Contributions of Medial Temporal Lobe and Striatal Memory Systems to Learning and Retrieving Overlapping Spatial Memories

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Many life experiences share information with other memories. In order to make decisions based on overlapping memories, we need to distinguish between experiences to determine the appropriate behavior for the current situation. Previous work suggests that the medial temporal lobe (MTL) and medial caudate interact to support the retrieval of overlapping navigational memories in different contexts. The present study used functional magnetic resonance imaging (fMRI) in humans to test the prediction that the MTL and medial caudate play complementary roles in learning novel mazes that cross paths with, and must be distinguished from, previously learned routes. During fMRI scanning, participants navigated virtual routes that were well learned from prior training while also learning new mazes. Critically, some routes learned during scanning shared hallways with those learned during pre-scan training. Overlap between mazes required participants to use contextual cues to select between alternative behaviors. Results demonstrated parahippocampal cortex activity specific for novel spatial cues that distinguished between overlapping routes. The hippocampus and medial caudate were active for learning overlapping spatial memories, and increased their activity for previously learned routes when they became context dependent. Our findings provide novel evidence that the MTL and medial caudate play complementary roles in the learning, updating, and execution of context-dependent navigational behaviors.

Keywords: caudate, fMRI, hippocampus, navigation, parahippocampal

Episodic memories are composed of distinct events in time and space, yet our memories often share information with other experiences. We draw upon memories to guide our decisions and actions, but overlap between representations is a source of interference that can lead to errors in memory-guided behavior. The brain must be able to represent these overlapping memories in a manner that allows subsequent retrieval of distinct representations, and researchers have focused on the medial temporal lobe (MTL) as critical to this function. Within the MTL, the parahippocampal cortex may represent contextual information (Bar and Aminoff 2003; Davachi 2006; Eichenbaum et al. 2007; Brown et al. 2010) that the hippocampus could associate with specific events, facilitating retrieval of unique episodes despite interference from overlapping memories (Agster et al. 2002; Hasselmo and Eichenbaum 2005; Zilli and Hasselmo 2008; Brown et al. 2010).

Selecting situationally appropriate behaviors based on overlapping experiences may rely not only on the MTL but also on components of the complementary striatal memory system (Foster and Knierim 2011). In particular, the medial caudate is thought to support translation of mnemonic information into goal-directed action (Devan and White 1999; Johnson et al. 2007; Brown et al. 2012). Activity in the caudate rapidly updates to reflect changes in behavioral contingencies in primates (Pasupathy and Miller 2005), and the medial dorsal striatum is important for acquiring alternative behaviors in maze environments in rodents (Ragozzino et al. 2002; DeCoteau et al. 2007; Thorn et al. 2010). In humans, the caudate has been implicated in shifts in response strategy and stimulus–outcome associations due to changes in task rules (Monchi et al. 2001, 2006; Xue et al. 2008; Graham et al. 2009). These data suggest that the medial caudate may be critical for the learning and flexible expression of context-dependent spatial behaviors in humans by representing and updating alternative behavioral programs in different situations.

Despite considerable interest in the neural representation of overlapping navigational information (e.g., Wood et al. 2000; Hasselmo and Eichenbaum 2005; Smith and Mizumori 2006; Johnson and Redish 2007; Zilli and Hasselmo 2008; Hasselmo 2009), fundamental questions remain regarding this process in humans. Whether learning overlapping navigational representations and behaviors recruits the hippocampus and medial caudate, and whether this process relates more strongly to hippocampal and striatal function than encoding distinct non-overlapping spatial associations, has not been demonstrated in humans. Furthermore, in the real world, overlapping navigational routes are typically learned separately from one another, often with a considerable temporal delay between experiences. Prior research suggests that specific well-learned routes have limited dependence on the hippocampus (Hartley et al. 2003). It is not known whether such stable representations of distinct routes are updated to recruit the hippocampus more strongly when subsequent experiences introduce overlapping associations and a need for context-dependent retrieval. Similarly, it is not known whether unambiguous, well-learned navigational decisions become more dependent on the medial caudate when competing behavioral associations are introduced. For example, when turning left has been previously reinforced for a location, but you subsequently learn that turning right is correct in a different context or situation, does the medial caudate become active for flexibly selecting between the 2 responses?

The present fMRI experiment was designed to test whether activity in the MTL and medial caudate relates more strongly to learning navigational routes that overlap with familiar spatial memories than learning novel distinct route representations, and to examine how recruitment of the hippocampus and medial caudate for retrieval of well-learned spatial memories changes with the introduction of overlapping alternative routes. Participants learned a series of virtual mazes outside...
of the scanner. Twenty-four hours later, participants navigated the familiar routes during fMRI scanning, while also learning a series of novel virtual mazes. Critically, some of the novel routes shared locations with mazes already well learned from training the previous day. Using a region-of-interest (ROI) analysis approach, fMRI signal for overlapping mazes was compared with that of closely matched non-overlapping mazes during different stages of the task.

Within the MTL system, we hypothesized that the parahippocampal cortex would represent the relationship between the starting location and upcoming context-dependent decision-points in the overlapping condition. It is this unique association between the starting point and subsequent intersection that serves as a contextual signal for distinguishing each overlapping maze. In contrast, these relationships are not necessary for retrieval (navigation) of subsequent locations in non-overlapping mazes. We predicted that the parahippocampal cortex would be more strongly recruited for overlapping maze contextual cues than non-overlapping maze cues, reflecting activation of the association between the starting location and the upcoming route environment.

For the overlapping component of the routes, we predicted that the posterior hippocampus would be recruited for learning to navigate context-dependent decision points, helping to encode a novel navigational memory and context that incorporates familiar locations. A growing body of literature also implicates the posterior hippocampus in explicit sequence retrieval (Ross et al. 2009), and spatial mnemonic processes (Fanselow and Dong 2010), including context-dependent coding of overlapping trajectories based on future routes (Wood et al. 2000; Ferbinteanu and Shapiro 2003; Lee et al. 2006; Smith and Mizumori 2006), context-guided route retrieval (Brown et al. 2010), and separate retrieval of potential route options during decision-making periods (Johnson and Redish 2007). With the introduction of competing behavioral associations for the overlapping intersections, navigation of familiar overlapping routes may come to recruit the hippocampus for directed retrieval of the correct turn to reach the next location in the current context. This is in contrast to well-learned non-overlapping routes, which we expected to rely minimally on hippocampal-dependent forms of memory (with performance potentially supported by unique associations stored in the cortex and learned stimulus-behavior pairings). Therefore, we predicted that posterior hippocampal activity would increase for previously learned routes when a need for context-dependent retrieval is introduced, to become significantly greater than activity for navigation of familiar non-overlapping routes. Finally, we hypothesized that the medial caudate would play a complementary role to the hippocampus, being recruited during the acquisition of novel alternatives to previously learned behaviors in overlapping mazes, and updating participation in the selection of familiar navigational behaviors when alternative actions have been introduced.

Materials and Methods

Participant Pool
Twenty-one participants were recruited for the experiment. Two participants were excluded due to excessive head motion. Three participants were excluded due to technical issues with the MRI scanner. A total of 16 participants were included in the final analysis (7 males and 9 females, 3 left handed and 13 right handed). Participants were healthy young adults, with no history of neurological or psychiatric disorder. Participants were compensated for their participation at a rate of $10 per hour. The mean participant age was 20 years old (SD 2.7 years). Informed consent was obtained from each participant in a manner approved by the Partners Human Research Committee and the Boston University Institutional Review Board.

Virtual Navigation Design
Twenty virtual mazes (see Fig. 1) were constructed using POV-Ray Version 3.6.2 (http://www.povray.org [date last accessed 14 February 2013]), a 3D ray-tracer modeling program. Mazes were described to participants as being different routes in a large outdoor labyrinth, similar to different routes among a city. Participants navigated the virtual routes from a ground-level first-person perspective and behavioral performance (accuracy and reaction time) was recorded using E-Prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA, USA). Every maze was comprised of 3 hallways and 3 intersections. Each intersection contained unique, clearly identifiable objects that served as distinguishing features between the locations. The 20 mazes were divided into 2 groups. Ten of the mazes were “non-overlapping,” and did not share any hallways or intersections with each other and were therefore completely distinct. The other 10 mazes were “overlapping” mazes. The overlapping mazes were split into 5 pairs that each began and ended at distinct, non-overlapping locations, but converged in the middle to share the second hallway with another maze.

Participants began navigation of each maze with a 2 s cue period, during which participants viewed the starting intersection of the maze without moving. During the cue period, wooden barriers blocked visibility down the hallways off the intersection so that the only visual information available to participants was the unique landmark of the starting location. Following the cue, the wooden barriers fell away and participants could make their initial navigational response. At each intersection, participants responded with a button press of 1 to turn left, 2 to go straight ahead, and 3 to turn right. The correct choice was the next hall in the sequence of spatial locations comprising a maze. Navigational demands were matched between overlapping and non-overlapping mazes, with the number of left, right, and straight choices counterbalanced across the mazes and experimental conditions. Participants were not allowed to make exploratory turns to view the hallways to the left and the right of the current intersection, meaning landmarks down those halls were not visible until after the navigational response for the current intersection had been made and the turn completed. This meant that navigational turns required knowledge of the correct turn for the current landmark to reach the next location in the route.

Following a correct navigational choice, participants would turn down the next hallway and travel to the subsequent intersection. Turns were made in 2 simulated steps, with each step incorporating 45° of rotation, such that the participant would come out of the turn centered and facing directly down the next hallway. Turns took 1 s. Movement down a hallway was simulated with a video of POV-Ray-generated images. Each hallway took 2 s to traverse. Following an incorrect navigational choice, participants received correctional feedback.

The exact timing of behavioral responses and stimulus presentation was logged in E-Prime to allow accurate modeling of the task. The total duration of a maze varied with the response times at each intersection. Each maze was followed by an 8 s inter-trial interval (ITI) during which participants viewed a fixation point in the center of a black screen.

Experiment Protocol
The experiment was broken into two phases: a pre-scan training session, followed the next day by the fMRI experiment.
the participant failed to respond were treated as incorrect for both the correctional movement as with an incorrect response. Trials in which participants did not respond within 5 s, they were given a visual prompt maximum of 5 s to respond at each intersection. In cases where participants rotated in the correct direction and sent down the correct hall. To further control the timing of the task, participants were allowed a 4-way intersection with 1 uniquely identifiable landmark object placed at the corners. Only knowledge of the routes distinguished the overlapping intersections as different from non-overlapping intersections.

**Pre-Scan Training**
The day before scanning, participants were guided through a sample pair of overlapping routes (different from those used in the actual task) by the experimenter to ensure participants understood the mechanics of the navigational task. Participants were then trained to a criterion of 100% correct on 10 of the virtual routes they would navigate in the scanner. Participants initially learned each maze one at a time, repeatedly navigating a maze until they met a training criterion of 4 consecutive perfect trials. Once criterion was met on one maze, participants would learn the next maze. The order in which the 10 mazes were learned was randomized across participants. Following individual training on the mazes, participants were given 5 training runs in which all 10 mazes were navigated once per run in a randomized order, similar to the fMRI task they would be given the following day. The final 2 training runs were required to be error-free to ensure participants had mastered the 10 mazes. Participants were instructed to attend the Cue period of every maze, as it identified which route they were to follow on a given trial.

The 10 training day mazes were learned as distinct routes that did not overlap with one another. Critical to the experiment, 5 of these routes would become overlapping the following day during fMRI scanning when they came to share common hallways with novel alternative routes (see Fig. 1b). The remaining 5 mazes learned during training would remain non-overlapping during the scanning task. Participants were aware that 5 of the routes learned during training would become overlapping in the scanner, but did not know which of the training day mazes would become overlapping and which would remain non-overlapping. Participants were instructed during training to simply focus on mastering the 10 distinct, currently non-overlapping, routes. Which overlapping and non-overlapping condition mazes were learned during training was randomized across subjects.

**Feedback**
Participants learned to correctly navigate the virtual mazes by receiving visual feedback for navigational errors. After an incorrect navigational choice at an intersection, text reading "Wrong!" in red letters was overlaid on the scene along with a green arrow indicating the correct direction for that decision point. Participants were then rotated in the correct direction and sent down the correct hall. To further control the timing of the task, participants were allowed a maximum of 5 s to respond at each intersection. In cases where participants did not respond within 5 s, they were given a visual prompt to respond and were provided with the same feedback arrows and correctional movement as with an incorrect response. Trials in which the participant failed to respond were treated as incorrect for both the training and scanning components of the study. Feedback was provided during all components of the study.

**fMRI Scanning Task**
Participants performed the fMRI scanning task ~24 h and 1 sleep cycle after prescan training to facilitate consolidation of the mazes learned during training. On the scanning day, prior to being placed in the scanner, participants were given an additional warm-up run through the ten familiar mazes. During the warm-up run, the 10 mazes learned during prescan training were presented once each in a randomized order. Within the scanner, participants performed 10 runs of the experiment. During each run, participants navigated once through each of the 10 mazes they had learned during training, as well as once through each of the 10 novel mazes with which they had no prior experience. By attending the correctional feedback for errors, participants gradually learned the 10 new mazes across runs. Mazes of the different experimental conditions were presented in an interleaved manner, with the order counterbalanced across runs, and the order of the runs randomized across participants.

Because participants learned 1 route from each pair of overlapping mazes during training, if the well-learned route was navigated in the first run of the scanning task before participants had encountered its new overlapping counterpart, participants would still process the trained route as non-overlapping for that first trial. To control for this, we ensured that the new overlapping mazes occurred before their well-learned counterpart in the first run by switching their placement in the maze presentation order where necessary.

In the non-overlapping mazes, the intersections required the same navigational choices in every trial. In the overlapping mazes, the starting Cue intersections were also always associated with the same navigational choices, but the second and third intersections were overlapping locations between the mazes. The correct turn at the overlapping intersections differed depending on which route was being followed in a given trial, identified by the unique starting location of the maze. Participant reports along with behavioral measures (see Post-Scan Interview results) indicated that participants used feedback from the second intersection to guide behavior at the third intersection in the overlapping mazes. We therefore refer to the second intersection in the mazes as the "Critical Decision" and the third intersection in the mazes as the "Secondary Overlapping Decision." We focus this report on the Cue and Critical Decision components of the environments.

Importantly, construction of the overlapping intersections was no different from the non-overlapping intersections: each was a 4-way intersection with 1 uniquely identifiable landmark object placed at the corners. Only knowledge of the routes distinguished the overlapping intersections as different from non-overlapping intersections.
Accuracy and reaction time were recorded for each navigational choice made. The 20 mazes were divided into 4 experimental conditions for behavioral and fMRI analysis (Fig. 1b): 1) The 5 mazes learned during pre-scan training that became overlapping in the scanner comprised the OverlappingOld (OLOld) condition. 2) The 5 mazes learned during prescan training that remained non-overlapping in the scanner comprised the Non-overlappingOld (NOLOld) condition. 3) The 5 mazes learned within the scanner that overlapped with the OLOld routes comprised the OverlappingNew (OLNew) condition. 4) The 5 non-overlapping mazes learned within the scanner comprised the Non-overlappingNew (NOLNew) condition. There were 50 trials per experimental condition.

Post-Scan Interview

After scanning, participants were interviewed about the experimental task. Participants were asked to elaborate on their use of the landmark objects in their navigational decisions, and their strategy for accurately navigating the Critical and Secondary Overlapping Decision periods.

Image Acquisition

Images were acquired at the Athinoula A. Martinos Center for Biomedical Imaging of the Massachusetts General Hospital in Charlestown, MA, using a 3 Tesla Siemens MAGNETOM TrioTim scanner with a Siemens 32-channel matrix head coil. High-resolution T1-weighted multiplanar rapidly acquired gradient echo (MP-RAGE) structural scans were acquired using generalized autocalibrating partially parallel acquisitions (GRAPPA) (TR = 2530 ms; TE = 3.31 ms; flip angle = 7; slices = 176; resolution = 1 mm isotropic). T2*-weighted BOLD images were acquired using an echo-planar imaging (EPI) sequence (TR = 2000 ms; TE = 30 ms; flip angle = 85; slices = 32, resolution = 3.0 × 3.0 × 4.0 mm). Functional image slices were aligned along the anterior/posterior commissure line.

fMRI Preprocessing

Imaging analysis was conducted using SPM8 (Wellcome Department of Cognitive Neurology, London, UK). All BOLD images were reoriented so the origin [i.e., coordinate xyz (0 0 0)] was at the anterior commissure. Images were then slice-time corrected to the first slice acquired in time. Motion correction was conducted and included realigning the BOLD images to the first functional image acquired and unwarping the BOLD images to correct for movement-by-susceptibility artifact interactions (Andersson et al. 2001). The high-resolution structural images were then coregistered with the mean BOLD image obtained during motion correction and segmented into white and gray matter images and bias-corrected. The bias-corrected structural images and coregistered BOLD images were spatially normalized into standard Montreal Neurological Institute (MNI) space using the Diffeomorphic Anatomical Registration using Exponentiated Lie algebra (DARTEL) algorithm (Ashburner 2007) for improved inter-subject registration. BOLD images were resampled during normalization to 2 mm³ isotropic voxels and spatially smoothed using a 6 mm Full-width at half-maximum Gaussian kernel.

Statistical Analysis of data

Because of our strong a priori predictions for this task, the primary fMRI data analyses were conducted using a targeted ROI approach. On the basis of prior experiments in humans and animals, we examined activations for context-dependent Critical Decisions with specific ROIs in the tail of the hippocampus and medial caudate, and activations in posterior parahippocampal cortex related to processing overlapping maze contextual cues. In order to identify which other brain regions contribute to overlapping route navigation, we also conducted corresponding whole-brain analyses of the fMRI data.

To better characterize the function of our ROIs and their relationship to learning, we analyzed the data in 4 ways:

1. Averaged overlapping versus non-overlapping analysis—this analysis examined whether the hippocampal tail, medial caudate, and parahippocampal cortex had generally greater activation, collapsed across trials, for context-dependent overlapping maze navigation than non-overlapping maze navigation.
2. Early versus Late task phase analysis—this analysis examined whether disambiguation-related (overlapping > non-overlapping) activation differences in our hippocampal and medial caudate ROIs for Critical Decisions changed from early learning to late trials of the experiment.
3. Within-subjects regression of activity and learning curves—this analysis examined whether activations in the hippocampus and medial caudate for new mazes decreased in the manner proportional to improving Critical Decision accuracy across trials, and whether decreases in activity with learning relate more strongly to overlapping than non-overlapping maze learning curves.
4. Between-subjects activity-accuracy regression analysis—in order to determine whether good overlapping route navigators are characterized by greater recruitment of our hippocampal tail and medial caudate ROIs, this regression analysis examined whether participants who performed better on Critical Decisions had stronger activations in our ROIs than those who performed worse.

We conducted a corresponding analysis of the behavioral data. The details of our behavioral and functional analyses are provided below.

Analysis of Behavioral data

Training Day Trials to Criterion

Mazes of both the OLOld and NOLOld conditions were learned as distinct, non-overlapping routes during pre-scan training, and participants were ignorant of which routes belonged to which condition. We compared the number of trials to reach training criterion between the 2 conditions to ensure that there were no differences in their difficulty. We compared the number of trials to reach criterion by entering individual subject’s data into a paired-sample t-test between the conditions.

Averaged overlapping versus non-overlapping analysis—scanning day behavior

To compare overall performance between experimental conditions of interest, we entered the Critical Decision accuracies and reaction times averaged across trials into 2 × 2 repeated-measures general linear model (GLM) analyses examining effects of training status (Old vs. New mazes) and condition (overlapping vs. non-overlapping mazes). Significant training status by condition interactions were examined with specific follow-up paired-sample t-tests comparing OLOld with NOLOld mazes, and OLNew with NOLNew mazes. This allowed us to determine whether significant differences between the overlapping and non-overlapping conditions were specific to well-learned or newly learned mazes. While there was no behavioral response for the 2 second Cue period of the task, we also compared accuracies for the subsequent "starting intersection" choices to determine that overlapping and non-overlapping maze Cues were comparable in terms of starting location recognition memory.

Early versus Late task phase analysis: scanning day behavior

To examine how learning affects activity differences in our hippocampal and medial caudate ROIs for Critical Decisions, we split the data into 2 bins: Early trials and Late trials (for similar approaches, see Shohamy and Wagner 2008; Ross et al. 2009). Using the behavioral data for the individual mazes, the Early phase was defined as the first 3 experimental runs, during which learning rates (improvement in accuracy from one run to the next) were the greatest for the OLOld maze Critical Decision points and their NOLNew maze counterparts. During this period, participants were making a comparable number of errors for the 2 conditions. The Late phase was comprised of the final 3 runs of the experiment, during which all participants were consistently performing at peak accuracy for the Critical Decision points of each condition. The trials from the middle 4 runs were not...
included in the Early versus Late analysis, because these runs encompassed a transitional period when some mazes were still being learned while others were not.

To examine whether knowledge of the mazes improved comparably from the early phase to the Late phase in the overlapping and non-overlapping mazes, average accuracies for the early and late bins were entered into a repeated-measures GLM analysis with task phase (Early vs. Late) and condition (OL vs. NOL) as factors. In order to directly compare the slopes between overlapping and non-overlapping mazes, we conducted this analysis separately for the Old and New mazes. The absence of a significant task phase by condition interaction would indicate accuracy changed comparably for the overlapping and non-overlapping conditions from early to late trials.

fMRI Analyses
ROI Definition
Prior examinations of overlapping representations in the brain strongly implicate the posterior extent of the hippocampus. Specifically, context-specific representations of overlapping locations lie in the dorsal hippocampus of rodents (Wood et al. 2000; Ferrébleau and Shapiro 2003; Lee et al. 2006; Smith and Mizumori 2006), which corresponds to the tail of the human hippocampus. Furthermore, sequential replay of spatial trajectories occurs in the dorsal hippocampus of rodents (Davidson et al. 2009; Gupta et al. 2010). Similarly, activations related to overlapping information processing localize predominantly to posterior regions of the hippocampus in prior human fMRI studies (Kumaran and Maguire 2006; Ross et al. 2009; Kuhl et al. 2010). We therefore reasoned that the posterior hippocampus may be particularly important for disambiguating overlapping representations. In particular, we hypothesized that the same region of the hippocampus that has been previously implicated in navigating familiar overlapping routes (Brown et al. 2010) might be important for learning overlapping routes and update its response for familiar representations as they become context-dependent. Coordinates for our hippocampal tail, medial caudate, and parahippocampal cortex ROIs were therefore derived from the 2010 study by Brown et al. The center coordinates for our left and right hippocampal tail ROIs were $x = 18, -34, z = -2$. The center coordinates for our medial caudate nucleus ROIs were $x = 14, 4, z = 14$. The center coordinates for our parahippocampal cortex ROIs were $x = 18, -40, z = -12$. The ROI volumes were created in 2 steps: we initially created spherical ROI volumes with a 5 mm radius centered on the coordinates listed above using the Wake Forest University (WFU) PickAtlas available for SPM (Maldjian et al. 2003, 2004). To minimize voxels residing in white matter, cerebrospinal fluid, and other brain areas from being included in data from our ROIs, the spherical ROIs were then masked by anatomical boundaries of the hippocampus, caudate, and parahippocampal cortex using an intersection between the spheres and AAL structural delineations in the WFU PickAtlas (Tzourio-Mazoyer et al. 2002). These anatomically constrained ROIs were then saved as masks to be used for the ROI analyses.

As noted above, our targeted ROI approach was paired with exploratory whole-brain analyses, which allowed us to characterize other brain regions that are important for the learning, updating, and retrieval of overlapping spatial memories.

Averaged overlapping versus non-overlapping model and analysis
Twenty-eight separate regressors were created for each participant to model the fMRI data. Maze components were modeled based on their conceptually different cognitive processes. Our analysis focused on data from regressors modeling 2 key maze components: the Cue period and the Critical Decision period. These maze components were modeled separately for each condition and training state (OLOld, OLOld, NOLnew, and NOTnew). Non-overlapping “counterpart” regressors were assigned to the Critical Decision period because there were no actual overlapping intersections in the non-overlapping condition.

The Cue period regressors represented the 2 s period in which participants viewed the distinct non-overlapping starting location of each maze without moving. The view of the other hallways was obstructed by wooden barriers during the Cue period. The Critical Decision period regressors contained both the time to traverse the hallway (2 s) and the time at the subsequent intersection preceding the navigational response. This ensured that parameter estimates computed for these regressors captured the navigational decision-making process underlying trials of both conditions.

In order to accurately capture the variance in the task, additional regressors were created for the remaining maze components (starting intersection, secondary overlapping decision period, and final hallway) for each condition and training state. The starting intersection regressor modeled the time at the starting intersection following the Cue period from the disappearance of the wooden barriers. The secondary overlapping decision and final hallway regressors modeled traversal of the last 2 hallways of each maze. As with the Critical Decisions, non-overlapping “counterpart” regressors were assigned to the secondary overlapping decision periods. A 21st regressor modeled the ITI period of the experiment, and a 22nd nuisance regressor accounted for incorrect trials and feedback periods. Finally, the 6 motion parameters calculated during motion correction were added to the model to account for this artifact.

Of note, regressors from the task were constructed as a series of square wave functions or “boxcars.” Boxcar onsets were defined by the onset of each event, with the duration of Critical Decision and secondary overlapping decision period boxcars being determined by the reaction time of participants for that particular trial. These parameters were convolved with the canonical hemodynamic response function in SPM8. The design matrix was then analyzed using the GLM approach.

To examine average activation differences between the overlapping and non-overlapping conditions, t-contrasts between the conditions for the 2 task components of interest (contextual cue period and critical decision period) were conducted for each participant. Group-averaged statistical parametric maps (SPMs) were created by entering the Overlapping greater than Non-overlapping condition contrast images from each participant into a one-sample t-test using participants as a random factor.

ROI analysis. To test whether our a priori ROIs are more strongly recruited on average for contextual Cue and Critical Decision periods of the overlapping mazes than the non-overlapping mazes, t-contrasts between the conditions were conducted within the combined volume of our a priori ROIs in SPM8. A voxelwise statistical threshold of $P < 0.01$ was applied to the contrast maps. To correct for multiple comparisons, we applied a cluster-extent threshold technique. We used the AlphaSim program in the AFNI software package (http://afni.nimh.nih.gov/afni/) to conduct a Monte Carlo simulation analysis on the combined voxels of our ROIs. From a 10 000 simulation analysis, a minimum voxel extent of 10 was determined to maintain a family-wise error rate of $P < 0.05$.

Whole-brain analysis. Similar to the ROI analysis, we applied a voxelwise statistical threshold of $P < 0.01$ to the group-level whole-brain contrast maps. We conducted a whole-brain Monte Carlo simulation analysis, masking out voxels beyond the group functional brain space using the ResMS header file. From a 10 000 simulation analysis, a minimum voxel extent of 109 was determined to maintain a family-wise error rate of $P < 0.05$.

Early versus Late task phase analysis
To test whether differences in activity between the Overlapping and Non-overlapping conditions in our hippocampal and medial caudate ROIs change in relation to learning the OLS to Critical Decisions, we split the data into 2 bins: early trials and late trials. Early and Late bins were defined based on the behavioral data, as described in the behavioral analysis section above. The Early phase contained fMRI data from the first 3 experimental runs, while the Late phase was comprised of the final 3 runs of the experiment. For this analysis, we modified the model used for the averaged overlapping versus non-overlapping analysis, splitting the trials of the Critical Decision period into separate “task phase” regressors for Early and Late trial bins. For this analysis, Critical Decision error trials were included in
the Early and Late regressors. Including error trials in the task phase regressors allowed us to examine the relationship between the fMRI data and corresponding behavioral accuracies.

Parameter estimates were extracted from our hippocampal and medial caudate ROIs for both Early and Late trials of each condition, and entered into a repeated-measures GLM analysis with Task Phase and Condition as factors. Using parameter estimate extractions allowed us to visualize how activations in our ROIs change across task phases. In order to compare the slopes between overlapping and non-overlapping mazes, we conducted this analysis separately for the Old and New mazes. Before considering the main effects and interaction effects as significant, we applied Bonferroni correction for multiple comparisons to $P < 0.05$, correcting for the fact that the factors were tested 4 times (i.e., the ANOVA was conducted for each ROI) within mazes of a given Training Status (Old or New). Significant ANOVA effects were thresholded at $P < 0.0125$.

When significant main effects of Condition or Task Phase by Condition interactions were present, they were examined in detail with specific follow-up paired-sample $t$-tests between the Overlapping and Non-overlapping conditions for Early and Late trials. This allowed us to determine whether significant differences between the Overlapping and Non-overlapping conditions were specific to 1 task phase or both.

**Whole-brain analysis.** We conducted a whole-brain analysis of Early and Late task phase activity in SPM to evaluate which brain regions lying outside our specific ROIs are recruited for overlapping mazes during different stages of the task. We entered contrast images from each subject comparing the Overlapping and Non-overlapping conditions for Early and Late task phases into a group-level analysis, in the same manner as with the Averaged Overlapping versus Non-overlapping Analysis above. This allowed for separate evaluation of which areas are more strongly active for overlapping mazes during each task phase. We applied a voxelwise statistical threshold of $P < 0.01$ to the group-level whole-brain contrast maps, with a minimum voxel extent of 109 to ensure a family-wise error rate of $P < 0.05$.

**Within-subjects regression of activity and learning curves**
The degree to which activity decreases across trials in a manner correlated with improving accuracy serves as a metric for whether recruitment of a brain region relates to learning. We wanted to examine whether activations in our hippocampal and medial caudate ROIs relate to learning novel overlapping mazes in this manner. Similar to the Early versus Late task phase analysis, we modified the model used for the Averaged Overlapping versus Non-overlapping analysis to include error trials in the Critical Decision regressors. We conducted a parametric analysis in SPM at the individual subject level, using subject-specific Critical Decision learning curves as regressors for run-by-run Critical Decision activity. Since performance for individual Critical Decision trials was a binary measure, to obtain a continuous measure of performance the data points in the learning curve regressors were created using the average proportion of correct trials for each learning block (run). Because we were interested in activity that is higher during periods of greater learning and decreases in proportion to improving performance, each accuracy data point was subtracted from 1 to create a learning curve that was inverted (Fig. 5b).

We conducted a complementary regression for Non-overlapping mazes. A significant positive linear relationship in this regression indicates that activity is greatest during early learning and decreases across runs in a manner corresponding to improving accuracy.

Individual subject regression maps reflecting this relationship were then entered into 2 types of group-level analyses: 1) An ROI analysis using 1-sample $t$-tests against zero, testing whether there was a significant linear relationship between activity and individual subject learning curves in our hippocampal and medial caudate ROIs. 2) A $t$-test contrasting OLnew and NOLnew regression maps, masked to voxels showing a statistically significant linear relationship at $P < 0.01$ in the 1-sample OL > zero $t$-test. This analysis tested whether the regression of activity against the learning curve is more strongly positive for OLnew than for NOLnew mazes. These analyses were thresholded at $P < 0.01$, with a voxel extent of 10 to maintain a family-wise error rate of $P < 0.05$.

We also conducted a whole-brain exploratory analysis contrasting OLnew and NOLnew mazes, masked to voxels showing a statistically significant linear relationship at $P < 0.01$ in a whole-brain 1-sample OL > zero $t$-test. The OL > zero $t$-test was thresholded at $P < 0.01$ with a voxel extent of 109 to maintain a family-wise error rate of $P < 0.05$. The OL > NOL maze contrast was thresholded at $P < 0.01$, and needed to overlap with clusters from the OL > zero $t$-test by at least 45 voxels (equivalent to a family-wise error rate of $P < 0.05$ within this conjunction search volume). This analysis identified brain regions beyond our ROIs whose activity significantly tracked the overlapping maze learning curves, and did so in a significantly more positive manner for overlapping than non-overlapping mazes.

**Between-subjects activity-accuracy regression analysis**
We reasoned that if overlapping maze learning and decision-making is more reliant on processes supported by the hippocampal tail and medial caudate, how well participants perform on the overlapping routes might relate to how strongly they recruit our ROIs. To determine whether high-performance navigators are characterized by their recruitment of our ROIs, we entered the individual subject beta maps into a second-level multiple regression analysis in SPM, using Critical Decision performance as a covariate. All participants were performing at ceiling in both the Overlapping and Non-overlapping conditions by the end of the experiment, but there was sufficient behavioral variability for this analysis during early learning (Early task phase) of the OLnew and NOLnew Critical Decisions.

We asked 2 questions: 1) Using OLnew Critical Decision accuracy as a regressor with OLold activity, we tested whether participants who perform better on the newly encountered overlapping mazes recruit our ROIs more strongly for the familiar OLold decisions. 2) Using OLnew Critical Decision accuracy as a regressor with OLnew activity, we tested whether participants who perform better on the newly encountered overlapping mazes recruit our ROIs more for those same decisions.

This analysis was conducted in SPM8 using our ROIs as a search volume. Relationships between subject performance and activity were thresholded at $P < 0.01$ with a voxel extent of 10 to maintain a family-wise error rate of $P < 0.05$.

**Results**

**Behavioral Results**

**Training day Trials to Criterion**
Participants learned OLold and NOLold mazes quickly during training, reaching criterion (4 consecutive perfect trials) in an average of 5.24 trials for the OLold condition (SEM = 0.09) and 5.23 trials for the NOLOld condition (SEM = 0.11). There was no difference in the number of trials to criterion for the 2 conditions ($t_{15} = 0.082, P > 0.936$), consistent with the fact that mazes of both conditions were learned as “non-overlapping routes” during training.

**Post-scan Interview**
All participants reported using the landmark objects to identify and aid in navigating the virtual routes. Participants reported a predominantly prospective strategy at the overlapping decision points, associating the Critical Decisions with the Secondary Overlapping Decisions. Linking the 2 decision-points in memory allowed participants to use feedback for choices at the Critical Decision point to select the subsequent third intersection behavior. Consequently, the majority of “disambiguation errors” (erroneously selecting the alternative behavior for an overlapping intersection) occurred...
for the Critical Decision period rather than the Secondary Overlapping Decision period. We focus our report on the starting Cue period and the Critical Decision period of the mazes.

**Averaged Overlapping versus Non-overlapping analysis: scanning day behavior**

To compare overall performance between experimental conditions of interest, we entered average Critical Decision accuracies and reaction times into 2 × 2 repeated-measures GLM analyses examining effects of Training Status (Old vs. New mazes) and Condition (Overlapping vs. Non-overlapping mazes). The results demonstrate that average behavioral performance was closely-matched between conditions.

**Starting intersection behavior.** There was no behavioral measure for the Cue periods of the experiment. However, participants navigated the starting intersections following the Cue period of the OLOld mazes with 99.6% accuracy (SEM 0.3), the NOLOld mazes with 99.8% accuracy (SEM 0.2), the OLNew mazes with 84.6% accuracy (SEM 1.6), and the NOLNew mazes with 86.8% accuracy (SEM 1.9). The GLM analysis revealed a significant main effect of Training Status (Old vs. New) ($F_{(1,15)} = 112.8$, $P < 2.2 \times 10^{-8}$), but no significant main effect of Condition (OL vs. NOL) ($F_{(1,15)} = 1.291$, $P > 0.274$), and no significant Training Status by Condition interaction ($F_{(1,15)} = 1.065$, $P < 0.318$). These results indicate that the average accuracy for the starting intersection did not differ between the OL and NOL conditions, and this relationship did not differ for Old and New mazes. Average accuracy differed based on Training Status because the New mazes were learned across trials within the scanner. These data ensure that participants had comparable recognition memory for the starting Cue locations of the 2 conditions.

**Critical Decision Accuracies.** Participants navigated the Critical Decision periods of the OLOld mazes with 96.8% accuracy (SEM 1.5), the NOLOld mazes with 99.6% accuracy (SEM 0.3), the OLNew mazes with 82.9% accuracy (SEM 2.3), and the NOLNew mazes with 86.4% accuracy (SEM 1.6). The GLM analysis revealed a significant main effect of Training Status ($F_{(1,15)} = 107.4$, $P < 3.1 \times 10^{-8}$), but no significant main effect of Condition ($F_{(1,15)} = 3.72$, $P > 0.073$), and no significant Training Status by Condition interaction ($F_{(1,15)} = 0.06$, $P > 0.810$). These results indicate that the average accuracy for the Critical Decisions did not differ significantly between the OL and NOL conditions, and this relationship did not differ for Old and New mazes. The average accuracy did differ based on the training status, because the New mazes were learned across trials within the scanner.

**Critical Decision Reaction times.** Critical Decision period reaction times were 386.7 ms (SEM 23.30) for the OLOld mazes, 352.9 ms (SEM 24.02) for the NOLOld mazes, 519.4 ms (SEM 40.51) for the OLNew mazes, and 452.1 ms (SEM 30.55) for the NOLNew mazes. The GLM analysis revealed a significant main effect of Training Status ($F_{(1,15)} = 17.55$, $P < 0.001$), as well as a significant main effect of Condition ($F_{(1,15)} = 12.65$, $P < 0.003$), but no significant Training Status by Condition interaction ($F_{(1,15)} = 1.724$, $P > 0.209$). These results indicate that average reaction times for the Critical Decisions were slower for the OL condition than the NOL condition, consistent with the requirement for a context-dependent decision at this point in the overlapping mazes. Average reaction time differed based on Training Status, because the New mazes were learned within the scanner.

**Early versus Late task phase analysis: scanning day behavior**

To examine how learning affects activity differences in our hippocampal and medial caudate ROIs for Critical Decisions, we split the data into 2 bins: Early trials and Late trials. To help ensure that accuracy was not a confound when interpreting divergent fMRI activation levels for the Overlapping and Non-overlapping condition from Early to Late trials, average accuracies for the Early and Late bins were entered into a repeated-measures GLM analysis with Task Phase (Early vs. Late) and Condition (OL vs. NOL) as factors. The Task Phase analysis revealed that knowledge of the Critical Decision points changed in the same manner from Early trials to Late trials for the OL and NOL conditions (i.e., the slopes were matched between conditions) (summarized in Figs 3d and 4d).

**Early vs. Late analysis of Old maze performance (OLOld and NOLOld).** Accuracy of the Old mazes did not change differently for the OL and NOL conditions from Early to Late trials, indicated by no significant Task Phase by Condition interaction ($F_{(1,15)} = 1.093$, $P > 0.312$). There was a significant main effect of Condition ($F_{(1,15)} = 6.404$, $P < 0.023$). There was no significant main effect of Task Phase ($F_{(1,15)} = 2.304$, $P > 0.150$). These results indicate that knowledge of the Old maze Critical Decisions did not change for the OL and NOL mazes from Early to Late trials.

**Early vs. Late analysis of New maze performance (OLNew and NOLNew).** Accuracy of the New mazes did not change differently for the OL and NOL conditions from Early to Late trials, indicated by no significant Task Phase by Condition interaction ($F_{(1,15)} = 0.139$, $P > 0.715$). There was no significant main effect of Condition ($F_{(1,15)} = 0.246$, $P > 0.627$). There was a significant main effect of Task Phase ($F_{(1,15)} = 161.800$, $P < 1.9 \times 10^{-8}$). These results indicate that knowledge of the New maze Critical Decisions improved to the same degree for the OL and NOL mazes from Early to Late trials.

**fMRI Results**

**Averaged OL versus NOL Analysis**

To test whether our *a priori* ROIs were more strongly recruited on the average for contextual Cue and Critical Decision periods of the overlapping mazes than the non-overlapping mazes, *t*-contrasts comparing average activity across trials between the conditions were conducted within the combined volume of our *a priori* ROIs in SPM8. Significant results are reported at a voxelwise threshold of $P < 0.01$, cluster threshold corrected for multiple comparisons to $P < 0.05$.

**Cue period.** Every maze of both the OL and the NOL conditions began at a unique, non-overlapping starting intersection (termed the Cue period). During the Cue period,
observed that the activity in the medial caudate extended into but to which competing associations were then introduced. Critical Decision period for OLOld mazes required participants to which competing associations were then introduced. Critical Decision period for OLOld mazes required participants to select the appropriate behavior for the current trajectory (e.g., “Do I turn left this time, or do I turn right?”). Importantly, the Critical Decision period for OLOld mazes required participants to execute the same highly familiar behavior learned during pre-scan training, while the Critical Decision period for OLNNew mazes required participants to execute a newly learned alternative to the OLOld behavior.

The same regions of the left hippocampal tail (xzy = −18, −34, −2; t = 4.06) and bilateral medial caudate (left caudate: xzy = −14, 0, 16, t = 3.64; right caudate: xzy = 12, 6, 12; t = 3.39) recruited for navigation of familiar overlapping routes (Brown et al. 2010) were both significantly more strongly recruited on average for navigational decision points that were previously well learned as distinct representations, but to which competing associations were then introduced (OLOld Critical Decisions). The same region of the medial caudate (reported in Brown et al. 2010) was also more strongly recruited on average for novel OL than NOL Critical Decisions in both hemispheres (left: xzy = −12, 2, 14, t = 4.65; right: xzy = 14, 2, 18, t = 6.50).

Other brain regions. Whole-brain analyses of contrasts between the OL and NOL mazes revealed multiple brain areas that are important for the learning and execution of context-dependent behavior. A summary of whole-brain activation differences between the overlapping and non-overlapping conditions is given in Tables 1 and 2. We observed that the activity in the medial caudate extended into the nucleus accumbens for the Critical Decision period of OLNNew mazes. Consistent with involvement of the ventral striatum in reward processing and behavioral flexibility (Johnson et al. 2007; Turnock and Becker 2008), the nucleus accumbens may be important in the present study for the feedback-based learning of alternative behaviors in a novel context. We also observed activations in several cortical areas associated with visual, spatial, and mnemonic processing, including the retrosplenial cortex, which has been implicated in visualization, construction, and identification of complex visual scenes and spatial information (Burgess et al. 2001; Addis et al. 2007; Epstein and Higgins 2007; Hassabis et al. 2007).

Critical Decision period. The Critical Decision period in this experiment represented the first of two overlapping intersections in the mazes. To correctly navigate the Critical Decision point of overlapping mazes, participants needed to select the appropriate behavior for the current trajectory (e.g., “Do I turn left this time, or do I turn right?”). Importantly, the Critical Decision period for OLOld mazes required participants to execute the same highly familiar behavior learned during pre-scan training, while the Critical Decision period for OLNNew mazes required participants to execute a newly learned alternative to the OLOld behavior.

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OverlappingOld activity was significantly greater than Non-overlappingOld activity ($t_{(15)} = 3.289, P < 0.005$) (Fig. 3a). Although the Secondary Overlapping Decisions are not a focus of this report, we note that the level of hippocampal activity observed in the Late task phase for the OverlappingOld Critical Decisions (average parameter estimate: 0.39) is not observed for the Secondary Overlapping Decisions (average parameter estimate: −0.02). This provides insight into the processes underlying Critical Decision activity—two alternative behaviors are associated with the Secondary Overlapping Decision point, but in contrast to the significant OL > NOL Critical Decision activity difference, comparison of Secondary Overlapping Decision parameter estimates with the non-overlapping maze Critical Decision counterparts using a paired-sample $t$-test demonstrated a highly non-significant difference ($t = −0.183, P = 0.858$). This indicates that having 2 alternative navigational associations for the current location alone is not the driving force behind the hippocampal activation difference with non-overlapping maze Critical Decision counterparts, and suggests the hippocampal activity is related to the explicit contextually guided retrieval process occurring for the Critical Decision. This retrieval could possibly encompass the associations for both overlapping intersections, as suggested by reports that participants used the Critical Decision to guide the Secondary choice.

In the right hippocampal tail ROI, there was no main effect of Condition ($F_{(1,15)} = 0.724, P < 0.408$). There was no main effect of Task Phase ($F_{(1,15)} = 0.140, P < 0.713$). There was no Condition by Task Phase interaction ($F_{(1,15)} = 0.468, P < 0.504$).

In the left caudate ROI, there was a trend toward a main effect of Condition ($F_{(1,15)} = 3.919, P < 0.066$). There was no main effect of Task Phase ($F_{(1,15)} = 0.485, P < 0.497$). However, there was a significant Condition by Task Phase interaction ($F_{(1,15)} = 15.911, P < 0.001$), surviving Bonferroni correction to $P < 0.05$ for the 4 ROIs tested. Planned follow-up $t$-tests between the conditions for the 2 task phases revealed that activity in the left caudate did not significantly differ between the OLold and NOLold mazes during Early trials ($t_{(15)} = 0.498, P < 0.626$), but was significantly greater for the OLnew than NOLnew mazes after the OLnew counterpart mazes had been learned ($t_{(15)} = 3.299, P < 0.005$) (Fig. 3b).

In the right caudate ROI, there was no main effect of Condition ($F_{(1,15)} = 1.365, P < 0.261$). There was no main effect of Task Phase ($F_{(1,15)} = 0.058, P < 0.813$). However, there was a significant Condition by Task Phase interaction ($F_{(1,15)} = 17.191, P < 0.001$), surviving Bonferroni correction to $P < 0.05$ for the 4 ROIs tested. Planned follow-up $t$-tests between the conditions for the 2 learning phases revealed that activity in the right caudate did not significantly differ between the OLold and NOLold mazes during early learning ($t_{(15)} = 1.239, P < 0.254$), but was significantly greater for the OLnew than NOLnew mazes after the OLnew counterpart mazes were learned ($t_{(15)} = 3.354, P < 0.004$) (Fig. 3b).

**Early versus Late New maze activity (OLnew and NOLnew).** There was no main effect of Condition in either the left or right hippocampal tail ROIs (left: $F_{(1,15)} = 0.814, P < 0.381$; right: $F_{(1,15)} = 0.006, P < 0.957$). There were no main effects of Task phase (left: $F_{(1,15)} = 1.550, P < 0.232$; right: $F_{(1,15)} = 1.001, P < 0.335$). There were no significant Condition by Task Phase interactions although there was a trend toward significance in the Left hippocampal tail ROI (left: $F_{(1,15)} = 3.292, P < 0.090$; right: $F_{(1,15)} = 1.802, P < 0.199$). Consistent with the Averaged Overlapping versus Non-overlapping analysis results, these data indicate that activity in this region of the hippocampal tail does not differ on average between OL and NOL navigational decisions during learning. However, the whole-brain analysis revealed overlapping maze activity centered over our left hippocampal tail ROI specifically during early learning (with significance exceeding $P < 0.01$). Parameter estimates from this ROI volume are therefore displayed in Figure 4a for illustration of the general pattern of activity from Early to Late trials in this a priori ROI. It is important to note that while the group average of the OL maze parameter estimates appears as a relatively flat line, activity at the single-subject level had a generally decreasing trend from Early to Late trials in the hippocampus (reflected in the learning curve regression results below and in Fig. 5a).

In the left caudate ROI, there was a significant main effect of Condition ($F_{(1,15)} = 16.725, P < 0.001$), surviving Bonferroni correction to $P < 0.05$ for the 4 ROIs tested. There was no main effect of Task Phase ($F_{(1,15)} = 1.100, P < 0.311$). There was a significant Condition by Task Phase interaction ($F_{(1,15)} = 12.443, P < 0.003$), surviving Bonferroni correction to $P < 0.05$ for the 4 ROIs tested. Planned follow-up $t$-tests between the conditions for the 2 learning phases revealed that activity in the left caudate was significantly greater during
Early and Late task phase whole-brain analysis. Similar to the Averaged Overlapping vs. Non-overlapping Whole-brain analysis, multiple brain areas were identified as important for spatial disambiguation in different stages of learning. A summary of whole-brain activation differences between the overlapping and non-overlapping conditions split out for Early and Late trials is given in Table 3. The finding that the hippocampal tail and medial caudate are recruited for late trials of the OLNew mazes is also observed at the whole-brain level, with activations colocalized with our a priori ROI volumes (Fig. 3c).

Critically, the whole-brain analysis identified a large cluster of hippocampal activity centered over our a priori left hippocampal tail ROI that was more strongly active specifically during early learning of OLNew than NOLNew mazes. We also observed several other clusters of hippocampal activity that were greater for early trials of OLNew mazes. These data demonstrate a strong difference in hippocampal recruitment when learning to navigate familiar locations in the context of a novel overlapping route over learning completely novel, but non-overlapping, representations (Fig. 4c). In addition to hippocampal activity during early overlapping maze learning, we observed extensive activations in the medial caudate at the whole-brain level centered over our a priori ROI volumes.

We also observed activity in the dopaminergic midbrain for early learning of overlapping mazes. The dopaminergic midbrain has been shown to support integrative encoding of overlapping item associations (Shohamy and Wagner 2008). Our finding of robust activity around the ventral tegmental area for early learning of OLNew mazes suggests that learning overlapping spatial representations utilizes dopaminergic midbrain function more than entirely novel, but non-overlapping, associations. Such recruitment of dopaminergic midbrain areas could facilitate learning in both the hippocampal and striatal memory systems discussed here.

During early learning of novel overlapping mazes, recognition of the familiar location could activate the previously learned (OLOld) associations. Because there are no previously learned associations for NOLNew mazes, this process would not occur during Early trials for non-overlapping mazes. Such learning of the OLNew than NOLNew mazes ($t_{15} = 6.197$, $P < 1.7 \times 10^{-5}$), but did not differ between the 2 conditions after the new decisions were learned ($t_{15} = 0.768$, $P = 0.454$) (Fig. 4b).

In the right caudate, there was a significant main effect of Condition ($F_{1,15} = 5.762$, $P = 0.030$), although this did not survive Bonferroni correction for multiple comparisons. There was a main effect of Task Phase approaching significance ($F_{1,15} = 4.283$, $P = 0.056$). There was a significant Condition by Task Phase interaction ($F_{1,15} = 10.962$, $P < 0.005$), surviving Bonferroni correction to $P < 0.05$ for the 4 ROIs tested. Planned follow-up $t$-tests between the conditions for the 2 learning phases revealed that activity in the right caudate was significantly greater during early learning of the OLNew than NOLNew mazes ($t_{15} = 4.121$, $P < 0.001$), but did not differ between the 2 conditions after the new decisions were learned ($t_{15} = 0.190$, $P = 0.852$) (Fig. 4b).

Figure 3. Activations for the Critical Decisions of the well-learned mazes which become overlapping in the scanner. Asterisks denote statistically significant differences between OL and NOL conditions. (a) Activity in the left hippocampal tail does not discriminate between the familiar OLOld and NOLOld decisions in Early trials of the task, but increases across trials in the overlapping condition to become more active than the non-overlapping condition ($P < 0.005$). (b) Activity in the bilateral medial caudate does not discriminate between the familiar OLOld and NOLOld decisions in Early trials of the task, but increases in the overlapping condition and decreases in the non-overlapping condition across trials to be more active for Late phase overlapping decisions (left = $P < 0.005$, right = $P < 0.004$). (c) Whole-brain analysis image of activity significantly greater for OLOld mazes in Late trials. Activity centered over the a priori medial caudate ROI is denoted with green arrows. Activity in the left hippocampal tail ROI was also significantly greater for OLOld mazes in Late trials at the whole-brain analysis level (not shown). This whole-brain analysis image has a statistical threshold of $P < 0.01$ corrected for multiple comparisons to $P < 0.05$. (d) Behavioral accuracy corresponding to Early and Late task phases. Importantly, knowledge of the OLOld and NOLOld decisions does not change across task phases.
retrieval could benefit participants, helping them to learn how the novel overlapping route relates to the broader environment. In order to determine whether activation differences in our ROIs for Early OLNew and NOLNew trials can be attributed to the magnitude of activity for reactivation of the previously learned association, or whether encoding of the overlapping routes contributes to the magnitude of OLNew activity, we conducted a follow-up analysis directly contrasting Early OLNew and Early OLOld activations in SPM8 within our combined ROI volume (using a voxelwise threshold of $P < 0.01$, cluster extent corrected for multiple comparisons to $P < 0.05$). This test measured whether activations during
New mazes – minimum cluster size of 109 voxels.

Activation clusters survived cluster-threshold correction for multiple comparisons to test this idea, we reversed the group-level contrast of NOLNew activity in the medial caudate (9.42, 36, 50, 4.06) that tracked the learning curves at Early versus Late task phase analysis, supporting the prediction that overlapping maze activity in the medial caudate ROIs more active during early learning of OLNew hippocampal tail ROI had a stronger positive relationship with the overlapping maze learning curves across runs ($t_{12, 6, 10, 10, 6, 12} = 4.42$). This finding suggests that if reactivation of the pre-existing memories for the same locations.

Importantly, the follow-up analysis revealed that not only were our left hippocampal tail and bilateral medial caudate ROIs more active during early learning of NOLNew hippocampal tail ROI at the whole-brain level (Fig. 5b) decreases across runs with performance, rather than decreases. At a reduced threshold of $P < 0.05$, activity in the left hippocampus ($xyz = -20, -36, 12; t = 1.77$) and left medial caudate ($xyz = -16, 6, 18; t = 2.73$) ROIs increased with performance (i.e., showed a negative relationship with the learning curve regressors).

Within-subjects regression of activity and learning curves
To examine whether activations in our hippocampal and medial caudate ROIs relate to learning by decreasing across trials in a manner proportional to improving accuracy, we conducted a parametric analysis in SPM using inverted subject-specific Critical Decision learning curves as regressors for run-by-run Critical Decision activity. A significant positive relationship with the learning curves (Fig. 5b) indicates that activity is higher when learning is greatest, and decreases and levels off as accuracy improves and stabilizes in later trials.

The ROI-based regression analysis (OL > zero contrast) revealed that not only is the left hippocampal tail active during early learning of overlapping maze Critical Decisions, but also the activity decreases in a manner predicted by the inverted learning curves across runs ($xyz = -16, -38, 0; t = 3.62$). Although results of the Early versus Late task phase analysis indicate that overlapping maze activity in the medial caudate decreases more dramatically than hippocampal activity from Early to Late trials, medial caudate activity did not correlate with the overlapping maze learning curves at $P < 0.01$. However, activity in the left caudate ROI had a significant relationship with overlapping maze learning curves at a reduced voxelwise threshold of $P < 0.02$ ($xyz = -10, 6, 12; t = 2.66$).

In contrast, non-overlapping maze activity in our ROIs did not track learning in this manner, even at a liberal voxelwise threshold of $P < 0.05$. Because we observed an increasing trend in NOLNew hippocampal tail activity in the Early versus Late task phase analysis, we reasoned that NOLNew activity might relate to more strongly to retrieval than learning. To test this idea, we reversed the group-level contrast of NOLNew regressions against zero, testing whether activity increases across runs with performance, rather than decreases. At a reduced threshold of $P < 0.05$, activity in the left hippocampus ($xyz = -20, -36, 12; t = 1.77$) and left medial caudate ($xyz = -16, 6, 18; t = 2.73$) ROIs increased with performance (i.e., showed a negative relationship with the learning curve regressors).

Direct comparison of the overlapping and non-overlapping maze regression maps, masked to voxels showing a significant relationship between overlapping maze activity and the learning curves, confirmed that activity in the left hippocampal tail ROI had a stronger positive relationship with the overlapping learning curves than the non-overlapping learning curves ($xyz = -22, -38, 0; t = 4.50$). Voxels in the left medial caudate that tracked the learning curves at $P < 0.02$ also had a stronger positive relationship with overlapping than non-overlapping learning curves at $P < 0.01$ ($xyz = -16, 6, 18; t = 3.57$).

These results complement those of the Early versus Late task phase analysis, supporting the prediction that overlapping maze-specific activity in the hippocampal tail and medial caudate during the Early task phase relates to learning to navigate context-dependent decision points across trials.

**Regression of activity and learning curves, whole-brain analysis.** The finding that activity in the hippocampus tracks overlapping maze learning across runs was also observed at the whole-brain level (Fig. 5a). Activity in the bilateral hippocampal tail, and left hippocampal body and head, decreased across runs in a manner proportional to increasing accuracy at $P < 0.01$ and the relationship with the inverted learning curves was significantly more positive for the overlapping than the non-overlapping condition at $P < 0.01$. Furthermore, activity in a component of the medial caudate rostral to our a priori ROI also had a stronger positive

| Table 3 | Early vs. Late Critical Decisions |
|-----------------|--------|--------|--------|--------|--------|--------|
| Brain region    | Left ($t$-value) | (MNI x,y,z) | Right ($t$-value) | (MNI x,y,z) |
| Old mazes – Early: | | | | |
| Premotor cortex | 4.45 | -28, 52, 2 | - | - |
| Occipitoparietal sulcus | - | - | 4.12 | 18, -56, 26 |
| Intraparietal sulcus | 3.96 | -32, -42, 46 | - | - |
| Old mazes – Late: | | | | |
| Hippocampal tail | 2.9 | -18, -34, 4 | - | - |
| Medial caudate | 4.04 | -12, 21, 4 | 3.68 | 14, 21, 16 |
| Dorsolateral prefrontal cortex | 5.66 | -20, 24, 34 | 5.6 | 48, 32, 24 |
| Anterior Middle frontal gyrus | - | - | 3.88 | 32, 54, 14 |
| Inferior frontal sulcus | - | - | 5.63 | 46, 32, 10 |
| Premotor cortex | 5.97 | -38, -25, 8 | - | - |
| Supplementary motor cortex | 5.03 | -6, 14, 44 | - | - |
| Angular gyrus | 6.94 | -26, -72, 46 | - | - |
| Intraparietal sulcus | 5.2 | -34, -54, 40 | 6.92 | 34, -46, 38 |
| Precuneus | 5.99 | -2, -70, 42 | 4.53 | 14, 56, 32 |
| Calcarine sulcus | - | - | 7.38 | 14, -80, 10 |
| Cerebellum | 4.64 | -36, -60, -38 | 4.06 | 28, 58, -30 |
| New mazes – Early: | | | | |
| Hippocampal tail | 3.48 | -18, -36, 0 | 5.43 | 28, 38, 0 |
| Hippocampus body | 4.77 | -22, -30, 14 | 3.65 | 28, -26, -16 |
| Parahippocampal cortex | 3.75 | -30, -34, -14 | 3.68 | 18, -34, -12 |
| Medial caudate | 6.1 | -10, 10, 12 | 5.47 | 16, 21, 10 |
| Ventromedial / Substantia Nigra | - | - | 6.49 | 6, -10, -10 |
| Retrosplenial cortex | 5.29 | -10, -44, 2 | 4.29 | 10, -42, 4 |
| Dorsolateral prefrontal cortex | 9.42 | -36, 20, 50 | - | - |
| Ventromedial prefrontal cortex | - | - | 3.46 | 12, 50, -12 |
| Anterior Middle frontal gyrus | - | - | 4.06 | 34, 60, 18 |
| Inferior frontal gyrus | 5.74 | -38, 48, -2 | - | - |
| Supplementary motor cortex | 5.83 | -2, -60 | - | - |
| Anterior insula | 5.47 | -32, 20, 6 | 6.21 | 28, 20, 10 |
| Angular gyrus | 12.48 | -34, -76, 32 | 7.49 | 36, -68, 84 |
| Posterior cingulate | 4.89 | -8, -24, 30 | - | - |
| Precuneus | 9.76 | -6, -62, 22 | 7.47 | 10, -62, 30 |
| Middle temporal gyrus | 14 | -62, -40, -10 | - | - |
| Lateral occipital gyrus | 5.37 | -16, -96, 14 | - | - |
| Calcarine sulcus | - | - | 4.74 | 14, 94, 2 |
| Cerebellum | 4.92 | -34, -46, -36 | 5.25 | 18, -78, -26 |

*The coordinates reflect cluster-center voxels. $t$-values reflect a statistical threshold of $P < 0.01$. Activation clusters survived cluster-threshold correction for multiple comparisons to $P < 0.05$ with a minimum cluster size of 109 voxels.
relationship with overlapping than non-overlapping maze learning curves. It is noteworthy that activity in the parahippocampal cortex, retrosplenial cortex, and dorsolateral prefrontal cortex, that was greater for OLOld than NOLNew mazes during the Early task phase, also had a stronger positive relationship with overlapping than non-overlapping maze learning curves. A summary of significant differences between OLNNew and NOLNew regressions is provided in Table 4.

Between-subjects activity-accuracy regression analysis
To determine whether good overlapping route navigators are characterized by greater recruitment of our ROIs during early learning, we entered the individual subject beta maps from the Early task phase into a second-level multiple regression analysis in SPM, using Critical Decision performance from this period as a covariate.

Results of this analysis revealed a strong relationship between activity in the medial caudate and each subject’s performance during Early task phase Critical Decisions. At a voxelwise threshold of \( P < 0.01 \), cluster threshold corrected to \( P < 0.05 \), participants who performed better during early learning of OLNNew mazes recruited the medial caudate more strongly for the familiar decisions that have become overlapping (OLOld) (left caudate: \( xyz = -14, 14, 16, t = 5.67 \); right caudate: \( xyz = 14, 4, 12, t = 4.84 \)) (Fig. 6a). A positive relationship between OLNNew performance and OLOld activity was observed in the left hippocampal tail at a reduced voxelwise threshold of \( P < 0.02 \) (\( xyz = -14, 4, 16, t = 3.38 \)).

Similarly, participants who performed better during early learning of OLNNew mazes recruited the medial caudate more for those decisions (right caudate: \( xyz = 18, 6, 14, t = 3.35 \)) (Fig. 6b). A positive relationship between OLNNew Performance and OLNNew activity was also observed in the left medial caudate at a reduced voxelwise threshold of \( P < 0.02 \) (\( xyz = -14, 8, 12, t = 2.76 \)).

No positive relationship was observed between how well participants performed on the non-overlapping mazes and how strongly they recruited our ROIs, even with voxelwise thresholds reduced to \( P < 0.05 \). Instead, we actually observed the opposite relationship between performance and activity in our ROIs: participants who performed better on NOLNew mazes actually recruited the right medial caudate less for NOLOld mazes (\( xyz = 16, 2, 14, t = 4.43 \)). This relationship was also observed in the right hippocampal tail ROI (\( xyz = 20, -32, -4, t = 3.04 \)). Although the NOLOld and NOLNew decisions were not directly related to one another, these results indicate that participants who perform better during early learning of non-overlapping decisions also recruit these structures less during retrieval of distinct familiar associations.

These results support the prediction that how well people navigate context-dependent overlapping mazes relates to how strongly they recruit the medial caudate, and to a lesser extent, the hippocampal tail. They also indicate that people who are efficient non-overlapping maze learners recruit these areas less at retrieval, suggesting that overreliance on these areas may be maladaptive for unambiguous decisions.

**Discussion**
The results of the present experiment demonstrate that within the MTL system, the parahippocampal cortex plays a specific role in representing novel spatial contextual information used to guide flexible navigation, while the hippocampal tail is recruited for learning novel overlapping routes as well as retrieving familiar navigational decisions following the introduction of interfering memories. The medial caudate showed a similar sensitivity to the overlapping maze task demands, being strongly active for learning novel overlapping routes, and updating participation in navigation of familiar routes when they become overlapping. The hippocampus may be particularly important for flexible decision-making through its ability to disambiguate overlapping representations, while the striatum may support the “disambiguation of actions”, helping to flexibly represent alternative behavioral output in different circumstances.

**Parahippocampal Cortex Processes Novel Overlapping Maze Contextual Cues**
The results support a particularly important role for the parahippocampal cortex in representing contextually significant spatial information, consistent with models of MTL function (Davachi 2006; Eichenbaum et al. 2007; Eichenbaum et al. 2011). We show that the parahippocampal cortex is the only brain region more strongly active across trials for newly learned cues used to guide context-dependent decisions than cues for unambiguous events. Our data demonstrate that parahippocampal activity reflects the associations of overlapping maze cues during learning (OLNew), but parahippocampal responses for familiar scenes that were learned prior to being associated with context-dependent decisions (OLOld cues) do not differ on average from responses for non-overlapping maze cues. This finding suggests that the navigational importance of overlapping maze cues is only reflected by parahippocampal cortex activity if they are associated with context-dependent decisions at the time of encoding.

Previous research has implicated the parahippocampal cortex in source memory and the representation of context (Bar and Aminoff 2003; Davachi et al. 2003; Ranganath et al. 2003; Ekstrom and Bookheimer 2007; Ross and Slotnick 2003; Ekstrom and Bookheimer 2007; Brown et al. 2011).
2008; Jenkins and Ranganath 2010), while other studies highlight its role in processing scenes, landmarks, and spatial information (Epstein and Kanwisher 1998; O’Craven and Kanwisher 2000; Burgess et al. 2001; Hartley et al. 2003; Rosenbaum et al. 2004; Epstein et al. 2007; Howard et al. 2011; Mullally and Maguire 2011). Given the spatial nature of the present experiment, the cue locations could serve as a spatial context for the overlapping mazes both through the association between cue and critical choice landmarks as well as the unique spatial relationship between the locations. By perceptually isolating the Cue period of the task and directly comparing the OL and NOL conditions, our experiment allowed us to examine how parahippocampal cortex processes spatial information that serves as a cue for context-dependent decisions.

The parahippocampal cortex has been shown to be active for encoding landmarks at navigational choice points (Janzen and van Turennout 2004). However, in the present experiment the cue landmarks were equally important for the initial navigational choices of both the OL and NOL conditions. Furthermore, cue periods were perceptually comparable between the conditions because all mazes began at non-overlapping locations with participants’ views restricted to the starting landmarks. The key difference between the conditions was that in the NOL condition the cue landmarks were only necessary for the initial navigational decision, while in the OL condition the cues were also necessary to distinguish between episodes during the Critical Decisions. Therefore, the design targeted brain responses influenced by the associations of the present cue, rather than visuospatial features of the scene itself. Recent data show that the parahippocampal cortex responds to scenes differently depending on their temporal associations (Turk-Brown et al. 2012).

Similarly, our results demonstrate that parahippocampal cortex is not only important for processing navigational relevant landmarks, but parahippocampal activity is greatest when processing contextual cues with associations important for flexible navigational decisions during encoding.

Hippocampus Supports Retrieval of Routes that Become Overlapping

Models of MTL function predict the hippocampus is critical for retrieval of specific representations that overlap with other memories (Hasselmo and Eichenbaum 2005; Zilli and Hasselmo 2008). Our results support this prediction by demonstrating that the human hippocampus becomes more active for retrieval of familiar routes with the introduction of alternative overlapping associations. The hippocampus is thought to code representations that share common elements with contextual information, facilitating subsequent retrieval of distinct episodes (Wood et al. 2000; Agster et al. 2002; Ferbinteanu and Shapiro 2003; Lee et al. 2006; Smith and Mizumori 2006; Brown et al. 2010; Ginther et al. 2011; MacDonald et al. 2011).

In the real world, overlapping memories are typically learned in a progressive manner, with one experience following another. A key feature of our experimental design was the ability to examine whether navigational memories that were learned as non-overlapping representations are updated with experience to reflect the fact that they have become overlapping. OLOld mazes were already learned as distinct routes from training day and underwent a 24-h consolidation period, but learning still occurs in these mazes during scanning insofar as participants acquire knowledge of alternative associations for the overlapping decision points. Our data reveal that hippocampal tail activity began at a similar level...
for OL\textsubscript{Old} and NOLOld Critical Decisions in early trials, consistent with both sets of mazes having been learned as distinct routes the previous day. Parameter estimates in the hippocampal tail for non-overlapping maze retrieval remained near zero across runs. However, activity increased for OL\textsubscript{Old} Critical Decisions after participants mastered the OL\textsubscript{New} mazes, introducing a need to disambiguate 2 associations for the same spatial location, while remaining minimal for non-overlapping routes. These findings indicate that not only is the hippocampus active for retrieval of concurrently learned overlapping memories (Brown et al. 2010), but the hippocampal recruitment for well-learned non-overlapping navigational memories increases as overlapping associations and a need for context-guided retrieval is introduced. That the hippocampal activity is only observed for the first of 2 context-dependent decision points in the overlapping mazes supports the idea that the activity relates specifically to the initial disambiguation of the current route from its alternative and the context-dependent retrieval associated with that process.

**Medial Caudate Supports Context-Dependent Navigation**

Learning the OL\textsubscript{New} mazes introduced alternative behaviors to OL\textsubscript{Old} decision points. While the basal ganglia have traditionally been associated with incremental habit learning, research suggests that the medial component of the caudate plays an important role in flexible and goal-directed behavior (Devan and White 1999; Ragozzino et al. 2002; Yin and Knowlton 2004; Yin and Knowlton 2006; DeCoteau et al. 2007; Thorn et al. 2010; Brown et al. 2012). Our results provide a novel demonstration that the medial caudate becomes more strongly recruited for selection of familiar behaviors as they become context-dependent, in contrast to a decreasing pattern of activity for distinct non-overlapping behaviors following continued practice. Responses in the medial caudate for Old mazes followed a similar trend to that of the hippocampus, with activity beginning at similar levels for the OL\textsubscript{Old} and NOLOld mazes in Early trials, but diverging in Late trials after the OL\textsubscript{New} behaviors had been learned. Even during early trials, however, we show that participants who knew the OL\textsubscript{New} mazes better recruited the medial caudate more for the OL\textsubscript{Old} mazes, while participants who performed worse on the OL\textsubscript{New} mazes recruited the medial caudate less. While OL\textsubscript{Old} activity in the medial caudate increased across runs with learning of the alternative OL\textsubscript{New} decisions, the corresponding decrease in medial caudate activity for NOLOld decisions across runs indicates that the dependence of non-overlapping decisions on medial caudate function decreases with continued practice. Our data demonstrate that recruitment of the medial caudate for familiar navigational decisions is sensitive to the introduction of competing behavioral alternatives, and strongly support a greater role for this striatal subcomponent in context-dependent behavior.

Our data from the OverlappingOld mazes speak more broadly to the question of how we are able to maintain behavioral flexibility through the continued acquisition of new experiences. We find that recruitment of the hippocampus and medial caudate for distinct familiar representations is limited. However, well-learned memories are susceptible to the introduction of novel interfering associations, and successful retrieval of such familiar associations and actions can recruit the hippocampus and medial caudate more when additional experiences introduce a need to distinguish between episodes. It is possible that the association of familiar locations with novel overlapping routes involves reconsolidation (Hupbach et al. 2007, 2008; Tronson and Taylor 2007; Sederberg et al. 2011) of previously encoded environmental features that are present in the novel context.

**Hippocampus and Medial Caudate Support Learning of Context-Dependent Behavior**

A fundamental prediction about hippocampal function in episodic memory is that the hippocampus is critical for encoding overlapping memories in a manner that facilitates subsequent retrieval of specific episodes. Our data support this prediction, demonstrating that the same region of the hippocampal tail active for overlapping maze retrieval is recruited during early learning of overlapping spatial representations, and is significantly more active for this process than learning distinct non-overlapping associations (despite there being more novel information in the non-overlapping routes). This activity is also greater during learning than for successful retrieval of the previously learned alternative associations (OL\textsubscript{Old}) in the Early task phase, and decreases across trials in a manner proportional to increasing performance. Activity in the hippocampus has been previously shown to correlate more strongly with the learning rate of non-spatial overlapping than non-overlapping sequences (Kumaran and Maguire 2006). Our data provide clear evidence that activity in the human hippocampus is greater during, and relates more directly to, learning to navigate context-dependent overlapping spatial representations than during learning of non-overlapping spatial associations.

We show that activity in the hippocampal tail decreases from run to run in relation to learning but still remains active for the newly learned overlapping mazes in the Late trials of the task. What is surprising, however, is that hippocampal recruitment for the novel non-overlapping mazes actually increases across trials. This is in apparent contrast to the data from the well-learned Old mazes in this study as well as data presented in Brown et al. (2010). However, it is consistent with the results of Ross et al. (2009), where we observed similar recruitment of the hippocampus for retrieval of overlapping and non-overlapping sequences within the same session that learning occurred. The present data suggest an interesting dynamic in hippocampal sequence retrieval: across the time-frame of the scanning task, hippocampal activity for non-overlapping mazes increases as participants acquire many different stimulus associations with the same 3 types of behavior (turning left, right, or going straight). In contrast, when non-overlapping mazes have been learned prior to scanning and undergone a consolidation period, reliance on the hippocampal tail is minimal for these unique representations (NOLOld), while remaining elevated for overlapping maze retrieval.

Analysis of the medial caudate in the OL\textsubscript{New} condition further supports a central role for this region in behavioral flexibility, with the medial caudate being more strongly recruited for learning novel overlapping than non-overlapping routes. This result is striking because learning NOLOld mazes required associating a novel behavior with a novel stimulus, while learning OL\textsubscript{New} mazes required associating an alternative behavior with a familiar stimulus, suggesting recruitment.

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1920 Learning and retrieving overlapping spatial routes · Brown et al.
of the medial caudate is driven by flexible learning demands more than the amount of novel information. Activity in the medial caudate was greatest during early learning of the OLNew mazes and decreased across trials in a manner proportional to increasing performance. This pattern of medial caudate activity resembles its role in reversal learning (Ragozzino et al. 2002), coming online early for the rapid acquisition of a novel behavioral rule (Pasupathy and Miller 2005). The findings from our between-subjects analysis also demonstrate that people who perform better during early learning of the OLNew mazes recruited the medial caudate more during this period. Interestingly, this pattern of activity differs from the increasing role of the caudate in the OLOld mazes as their decisions become context-dependent. However, the decreasing OLNew activations converge with the increasing OLOld activations in the Late period. Therefore, our data suggest recruitment of the medial caudate for learning context-dependent behaviors is greater than recruitment for flexible selection of context-dependent behaviors. Medial caudate activity for context-dependent behavior is greater, in turn, than recruitment for well-learned routes that do not require selection between alternative actions (NOLOld).

Conclusions

Our experimental data support models predicting a critical role for the MTL in both storing and retrieving overlapping memories. Specifically, our data indicate that the human para-hippocampal cortex processes contextually significant spatial information during learning. We demonstrate that well-learned navigational decisions recruit the hippocampus more strongly after learning competing overlapping associations introduces a need for context-dependent retrieval, and this effect is specific to the initial disambiguation point of the routes. Importantly, our data also provide novel evidence that learning overlapping routes activates the hippocampus more strongly than new non-overlapping spatial representations. Finally, our results emphasize a central role for the medial caudate in navigating overlapping routes, demonstrating particularly strong recruitment of the medial caudate during both learning and executing context-dependent behaviors.

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Notes

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