Tranel, D., Ponto, L.L., Hichwa, R.D., Damasio, A.R., 2001. Neural correlates of naming actions and of naming spatial relations. NeuroImage 13, 1053–1064.

DeCoteau, W.E., Gilbert, P.E., Kesner, R.P., 1998. Memory for spatial location: role of the hippocampus in mediating spatial pattern separation. J. Neurosci. 18, 804–810.

Doeller, C.F., King, J.A., Burgess, N., 2008. Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. Proc. Natl Acad. Sci. U. S. A 105, 5915–5920.

Ekstrom, A.D., Bookheimer, S.Y., 2007. Spatial and temporal episodic memory retrieval recruit dissociable functional networks in the human brain. Learn. Mem. 14, 645–654.

Epstein, R.A., Parker, W.E., Feiler, A.M., 2007. Where am I now? Distinct roles for parahippocampal and retrosplenial cortices in place recognition. J. Neurosci. 27, 6141–6149.

Gallistel, C.R., 1990. The Organization of Learning. MIT Press, Cambridge, MA.

Goodrich-Hunsaker, N.J., Hunsaker, M.R., Kesner, R.P., 2005. Dissociating the role of the parietal cortex and dorsal hippocampus for spatial information processing. Behav. Neurosci. 119, 1307–1315.

Hellige, J.B., Cumberland, N., 2001. Categorical and coordinate spatial processing: more on contributions of the transient/magnocellular visual system. Brain Cogn. 45, 155–163.

Jacobs, R.A., Kosslyn, S.M., 1994. Encoding shape and spatial relations: the role of receptive field size in coordinating complementary representations. Cogn. Sci. 18, 361–386.

Jager, G., Postma, A., 2003. On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence. Neuropsychologia 41, 504–515.

Janzen, G., van Tourennout, M., 2004. Selective neural representation of objects relevant for navigation. Nat. Neurosci. 7, 673–677.

Jason, G.W., Cowey, A., Weiskrantz, L., 1984. Hemispheric asymmetry for a visuospatial task in monkeys. Neuropsychologia 22, 777–784.

Klatzky, R.L., 1998. Allocentric and egocentric spatial representations: definitions, distinctions, and interconnections. In: Freska, C., Havbel, C. (Eds.), Spatial Cognition. : An Interdisciplinary Approach to Representing and Processing Spatial Knowledge. Springer, Heidelberg, pp. 1–17.

Kosslyn, S.M., 1987. Seeing and imagining in the cerebral hemispheres: a computational approach. Psychol. Rev. 94, 148–175.

Kosslyn, S.M., Koenig, O., Barret, A., Cave, C.B., Tang, J., Gabrieli, J.D.E., 1989. Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate relations. J. Exp. Psychol: Hum. Percept. Perform. 15, 723–735.

Kosslyn, S.M., Chabris, C.F., Marsolek, C.J., Koenig, O., 1992. Categorical versus coordinate spatial relations: computational analyses and computer simulations. J. Exp. Psychol. Hum. Percept. Perform. 18, 562–577.

Laeng, B., Okubo, M., Saneyoshi, A., Michimata, C., 2011. Processing spatial relations with different apertures of attention. Cogn. Sci. 35, 297–329.

Long, J.M., Kesner, R.P., 1998a. Effects of hippocampal and parietal cortex lesion of memory for egocentric distance and spatial location information in rats. Behav. Neurosci. 112, 480–495.

Long, J.M., Kesner, R.P., 1998b. Parietal cortex and a spatial cognitive map. Psychobiology 26, 162–166.

Martin, A., Haxby, J.V., Lalonde, F.M., Wiggs, C.L., Ungerleider, L.G., 1995. Discrete cortical regions associated with knowledge of color and knowledge of action. Science 270, 102–105.

Martin, R., Houssemand, C., Schiltz, C., Burnod, Y., Alexandre, F., 2008. Is there continuity between categorical and coordinate spatial relations coding? Evidence from a grid/no-grid working memory paradigm. Neuropsychologia 46, 576–594.

McDonald, R.J., White, N.M., 1994. Parallel information processing in the water maze: evidence for independent memory systems involving dorsal striatum and hippocampus. Behav. Neural Biol. 61, 260–270.

Mellet, E., Bricogne, S., Tzourio-Mazoyer, N., Ghaëm, O., Petit, L., Zago, L., Etard, O., Berthoz, A., Mozoyer, B., Denis, M., 2000. Neural correlates of topographic mental exploration: the impact of route versus survey perspective learning. NeuroImage 12, 588–600.

Michimata, C., Saneyoshi, A., Okubo, M., Laeng, B., 2011. Effects of the global and local attention on the processing of categorical and coordinate spatial relations. Brain Cogn. 77, 291–297.

Morgan, L.K., MacEvoy, S.P., Aguirre, G.K., Epstein, R.A., 2011. Distances between real-world locations are represented in the human hippocampus. J. Neurosci. 31, 1238–1245.

Morris, N., Jones, D.M., 1990. Memory updating in working memory: the role of the central executive. Br. J. Psychol. 81, 111–121.

Palermo, L., Bureca, I., Matano, A., Guariglia, C., 2008. Hemispheric contribution to categorical and coordinate representational processes: a study on brain-damaged patients. Neuropsychologia 46, 2802–2807.

Poldrack, R.A., Packard, M.G., 2003. Competition among multiple memory systems: converging evidence from animal and human brain studies. Neuropsychologia 41, 245–251.

Robertson, L., Treisman, A., Friedman-Hill, S., Grabowecky, M., 1997. The interaction of spatial and object pathways: evidence from Balint's syndrome. J. Cogn. Neurosci. 9, 295–317.

Roth, E.C., Hellige, J.B., 1998. Spatial processing and hemispheric asymmetry, contributions of the transient/magnocellular visual system. J. Cogn. Neurosci. 10, 472–484.

Ruotolo, F., van der Ham, I.J., Iachini, T., Postma, A., 2011. The relationship between allocentric and egocentric frames of reference and categorical and coordinate spatial information processing. Q. J. Exp. Psychol. 64, 1138–1156.

Saneyoshi, A., Kaminaga, T., Michimata, C., 2006. Hemispheric processing of categorical/metric properties in object recognition. Neuroreport 17, 517–521.

Shelton, A.L., Gabrieli, D.E., 2002. Neural correlates of encoding space from route and survey perspectives. J. Neurosci. 22, 2711–2717.

Slotnick, S.D., Moo, L.R., 2006. Prefrontal cortex hemispheric specialization for categorical and coordinate visual spatial memory. Neuropsychologia 44, 1560–1568.

Slotnick, S.D., Moo, L.R., Tesoro, M.A., Hart, J., 2001. Hemispheric asymmetry in categorical versus coordinate visuospatial processing revealed by temporary cortical activation. J. Cogn. Neurosci. 13, 1088–1096.

Squire, L.R., Zola, S.M., 1996. Structure and function of declarative and nondeclarative memory systems. Proc. Natl Acad. Sci. U. S. A 93, 13515–13522.

Sun, H.-J., Chan, G.S.W., Campos, J.L., 2004. Active navigation and orientation-free spatial representations. Mem. Cogn. 32, 51–71.

Trojano, L., Grossi, D., Linden, D.E.J., Formisano, E., Goebel, R., Cirillo, S., Elefante, R., Di Salle, F., 2002. Coordinate and categorical judgements in spatial imagery. An fMRI study. Neuropsychologia 40, 1666–1674.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single subject brain. NeuroImage 15, 273–289.

Van der Ham, I.J., Postma, A., 2010. Lateralization of spatial categories: a comparison of verbal and visuospatial categorical relations. Mem. Cognit. 38, 582–590.

van der Ham, I.J., Raemaekers, M., Van Wezel, R.J.A., Oleksiak, A., Postma, A., 2009. Categorical and coordinate spatial relations in working memory: an fMRI study. Brain Res. 1297, 70–79.

Van der Ham, I.J., Zandvoort, M.J., Frijns, C.J., Kappelle, L.J., Postma, A., 2011. Hemispheric differences in spatial relation processing in a scene perception task: a neuropsychological study. Neuropsychologia 49, 999–1005.

Van der Lubbe, R.H.J., Schölvinck, M.L., Kenemans, J.L., Postma, A., 2006. Divergence of categorical and coordinate spatial processing assessed with ERPs. Neuropsychologia 44, 1547–1559.

Vauclair, J., Yamazaki, Y., Gunturkun, O., 2006. The study of hemispheric specialization for categorical and coordinate spatial relations in animals. Neuropsychologia 44, 1524–1534.

Vogels, R., Saunders, R.C., Orban, G.A., 1994. Hemispheric lateralization in rhesus monkeys can be task-dependent. Neuropsychologia 32, 425–438.

Wager, T.D., Smith, E.E., 2003. Neuroimaging studies of working memory: a meta analysis. Cogn. Affect. Behav. Neurosci. 3, 255–274.

Wolbers, T., Wiener, J.M., Mallot, H.A., Büchel, C., 2007. Differential recruitment of the hippocampus, medial prefrontal cortex, and the human motion complex during path integration in humans. J. Neurosci. 27, 9408–9416.

Yamazaki, Y., Aust, U., Huber, L., Hausmann, M., Gunturkun, O., 2007. Lateralized cognition: asymmetrical and complementary strategies of pigeons during discrimination of the “human concept”. Cognition 104, 315–344.

Yin, H.H., Knowlton, B.J., 2006. The role of the basal ganglia in habit formation. Nat. Rev. Neurosci. 7, 464–476.