Spinning in the Scanner: Neural Correlates of Virtual Reorientation

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Recent studies have used spatial reorientation task paradigms to identify underlying cognitive mechanisms of navigation in children, adults, and a range of animal species. Despite broad interest in this task across disciplines, little is known about the brain bases of reorientation. We used functional magnetic resonance imaging to examine neural activity in adults during a virtual reality version of the reorientation task. Three environments that varied in the cues provided were studied: a rectangular room with 4 identical gray walls (Geometry), a square room with 3 gray walls and 1 red wall (Feature), and a rectangular room with 3 gray walls and 1 red wall (Feature + Geometry). Multiple areas within the medial temporal lobe (MTL) showed increased activation when a feature was present compared with when reorientation was based only on geometric cues. In contrast, reliance on geometric cues significantly activated a number of non-MTL structures, including the prefrontal cortex and inferior temporal gyrus. These results provide neural evidence for processing differences between the 2 types of cue as well as insight into developmental and comparative aspects of reorientation.

Keywords: spatial cognition, reorientation, fMRI

Navigation and orientation are accomplished using a range of environmental and self-generated cues (Gallistel, 1990). A spatial reorientation task first introduced for rats by Cheng (1986) has become an important source of data on how these cues are combined and has led to the integration of spatial cognition theory and method across comparative, developmental, and cognitive disciplines in psychology (reviewed by Cheng & Newcombe, 2005). In Cheng's (1986) experiments, rats learned the location of food in one corner of a rectangular arena with distinctive features near the food. After disrupting the rat's orientation, the researchers placed it back in the arena to search for the food. The search pattern revealed that the rats were primarily relying on the shape of the arena, rather than the distinctive features, to remember the food's location. That is, they divided their searches between the correct corner and its rotational equivalent in the rectangle (e.g., the two corners with a long wall on the left and a short wall on the right), even though a distinctive feature marked the correct corner. This reliance on the geometry of the search space was subsequently demonstrated in very young children (Hermer & Spelke, 1994, 1996). It is interesting, however, that human adults are able to integrate these geometric cues with feature information, leading to qualitatively different performance in adults than in both very young children and nonhuman animals (Hermer & Spelke, 1994; Ratliff & Newcombe, 2008).

The original account of geometric-cue dominance in animal and child populations involved an obligatory geometric module that was resistant to combination with feature cues (Cheng, 1986). Adults, it was suggested, successfully combine the two types of cue using language (Hermer-Vazquez, Spelke, & Katsnelson, 1999). Recent evidence suggests reservations about this story, however. For instance, characteristics of the feature such as distance from the subject, its stability, and the testing room's size are important in determining whether children use features in addition to room geometry (Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008). In addition, adults' relative reliance on geometric versus feature cues depends on the size of the room as well as prior experience with the cues (Ratliff & Newcombe, 2008). Finally, multiple animal species have been shown to combine feature and geometric cues in the absence of language (e.g., chicks: Vallortigara, Zanforlin, & Pasti, 1990; mountain chickadees: Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; fish: Brown, Spetch, & Hurd, 2007; pigeons: Kelly, Spetch, & Heth, 1998).

Given these challenges to the assumptions of a geometric module (see Cheng, 2008, and Twyman & Newcombe, in press), other potential explanations for the use of geometric and feature cues have been suggested. Newcombe and Ratliff (Newcombe & Ratliff, 2007; Ratliff & Newcombe, 2008) proposed an adaptive combination account whereby the feature and geometry cues that

are used at any given time are weighted on the basis of the organism's certainty in encoding them and learning history, along with the cues' salience and perceived reliability. The weights are combined in a Bayesian fashion so that cues perceived as less useful are weighted less. An associative model by Miller and Shettleworth (2007) proposed that cues in a particular corner become associated, and when a target is encoded in that corner, learning about both the geometry and the feature of the corner is facilitated. Subsequently encountering the same geometry cue at the rotationally correct corner leads organisms to search there, even though the feature cue may be incorrect. Finally, a view-based account has been proposed wherein animals encode the panoramic view into the arena from the rewarded corner and attempt to match it (Stürzl, Cheung, Cheng, & Zeil, 2008). Using computer simulations and images comparable to those constructed by rats' visual systems, the model produced rotational errors without reference to the overall shape of the enclosure.

As the preceding discussion illustrates, there is broad comparative interest in the cognitive mechanisms involved in the spatial reorientation task paradigm. This interest has not been matched by an understanding of the underlying neural mechanisms in either animals or humans, however. We know of no study that has directly addressed the brain regions involved when reorienting with feature and room geometry cues in this paradigm. In the current experiment, we combined functional magnetic resonance imaging (fMRI) measures of neural activity with an interactive virtual reality version of the reorientation task. It is unclear at this point how patterns of neural activity across the conditions of the task will help differentiate the current postmodular proposals to explain search behavior. Instead, our goal was to begin to answer fundamental, yet unanswered, questions about the mechanisms of reorientation behavior at the neural level by isolating the most prominent cues in the task and comparing their corresponding patterns of brain activation. In addition, beyond identifying areas involved in processing these cues, information about the roles of specific brain regions may help explain behavioral patterns, such as the failure of young children to use the feature to aid searching.

Brain regions engaged in other navigational and spatial tasks suggest a central role for the medial temporal lobe (MTL; see Burgess, 2008, for a recent review). Areas of particular interest are those that have been associated with processing information about environment shape, cues along the boundary of an environment, landmarks, and the linking of a target location with these cues. For instance, Epstein has proposed that an area of posterior parahippocampal cortex (referred to as the parahippocampal place area, or PPA) is particularly sensitive to the layout of scenes as defined by the stable, fixed features present in the scene (Epstein, 2005, 2008; Epstein & Kanwisher, 1998). Evidence for this spatial layout hypothesis comes from studies in which subjects view static images of scenes (e.g., rooms) with or without objects as well as the objects alone. The most important finding for the present study is similar activation in the PPA for images of empty rooms and those same rooms with objects, and greater activation for empty rooms versus the objects in isolation (Epstein & Kanwisher, 1998). This activation pattern was interpreted as an indication that the posterior parahippocampal cortex may be centrally involved in processing the shape of the room in the reorientation paradigm (Epstein, 2005, 2008; Epstein & Kanwisher, 1998). Moreover, this area may show significantly greater activation when room shape information is crucial in the absence of a feature cue.

The hippocampus has been a major focus of spatial cognitive processing for some years (O'Keefe & Nadel, 1978), and imaging data taken during active spatial tasks suggest a role for it in the reorientation task. For instance, Doeller, King, and Burgess (2008) used a virtual reality environment to investigate brain activation while subjects learned object locations in an arena relative to both a discrete landmark spatially distinct from a low wall forming the boundary of the search space and distal cues visible from the search space but beyond the wall. Subjects later replaced one of the objects in the space with the landmark moved relative to the boundary wall such that the target location indicated by the two cues conflicted. When subjects replaced the object at a location indicated by the boundary wall and its distal cues, there was significantly more activation in the right hippocampus than when they replaced the object at a landmark-indicated location. Therefore, the hippocampus was preferentially engaged when the location was encoded relative to the boundary of the search space and the distal orienting cues beyond it. Iaria, Petrides, Dagher, Pike, and Bohbot (2003) also observed increased hippocampal activation in a virtual radial maze task. When subjects encoded locations using distal landmarks around the maze, they observed increased hippocampal activation relative to a visuomotor control condition. Given that target localization in the reorientation task involves the floor-to-ceiling wall boundary in both feature and no-feature conditions in the current study, there may be equal hippocampal involvement in all conditions. If the crucial aspect of hippocampal involvement is an orienting cue, however, there should be more hippocampal activation in conditions in which a feature is present than when no feature is present.

In the present study we sought to resolve how these brain regions might be differentially associated with the use of featural versus geometric cues during reorientation in humans. Adults were scanned using fMRI at 3 Tesla as they performed a virtual spatial memory task that simulated the reorientation task. Each trial consisted of two phases, encoding and retrieval. In the encoding phase, subjects searched for a traffic pylon that was placed in a corner of a virtual room. Next, in the retrieval phase, they were moved to a randomly selected corner of the room and were required to pick up the traffic pylon from the center of the room and place it in the previously viewed location. Three experimental conditions were created by manipulating the geometric shape and/or visual features in the room: (a) a rectangle shape with all walls light gray and identical (Geometry [G] condition), (b) the same shape but with one short wall colored red (Feature + Geometry [FG] condition), or (c) a square shape with three light gray walls and one red wall (Feature [F] condition). If the virtual task is a valid analogue of the real-world reorientation task, subjects should direct a majority of searches to the correct and rotationally correct corners in the G condition and concentrate searches in the correct corner on F and FG trials.

We contrasted brain activation across the conditions in a pairwise fashion (G vs. F, FG vs. G, F vs. FG) separately for the encoding and retrieval phases of the trials, which allowed us to isolate brain areas uniquely engaged in the processing of geometric information, feature information, and the combination of those two information sources. In particular, the separation of encoding and retrieval phases in the analysis gave the potential for more precise

aligning of neural activation with the cognitive demands within each trial. First, it was predicted that if the hippocampus is preferentially involved in processing a feature that is part of the boundary, we should see more hippocampal activation in the F and FG conditions relative to the G condition. Next, if activation in parahippocampal cortex (e.g., the PPA) is particularly important when environment shape is the critical spatial cue, there should be increased activation in this region on G trials relative to F and FG trials. Finally, we conducted an exploratory whole-brain analysis to determine whether any non-MTL regions would be differentially activated across conditions.

Method

Subjects

Sixteen neurologically healthy adults (eight women, eight men) ages 18–31 years ($M = 23$ years) were recruited from the University of Western Ontario community. Fourteen were right-handed by self-report; one was left handed, and one reported mixed handedness. All procedures were approved by the University of Western Ontario Medical Research Ethics Board, and informed consent was obtained from each subject prior to testing.

Behavioral Task and Data Analysis

During scanning, subjects performed a navigation task implemented within a nonimmersive, interactive, virtual reality environment. A first-person perspective was rendered on a video display that was projected at 1024×768 resolution onto a screen mounted at the head of the scanner bore. Subjects viewed the display through a mirror placed above the head coil. The 3D environment was rendered in real-time using the Half-Life 2 game engine and the Source Software Development Kit (Valve Software, Bellevue, WA), using a Windows PC equipped with an AMD Athlon dual core processor and a 128-MB nVidia GeForce 8800 graphics processor. Movement was controlled via a four-button directional keypad, and a fifth button was provided to allow interaction with objects within the environment.

At the start of each trial, subjects were placed at the center of a room randomly facing one of the four walls. They were instructed to move about the room in order to determine the location of an object (a traffic pylon; see Figure 1). Movement was controlled using four directional arrow keys to move forward and backward and to turn left and right. After 10 s, the screen was cleared and blank. After 2 s, the retrieval phase began; subjects viewed the same room as in the encoding phase but were placed at a randomly predetermined corner facing into the room with the pylon in the center of the room (lower panel of Figure 1). Subjects picked up the pylon (via a keypress) and placed it in the place where they had previously viewed it in the encoding phase. This sequence was accomplished by moving toward the pylon using the directional keys on the keypad, pressing the "pick up/drop" key to pick it up, moving to the desired corner using the directional keys, and finally pressing the "pickup/drop" key again to drop the pylon. A total of 20 s was provided for the retrieval phase, at which point the screen again went blank in preparation for the next trial 10 s later.

In the FG condition, the room had a rectangular geometry such that there were two longer walls and two shorter walls (rendered as

Encoding

Geometry   Feature   Feature + Geometry

Retrieval

Geometry   Feature   Feature + Geometry
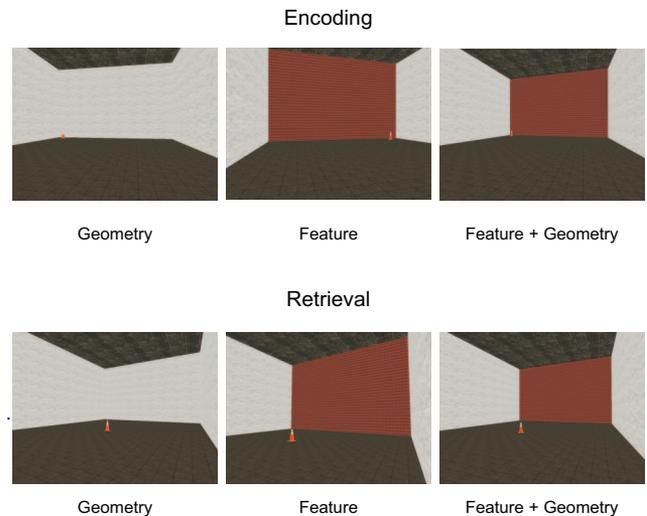
Figure 1. Views of the rooms used in the three conditions during the encoding (top panel) and retrieval (bottom panel) phases.

765×513 units of measure, where each unit corresponds to a perceived size of approximately 1.9 cm; therefore, the entire room appeared as 14.54 m $\times$ 9.76 m; the software provided an apparent eye-level that was approximately 64 units, or 1.21 m, above ground level, and provided 75° horizontal field of view). Three walls were shaded with a light gray cinderblock texture; the fourth wall, always one of the two shorter walls, was shaded with a red brick texture (see Figure 1). In the F condition, subjects viewed a room with a square geometry (513×513 units). Here, again, one of four walls was red so that it was distinct from the other three. In the G condition, subjects viewed a room with rectangular geometry identical to the FG condition but with all four walls shaded the same gray cinderblock texture. Lighting was uniform throughout the room, such that brightness and shadows could not be used as orientation cues. All rooms had a height of 326 units (6.19 m), with the floor shaded in a medium gray tile texture and the ceiling shaded in dark gray texture.

Subjects performed six runs of six trials each (two of each condition per run) for a total of 36 trials, 12 of each condition. Trials were presented in random order with the constraint that no condition was presented twice in a row, and each condition preceded and followed the other two conditions with equal frequency. The subject's initial orientation during the encoding and retrieval phases was also counterbalanced across conditions.

To verify the validity of the virtual task as a test of reorientation similar to previous behavioral studies, we characterized subjects' placements of the pylon in the retrieval phase as C (correct corner), N (near correct corner error), R (rotational error), or F (far corner error), as shown in Figure 2. Using the proportion of total searches in each corner, we conducted a series of a priori comparisons with one sample two-tailed t tests and a paired two-tailed t test. For both FG and F conditions, the proportion of placements in the correct corner was compared with chance (.25). The proportions of placements in the C and R corners on G condition trials were summed and compared with a chance value of .5. Finally, the proportion of placements in the C corner on F and FG trials was compared.

Feature

F	.08 (.001)	.84 (.02)	C
R	.01 (.01)	.07 (.02)	N

Geometry

F	.12 (.02)	.39 (.03)	C
R	.41 (.03)	.08 (.02)	N

Feature + Geometry

F	.015 (.01)	.97 (.01)	C
R	0 (0)	.015 (.01)	N

Figure 2. Mean proportion of pylon placements in each corner for F trials, G trials, and FG trials. Standard errors are shown in parentheses. Note that each corner served as the correct corner an equal number of times within each condition.

fMRI Data Acquisition and Analysis

Imaging was performed at 3 Tesla using a Siemens TIM Trio scanner with a 32-channel head-coil for transmit/receive. T2*-weighted functional scans were acquired in an axial orientation using single-shot echo-planar imaging (EPI) with an iPAT parallel acquisition sequence (generalized auto-calibrating partially parallel acquisition [GRAPPA]; acceleration factor = 2). We acquired 36 slices per volume (voxel size = 3 × 3 × 3.5 mm; FOV = 240 × 240 mm; TR = 2 s; TE = 30 ms), providing full coverage of the cerebrum and cerebellum. A total of 792 functional scans were acquired for each subject, divided over six runs (4.4 min per run). At the end of the session, a whole-head high-resolution 3D anatomical scan was acquired within the same orientation as the functional scans using a 3D pulse sequence weighted for T1 contrast (MPRAGE; GRAPPA acceleration factor = 2; voxel size = 1 × 1 × 0.875 mm; FOV = 256 × 240 mm; 192 slices; TR = 2.3 s; TE = 4.31 ms).

Data were analyzed using Analysis of Functional NeuroImages (AFNI; Cox, 1996). Functional scans were preprocessed as follows: Motion correction was performed concurrently with scanning, relative to the first functional scan of each sequence; slice timing was adjusted offline (AFNI *3dTshift*, quintic interpolation); finally, each volume was re-registered to the functional volume immediately preceding the anatomic scan (AFNI *3dvolreg*), to correct for movement between scanning runs. All subjects produced movements of less than 3 mm and 3° across runs.

Statistical parametric maps were created in two steps. The first step created a general linear model (GLM; AFNI *3dDeconvolve*, linear drift corrected) for each subject. Six GLM predictors were created, representing the crossing of encoding and retrieval phases of the F, G, and FG trial types. Each was modeled as a boxcar function convolved with a canonical hemodynamic response func-

tion. The encoding phase was modeled as the first 5 volumes (10 s) of the trial. The retrieval phase began at the seventh volume posttrial onset, and trial duration was tailored to each subject by computing his or her mean time to drop the pylon across all runs, producing a range of 4–7 volumes (8–14 s). Anatomical coregistration was performed by spatially transforming each subject's anatomical scan to standard 3D space (Talairach & Tournoux, 1988). This transformation was next applied to each subject's statistical maps, following resampling to 1 mm³ resolution. Finally, a spatial filter was applied (Gaussian blur, 5 mm FWHM). The second analysis step obtained groupwise statistical maps using a two-way repeated-measures analysis of variance (ANOVA) model (AFNI *3dANOVA3*) for main effects and interactions of the factors trial type (F, G, FG) and trial phase (encoding, retrieval). All statistical maps were thresholded at an uncorrected alpha level of $p = .001$.

The first set of analyses focused on activated voxels within bilateral MTL structures including the amygdala and hippocampus (identified using Pruessner et al., 2000), and temporopolar, perirhinal, entorhinal, and parahippocampal cortices (Pruessner et al., 2002). Given narrow anatomical restrictions and the a priori nature of this region of interest (ROI) analysis, a minimum cluster size was not enforced. We were also interested in whether non-MTL regions would show differential activation across conditions and consequently performed a largely exploratory whole-brain analysis. For this analysis, correction for multiple contrasts was obtained using a Monte Carlo simulation (AFNI AlphaSim; 10,000 iterations), which provided a corrected alpha level of $p < .05$ using a minimum cluster size of 243 mm³.

Results

Behavioral Task

Figure 2 shows the mean proportion of searches in each corner for each of the three conditions. Subjects placed the pylon in the C corner at a rate significantly above chance (.25) in the F condition, $t(15) = 25.30$, $p < .001$, and in the FG condition, $t(15) = 55.28$, $p < .001$. They also placed the pylon in the C and R corners significantly more than would be expected by chance (.50) in the G condition, $t(15) = 10.12$, $p < .001$. Additionally, we found more C corner placements in the FG condition than in the F condition, $t(15) = 5.41$, $p < .001$. An important finding is that the observed pattern of pylon placements in the virtual task is similar to results in prior reorientation studies involving navigating within actual enclosed spaces (e.g., Ratliff & Newcombe, 2008), confirming that the virtual tasks and the nonvirtual tasks are generally analogous.

Imaging

F versus G contrasts. The F versus G contrasts examined brain regions that showed a significant activation difference between the square room with one red wall and three gray walls (F) and the rectangular room with all walls gray (G). An initial ROI analysis was performed, restricted to areas of MTL, and revealed a number of significant clusters of activation for the F versus G contrast (see Table 1). In the encoding phase, we observed more activation on F trials in areas of left MTL including the amygdala/anterior hippocampus region and the parahippocampal cortex along the collateral sulcus

Table 1

Clusters of Significant Activation in the Region of Interest Analysis

Contrast			Region		Talairach coordinates			
Environment	Phase	Activation	L/R	Area	x	y	z	Size (mm^3)
F vs. G	Encoding	F > G	L	Amygdala/Anterior hippocampus	−24	−4	−11	134
			L	Parahippocampal cortex	−24	−43	−5	68
	Retrieval	F > G	R	Hippocampus	21	−10	−11	296
			R	Hippocampus	32	−24	−12	75
			L	Hippocampus	−27	−32	−6	40
			L	Hippocampus	−28	−42	1	81
FG vs. G	Retrieval	FG > G	L	Parahippocampal cortex	−15	−39	−3	104
			R	Hippocampus	25	−8	−20	98

Note. There were no significant differences in encoding in the FG versus G contrast, and no significant differences in either encoding or retrieval in the FG versus F contrast. Coordinates indicate location of peak activation for each cluster. L/R = left/right; F = Feature condition; G = Geometry condition; FG = Feature + Geometry condition.

(see Figure 3, left panel). In the retrieval phase of the trial (see Figure 3, right panel), we observed similarly greater MTL activation on F trials including multiple clusters of activation throughout the bilateral hippocampus.

The second analysis examined clusters of activation across all brain regions (see Table 2; note that, because this analysis was more exploratory in nature, all reported whole-brain contrasts employed a minimum cluster-size criterion correcting for multiple contrasts). We observed a number of significant acti-vation differences, including more motor-related areas on G trials during retrieval (left primary motor cortex and right supplementary motor area) and more parietal activation on F trials (bilateral postcentral gyrus and right inferior parietal areas). The G trials also yielded clusters of greater activity in left inferior frontal gyrus (see Figure 3, right panel), specifically in the pars orbitalis/triangularis region (BA 45), and a significant cluster in the right inferior temporal gyrus, just during the retrieval phase.
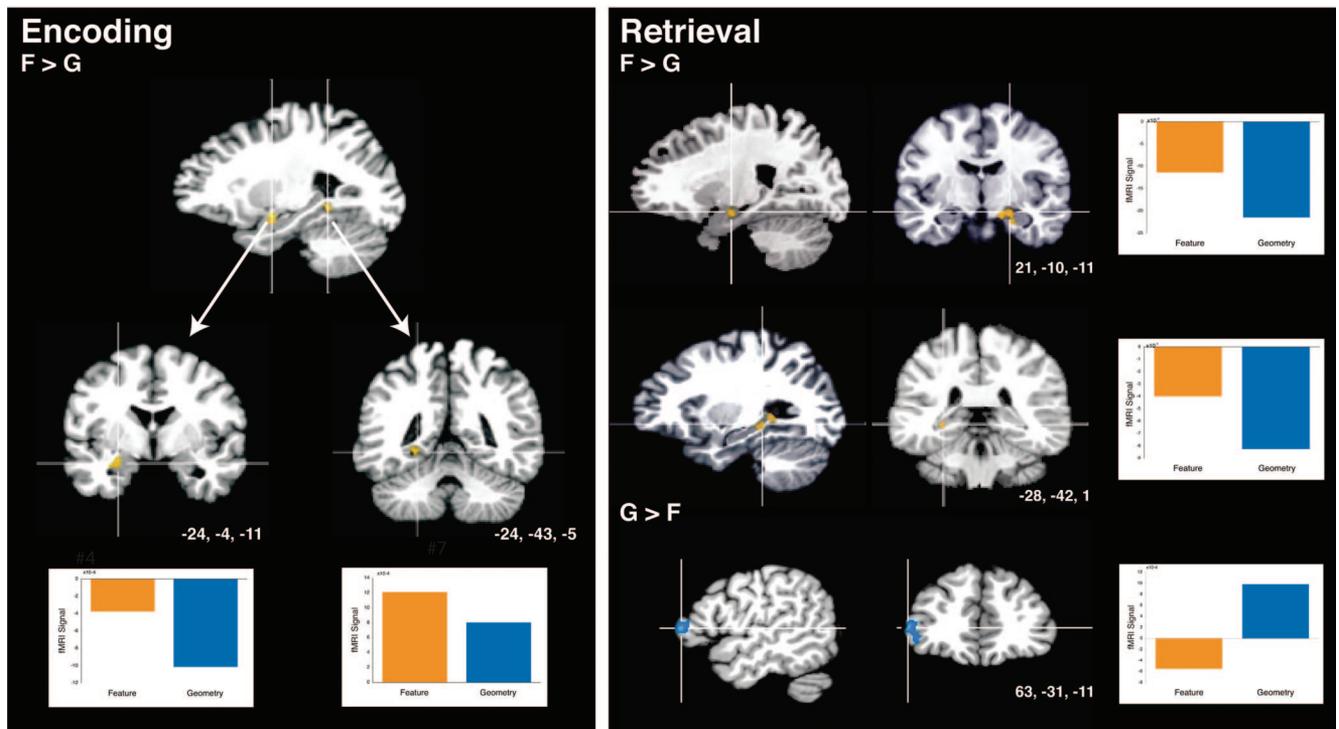
Figure 3. Brain regions showing significant activation differences in the F versus G contrast. Orange clusters: F > G; blue clusters: G > F. Statistical maps are overlaid on a Talairach-transformed standard brain. Statistical threshold set to $p < .001$. Bar charts show mean conditionwise beta weights for indicated clusters.

Table 2
Clusters of Significant Activation in the Whole-Brain Analysis

Contrast			Region		Talairach coordinates				
Environment	Phase	Activation	L/R	Area	x	y	z	Size (mm³)	BA
F vs. G	Encoding	F > G	L	Cuneus/posterior cingulate	−4	−73	12	668	23
	Retrieval	F > G	L	Cuneus	−10	−76	15	1052	18
			R	Cuneus	12	−88	24	582	19
			R	Insula	29	4	16	593	
			L	Postcentral gyrus	−23	−45	63	275	5
			R	Postcentral gyrus	23	−46	58	538	7
			R	Inferior parietal/postcentral gyrus	37	−24	27	277	2
			L	Insula	−36	7	3	254	
		G > F	L	Inferior frontal gyrus	−50	38	7	1236	45
			L	Precentral gyrus	−41	−1	34	474	6
			R	Inferior temporal gyrus	63	−31	−11	277	21
			R	Supplementary motor area	7	13	56	251	6
FG vs.G	Encoding	G > FG	L	Precentral gyrus	−20	−22	61	1779	6
			R	Precentral gyrus	51	−1	33	281	6
			L	Superior parietal	−25	−63	55	1707	7
			R	Superior parietal	14	−72	57	959	7
			R	Superior frontal gyrus	18	7	62	1096	6
			L	Postcentral gyrus	−43	−33	43	522	40
			R	Superior orbital gyrus	19	47	−3	361	10
			L	Lingual gyrus	−13	−88	−15	328	18
	Retrieval	G > FG	L	Dorsolateral prefrontal cortex	−46	47	6	254	46
			R	Anterior prefrontal cortex	40	54	11	1338	10
			R	Supplementary motor area	7	14	57	373	6
		FG > G	R	Middle cingulate	6	−28	46	328	31
			L	Middle cingulate	−7	6	39	283	32
			R	Insula	33	1	14	365	
			R	Posterior cingulate	6	−55	10	307	30
F vs. FG	Encoding	F > FG	L	Precentral gyrus	−22	−24	61	297	4
			R	Precentral gyrus	26	−9	51	293	6

Note. There were no significant differences in the retrieval phase for the F vs. FG contrast. Coordinates indicate location of peak activation for each cluster. L/R = left/right; BA = Brodmann area; F = Feature condition; G = Geometry condition; FG = Feature + Geometry condition.

FG versus G contrasts. The FG versus G contrasts examined brain regions that showed significant activation differences between the rectangular room with all walls gray (G) and the rectangular room with three gray walls and one red wall (FG). The ROI analysis revealed no significant activation differences during the encoding phase. The whole-brain analysis (see Table 2) revealed greater activation on G trials in a number of areas including motor areas (bilateral precentral gyrus extending dorsally to near the central sulcus, superior frontal gyrus/BA 6) and bilateral superior parietal cortex (BA 7). During the retrieval phase, the ROI analysis showed that the FG room resulted in significantly more activation in the left parahippocampal cortex and right anterior hippocampus (see Table 1 and Figure 4). The whole-brain analysis for the retrieval phase further revealed increased activation in the right supplementary motor area on G trials, as well as increased right anterior prefrontal cortex activation and left dorsolateral prefrontal cortex activation (see Figure 4 and Table 2).

F versus FG contrasts. The F versus FG contrast compared regions of activation on trials with a square room and one red wall (F) with a rectangular room with one red wall (FG). There were no significant activation differences in the ROI analysis for either encoding or retrieval phases. However, the whole-brain analysis (see Table 2) showed increased clusters of activation in the bilateral precentral gyrus during the encoding phase of F trials.

ROI and deactivation relative to rest. We also noted that for the significant clusters within the hippocampus described earlier, all reflected differences between two negative beta coefficients in the GLM model (see Table 1 and Figures 3 and 4). This appears to indicate task-related decreases in hippocampus activation relative to the resting baseline for both conditions of interest, but where the levels of activation for the two conditions were nevertheless significantly different. This is consistent with the tendency for MTL structures to show increased activity during baseline periods that involve relaxation (here, viewing a blank screen during the peritrial intervals) and highlights the difficulty in creating an appropriate baseline condition for MTL analyses (Stark & Squire, 2001). In particular, task-related deactivation has been demonstrated for the hippocampus in another virtual spatial navigation task, the Morris Water Tank task (Shipman & Astur, 2008). In the whole-brain analysis (see Table 2), only three areas showed a similar pattern of deactivation relative to rest, including bilateral cuneus and right inferior parietal lobe areas in the F versus G retrieval contrast and right posterior cingulate in the FG versus G retrieval contrast.

Movement analysis. Of some interest was why the G condition yielded increased activation in motor-related areas compared with the F and FG trials. We hypothesized that this was due to subjects moving around the virtual room more during G trials. To

Feature+Geometry vs. Geometry
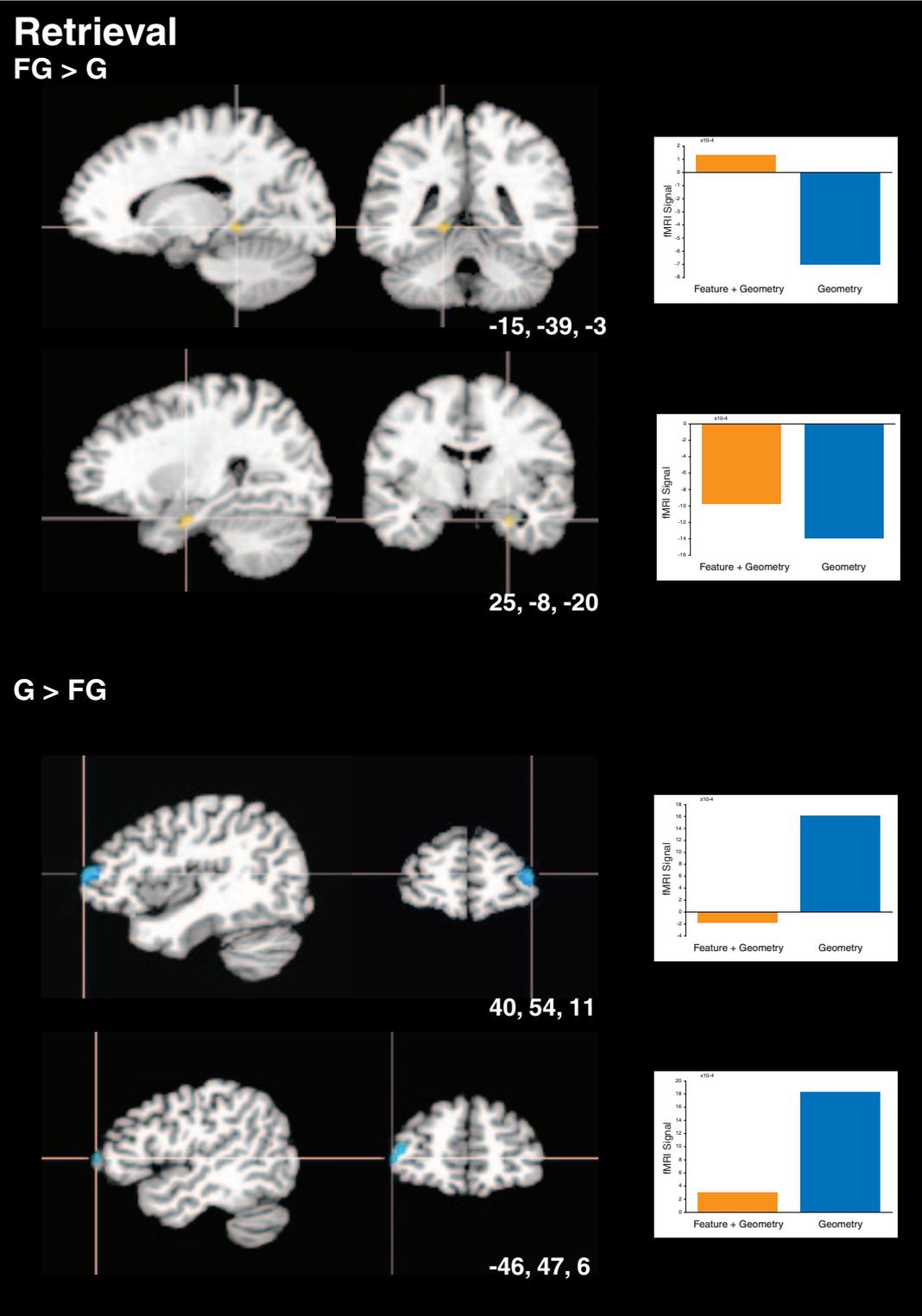
Figure 4. Brain regions showing significant activation differences in the FG versus G contrast. Orange clusters: FG > G; blue clusters: G > FG. Statistical maps are overlaid on a Talairach-transformed standard brain. Statistical threshold set to $p < .001$. Bar charts show mean conditionwise beta weights for indicated clusters.

address this, we analyzed the amount of movement throughout the environment (measured in arbitrary units of distance defined by the 3D rendering software) during the encoding and retrieval phases across conditions. It was expected that average movement distance on F trials (encoding: $M = 12.28$, $SD = 10.69$; retrieval: $M = 43.46$, $SD = 4.72$) would be lower than on the trials in the other rooms because of the smaller room size. A more meaningful comparison is the G room versus the FG room, because the rooms are identical in every way except for the single red wall in FG. Paired t tests showed that subjects moved around the room more during encoding on G trials ($M = 15.96$, $SD = 13.04$) than on FG trials ($M = 11.77$, $SD = 11.54$), $t(15) = 2.54$, $p < .05$, and also more during the retrieval phase of G trials ($M = 55.72$, $SD = 4.40$) than FG trials ($M = 51.30$, $SD = 4.61$), $t(15) = 3.88$, $p < .01$. To move around the room, subjects pressed keys on a keypad, meaning more movement was a result of more key presses. Given that the areas of increased activation included premotor and primary motor cortex and that a very large cluster was located in the left hemisphere, it is likely that these increased keypresses underlie the motor-related brain activation on G trials.

Discussion

In a virtual reality version of the geometric reorientation task, subjects studied the location of a pylon in a room and, after a short break that served to disrupt orientation, carried the pylon back to the remembered location. The room was rectangular with four gray walls (G condition), rectangular with three gray walls and one short red wall (FG condition), or square with three gray walls and one red wall (F condition). Behavioral results indicated that the virtual task produced the same pattern of responses as the 3-dimensional, "real-life" version of the task. Brain activation while performing the task was contrasted between conditions and revealed clusters of significant activation unique to each condition.

The Medial Temporal Lobe and Use of the Feature Cue

A consistent pattern emerged showing that bilateral hippocampal and left parahippocampal cortex regions were more engaged when the red feature wall was present (F and FG conditions) than when the room was entirely gray (G condition). This pattern suggests that the hippocampus is particularly engaged in processing a distinctive cue that is part of the environment boundary. If this activation was evident only in the F versus G contrast, it might be concluded that the difference was due to room size, as the F room was smaller. Because we also saw increased hippocampal activation on FG trials in the FG versus G contrast, where the room sizes were identical, this explanation is unlikely. The feature wall cue as a source of hippocampal activation in humans is consistent with findings from other imaging studies, such as the Doeller et al. (2008) finding of hippocampus activation for learning a location relative to a low wall with distal cues beyond it. The feature wall in the reorientation paradigm is more similar to the patterned wall used by Iaria et al. (2003) however, where activation in the hippocampus was also observed. In addition, Hartley, Trinkler, and Burgess (2004) suggested that the human hippocampus is responsible for both orientation and computation of a target location's distance from nearby walls. Consistent with this, the feature

in the current study can be used both for orienting (On which side of the room is the target location?) and for more precise localization that is landmark-like (the corner to the left of the red wall). The current task, however, does not allow a distinction between the neural mechanisms underlying the wall's use as a general orienting cue and as a more precise spatial reference. Nonetheless, the results provide clear evidence that the presence of a feature results in significant clusters of activation in the bilateral hippocampus not seen when only the geometry of the room is available for target localization.

An alternative hypothesis for the increased hippocampus activation on F and FG trials relative to G trials is the nature of the response required by the three conditions. On F and FG trials, there is one unambiguous correct corner, but on G trials, there are two potentially correct corners (e.g., the corners with a long wall on the left and a short wall on the right). Therefore, it could be the certainty of the response on F and FG trials that drives the relatively greater hippocampal activation rather than the use of the feature as a spatial cue. Table 1 reveals this is unlikely to be the case, however. If response certainty per se was responsible for greater hippocampal activation, we would expect similar amounts of activation in the F and FG conditions when each is compared with G. Instead, in the F condition, we found increased hippocampal activation in multiple clusters and in both encoding and retrieval phases of the trial, whereas there was one significant cluster during retrieval on FG trials. Rather than an effect of response certainty, this pattern could be interpreted to reflect the relative reliance on the feature in the different conditions: When it is the only informative cue (F trials), there are multiple clusters of activation, and when geometric information is also available (FG trials), there is less hippocampal activation. Whether the weighting of the feature produces a graded effect or not, however, the hippocampus activation revealed in the contrasts is most likely related to the presence of the feature cue and not the ambiguity of the response.

We also observed greater activation of left parahippocampal cortex on trials with the feature. It is unclear whether this region directly corresponds to the PPA region as it is reported elsewhere (e.g., Epstein & Kanwisher, 1998; Köhler, Crane, & Milner, 2002), as we did not functionally define the PPA using a separate localizer task and the activation was not bilateral. Nonetheless, it is clear that the observed region of parahippocampal cortex was not preferentially involved in the processing of environment shape when shape was the critical spatial cue. If that were the case, significant increases in activation should have been observed in this region on G trials relative to trials with the feature. On closer inspection, whether the prediction based on the pattern of PPA results reported elsewhere should require such an extreme geometric cue as the current G room is not clear. The stimuli used in the crucial comparison in Epstein and Kanwisher (1998) between furnished or empty rooms and arrays of objects are not completely comparable to the rooms in the current task. It is important that it is unlikely that the majority of the empty rooms in Epstein and Kanwisher had walls that were completely identical as were the walls on our G trials. In fact, the F and FG trials in the current experiment are as or more similar to the empty room photographs than the G trials. Of course, our virtual task is very different from the static images employed in studies of PPA, and it may be that PPA activation while viewing static images does not directly generalize to the current task. Further research will be required to

determine how PPA activation in response to static images and in the reorientation task are related.

We analyzed encoding and retrieval portions of the trials separately, and the majority of significant clusters of activation within MTL occurred in the retrieval phase (F > G, FG > G). There were differences in one encoding contrast, however, such that there was greater MTL activation on F trials relative to G trials. The fact that the F versus G contrast was the only one to produce both encoding and retrieval differences in MTL activation could be due to the lack of overlap between the cues in the two rooms. In the F room, the only informative cue was the feature wall, and in the G room, the only informative cue was room shape. This strongly suggests that feature use in isolation is sufficient to activate the hippocampus and parahippocampal cortex. In the FG versus G contrast, where room shape was identical but the FG room included the feature wall, the only MTL differences occurred in the retrieval phase when subjects were replacing the pylon. It is problematic to use the lack of a difference during encoding to conclude that encoding in these rooms is similar in terms of MTL involvement, although replacing the pylon on the basis of a spatial memory involving the feature was clearly associated with more right hippocampus and left parahippocampal cortex activation. Further research will be necessary to clarify exactly how encoding and retrieval differ with respect to MTL involvement in this task.

Implications of MTL Findings for the Development of Reorientation

The finding of the involvement of the hippocampus in feature-guided searching could inform thinking about children's performance in the reorientation task. Until about age 5 years, children are particularly sensitive to how the feature is presented in the task and fail to use it, for instance, if it is too close to them, as is the case in small rooms. One possibility is that the place learning function of the hippocampus—that is, its ability to encode a location relative to multiple environmental landmarks—is too immature to use the feature wall to guide searching. There is evidence, however, that place learning development is well under way earlier (before age 2 years) than adultlike performance on the reorientation task (Newcombe, Huttenlocher, Drummey, & Wiley, 1998; Sluzenski, Newcombe, & Satlow, 2004), although place learning does continue to develop into the early school years (Learmonth & Newcombe, 2010). This evidence, plus the fact that children are able to reorient successfully under some conditions of the task, suggests that place learning per se may not be the sole root of children's difficulty in small rooms.

Another, related, possibility is that children's failure in the reorientation task is related to the concurrent development of the hippocampus-mediated memory function of *binding*, or the general ability to encode the relations among to-be-remembered items (Cohen & Eichenbaum, 1993). Often conceived of as a process associated with transfer of information to long-term memory, hippocampus-mediated binding has also been demonstrated in tasks that require short-term memory, which is required by the reorientation task (Hannula & Ranganath, 2008; Olson, Page, Moore, Chatterjee, & Verfaellie, 2006). Recent data show that the process of binding undergoes development around the same time children are able to perform at adultlike levels under a variety of conditions in the reorientation task (Lloyd, Newcombe, & Doy-

dum, 2009; Sluzenski, Newcombe, & Kovacs, 2006). It is possible that as the general ability to encode relations between stimuli develops, so too does the breadth of stimuli that are perceived as relevant for encoding. Because the place learning function of the hippocampus is particularly tuned to large, distal features in the environment (Doeller et al., 2008; Iaria et al., 2003), it may take a combination of the development of the hippocampus-dependent processes of place learning and binding plus navigation experience for children to successfully use the less-optimal close feature wall in the small-room version of the task.

Geometric Cues and Regions of Activation

The G condition did not yield significantly greater activation within MTL; rather, we observed a number of clusters in the whole-brain analysis that appeared to be selective for this type of cue. Although we are cautious in interpreting this analysis, given its exploratory nature, there were some intriguing findings. First, we observed significant clusters of activation in areas associated with executive function including anterior prefrontal cortex and dorsolateral prefrontal cortex during the retrieval phase on G trials when compared with FG trials. The increased demand on executive function may be due to the ambiguous nature of having two correct responses on G trials (the correct and rotation error corners), which would result in an additional decision-making step made unnecessary when a feature was present.

Next, we found an increase in motor-related areas in the G condition when contrasted with the FG condition that was accompanied by more movement around the room in the G condition. This increased movement was probably due to the need to assess the length of the walls on G trials as opposed to determining the location of the red wall and moving toward the appropriate corner relative to it on FG trials.

Finally, we observed a large cluster of left inferior frontal gyrus activation in the pars orbitalis region for G trials relative to F trials. This region has been shown to be involved in verbal coding (Devlin, Matthews, & Rushworth, 2003) and may also be involved when choosing between competing representations (Thompson-Schill, 2003). It is interesting that such a region would be significantly activated on G trials, given the hypothesis that language is central to processing *feature* information in this task (Hermer-Vazquez et al., 1999). This notion has recently been weakened by evidence that non-language-related tasks interfere with feature processing as much as language-related ones do (Ratliff & Newcombe, 2008). With the focus on the role of language in feature use, little attention has been paid to how geometry is coded, however. Our results suggest that verbal coding could also be important when remembering a location in the featureless room.

Further questions remain about how to characterize the processing of geometric cues acquired from environment shape. The current data suggest that such processing seems to be less hippocampus dependent than feature use; it seems to recruit more executive resources; and it might be differentially supported by verbal coding. As stated earlier, it is doubtful that a geometric module exists, and the debate about a modular processing mechanism has deflected attention away from determining what, exactly, humans process about environment shape when reorienting. A recent debate in the comparative literature addresses this topic in animals (reviewed by Sutton, 2009). Some have proposed that

environment shape is represented in memory via an abstract representation of the principal axes of the space—for instance, the long and short axes that describe a rectangle (Cheng & Gallistel, 2005)—and a similar process has been suggested for humans completing a different but related spatial updating task (Kelly, McNamara, Bodenheimer, Carr, & Reiser, 2008). Others have suggested a more local view that includes the angle of the corner and the lengths of walls surrounding it (McGregor, Jones, Good, & Pearce, 2006; Pearce, Good, Jones, & McGregor, 2004; Tommasi & Polli, 2004). A comparative perspective is especially interesting, given the suggestion that adults may use a verbal coding strategy when relying on geometric spatial information, a strategy unavailable to nonhuman animals. For researchers to further understand the brain mechanisms involved in the reorientation task, a detailed examination of geometric information processing and a description of the conditions under which it is employed will be needed for humans.

References

Brown, A. A., Spetch, M. L., & Hurd, P. L. (2007). Growing in circles: Rearing environment alters spatial navigation in fish. *Psychological Science, 18,* 569–573. doi:10.1111/j.1467-9280.2007.01941.x

Burgess, N. (2008). Spatial cognition and the brain. *Annals of the New York Academy of Sciences, 1124,* 77–97. doi:10.1196/annals.1440.002

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23,* 149–178. doi:10.1016/0010-0277(86)90041-7

Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences, 12,* 355–361. doi:10.1016/j.tics.2008.06.004

Cheng, K., & Gallistel, C. R. (2005). Shape parameters explain data from spatial transformations: Comment on Pearce et al. (2004) and Tommasi & Polli (2004). *Journal of Experimental Psychology: Animal Behavior Processes, 31,* 254–259. doi:10.1037/0097-7403.31.2.254

Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review, 12,* 1–23.

Cohen, N. J., & Eichenbaum, H. (1993). *Memory, amnesia, and the hippocampal system.* Cambridge, MA: MIT Press.

Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research, 29,* 162–173. doi:10.1006/cbmr.1996.0014

Devlin, J. T., Matthews, P. M., & Rushworth, M. F. S. (2003). Semantic processing in the left inferior prefrontal cortex: A combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience, 15,* 71–84. doi:10.1162/089892903321107837

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the USA, 105,* 5915–5920. doi:10.1073/pnas.0801489105

Epstein, R. A. (2005). The cortical basis of visual scene processing. *Visual Cognition, 12,* 954–978. doi:10.1080/13506280444000607

Epstein, R. A. (2008). Parahippocampal and retrosplenial contributions to human spatial navigation. *Trends in Cognitive Sciences, 12,* 388–396. doi:10.1016/j.tics.2008.07.004

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature, 392,* 598–601. doi:10.1038/33402

Gallistel, C. R. (1990). *The organization of learning.* Cambridge, MA: The MIT Press.

Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: Features overshadow geometry. *Biology Letters, 1,* 314–317. doi:10.1098/rsbl.2005.0347

Hannula, D. E., & Ranganath, C. (2008). Medial temporal lobe activity predicts successful relational memory binding. *Journal of Neuroscience, 28,* 116–124. doi:10.1523/JNEUROSCI.3086-07.2008

Hartley, T., Trinkler, I., & Burgess, N. (2004). Geometric determinants of human spatial memory. *Cognition, 94,* 39–75.

Hermer, L., & Spelke, E. (1994). A geometric process for spatial representation in young children. *Nature, 370,* 57–59. doi:10.1038/370057a0

Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61,* 195–232. doi:10.1016/S0010-0277(96)00714-7

Hermer-Vazquez, L., Spelke, E. S., & Katsnelson, A. S. (1999). Sources of flexibility in human cognition: Dual-task studies of space and language. *Cognitive Psychology, 39,* 3–36. doi:10.1006/cogp.1998.0713

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *Journal of Neuroscience, 23,* 5945–5952.

Kelly, D. M., Spetch, M. L., & Heth, C. D. (1998). Pigeons' (*Columba livia*) encoding of geometric and featural properties of a spatial environment. *Journal of Comparative Psychology, 112,* 259–269. doi:10.1037/0735-7036.112.3.259

Kelly, J. W., McNamara, T. P., Bodenheimer, B., Carr, T. H., & Reiser, J. J. (2008). The shape of human navigation: How environmental geometry is used in the maintenance of spatial orientation. *Cognition, 109,* 281–286. doi:10.1016/j.cognition.2008.09.001

Köhler, S., Crane, J., & Milner, B. (2002). Differential contributions of the parahippocampal place area and the anterior hippocampus to human memory for scenes. *Hippocampus, 12,* 718–723. doi:10.1002/hipo.10077

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science, 13,* 337–341. doi:10.1111/j.0956-7976.2002.00461.x

Learmonth, A. E., & Newcombe, N. S. (2010). The development of place learning in comparative perspective. In F. L. Dolins & R. W. Mitchell (Eds.), *Spatial cognition, spatial perception* (pp. 520–538). New York, NY: Cambridge University Press.

Learmonth, A. E., Newcombe, N. S., Sheridan, N., & Jones, M. (2008). Why size counts: Children's spatial reorientation in large and small enclosures. *Developmental Science, 11,* 414–426. doi:10.1111/j.1467-7687.2008.00686.x

Lloyd, M. E., Newcombe, N. S., & Doydum, A. (2009). Memory binding in early childhood: Evidence for a retrieval deficit. *Child Development, 80,* 1321–1328. doi:10.1111/j.1467-8624.2009.01353.x

McGregor, A., Jones, P. M., Good, M. A., & Pearce, J. M. (2006). Further evidence that rats rely on local rather than global spatial information to locate a hidden goal: Reply to Cheng and Gallistel (2005). *Journal of Experimental Psychology: Animal Behavior Processes, 32,* 314–321. doi:10.1037/0097-7403.32.3.314

Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes, 33,* 191–212. doi:10.1037/0097-7403.33.3.191

Newcombe, N., Huttenlocher, J., Drummey, A. B., & Wiley, J. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. *Cognitive Development, 13,* 185–200. doi:10.1016/S0885-2014(98)90038-7

Newcombe, N. S., & Ratliff, K. R. (2007). Explaining the development of spatial reorientation. In J. M. Plumert & J. P. Spencer (Eds.), *The emerging spatial mind* (pp. 53–76). New York, NY: Oxford University Press.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* New York, NY: Oxford University Press.

Olson, I. R., Page, K., Moore, K. S., Chatterjee, A., & Verfaellie, M. (2006). Working memory for conjunctions relies on the medial temporal

lobe. *Journal of Neuroscience, 26,* 4596–4601. doi:10.1523/JNEUROSCI.1923-05.2006

Pearce, J. M., Good, M. A., Jones, P. M., & McGregor, A. (2004). Transfer of spatial behavior between different environments: Implications for theories of spatial learning and for the role of hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 30,* 135–147. doi:10.1037/0097-7403.30.2.135

Pruessner, J. C., Köhler, S., Crane, J., Pruessner, M., Lord, C., Byrne, A., . . . Evans, A. C. (2002). Volumetry of temporopolar, perirhinal, entorhinal, and parahippocampal cortex from high-resolution MR images: Considering the variability of the collateral sulcus. *Cerebral Cortex, 12,* 1342–1353. doi:10.1093/cercor/12.12.1342

Pruessner, J. C., Li, L. M., Serles, M., Pruessner, M., Collins, D. L., Kabani, N., . . . Evans, A. C. (2000). Volumetry of hippocampus and amygdale with high-resolution MRI and three-dimensional analysis software: Minimizing the discrepancies between laboratories. *Cerebral Cortex, 10,* 433–442. doi:10.1093/cercor/10.4.433

Ratliff, K. R., & Newcombe, N. S. (2008). Is language necessary for human spatial reorientation? Reconsidering evidence from dual task paradigms. *Cognitive Psychology, 56,* 142–163. doi:10.1016/j.cogpsych.2007.06.002

Shipman, S. L., & Astur, R. S. (2008). Factors affecting the hippocampal BOLD response during spatial memory. *Behavioural Brain Research, 187,* 433–441. doi:10.1016/j.bbr.2007.10.014

Sluzenski, J., Newcombe, N. S., & Kovacs, S. L. (2006). Binding, relational memory, and recall of naturalistic events: A developmental perspective. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 32,* 89–100. doi:10.1037/0278-7393.32.1.89

Sluzenski, J., Newcombe, N. S., & Satlow, E. (2004). Knowing where things are in the second year of life: Implications for hippocampal development. *Journal of Cognitive Neuroscience, 16,* 1443–1451. doi:10.1162/0898929042304804

Stark, C. E. L., & Squire, L. R. (2001). When zero is not zero: The problem of ambiguous baseline conditions in fMRI. *Proceedings of the National Academy of Sciences of the USA, 98,* 12760–12766. doi:10.1073/pnas.221462998

Stürzl, W., Cheung, A., Cheng, K., & Zeil, J. (2008). The information content of panoramic images: I. The rotational errors and the similarity of views in rectangular experimental arenas. *Journal of Experimental Psychology: Animal Behavior Processes, 34,* 1–14. doi:10.1037/0097-7403.34.1.1

Sutton, J. E. (2009). What is geometric information and how do animals use it? *Behavioural Processes, 80,* 339–343. doi:10.1016/j.beproc.2008.11.007

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: An approach to cerebral imaging.* New York, NY: Thieme Medical Publishers.

Thompson-Schill, S. L. (2003). Neuroimaging studies of semantic memory: Inferring "how" from "where." *Neuropsychologia, 41,* 280–292. doi:10.1016/S0028-3932(02)00161-6

Tommasi, L., & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick (*Gallus gallus*). *Animal Cognition, 7,* 53–59. doi:10.1007/s10071-003-0182-y

Twyman, A. D., & Newcombe, N. S. (2009). Five reasons to doubt the existence of a geometric module. *Cognitive Science.* Advance online publication. doi:10.1111/j.1551-6709.2009.01081.x

Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals' spatial representations: A test with chicks (*Gallus gallus domesticus*). *Journal of Comparative Psychology, 104,* 248–254. doi:10.1037/0735-7036.104.3.248