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Theta oscillations support active exploration in human spatial navigation

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ABSTRACT

Active navigation seems to yield better spatial knowledge than passive navigation, but it is unclear how active decision-making influences learning and memory. Here, we examined the contributions of theta oscillations to memory-related exploration while testing theories about how they contribute to active learning. Using electroencephalography (EEG), we tested individuals on a maze-learning task in which they made discrete decisions about where to explore at each choice point in the maze. Half the participants were free to make active decisions at each choice point, and the other half passively explored by selecting a marked choice (matched to active exploration) at each intersection. Critically, all decisions were made when stationary, decoupling the active decision-making process from movement and speed factors, which is another prominent potential role for theta oscillations. Participants were then tested on their knowledge of the maze by traveling from object A to object B within the maze. Results show an advantage for active decision-making during learning and indicate that the active group had greater theta power during choice points in exploration, particularly in midfrontal channels. These findings demonstrate that active exploration is associated with theta oscillations during human spatial navigation, and that these oscillations are not exclusively related to movement or speed. Results demonstrating increased theta oscillations in prefrontal regions suggest communication with the hippocampus and integration of new information into memory. We also found evidence for alpha oscillations during active navigation, suggesting a role for attention as well. This study finds support for a general mnemonic role for theta oscillations during navigational learning.

1. Introduction

When learning the layout of a new city, intuition suggests that active exploration may lead to greater spatial knowledge than passive travel. This idea has been demonstrated empirically (Chrastil and Warren, 2015); however, the neural correlates underlying this advantage are unclear. Here, we used EEG to test: 1) the neural correlates of active exploration, and 2) the more general role of theta oscillations in navigation.

1.1. *Mechanisms of Active Exploration*

From the cognitive perspective, one possible hypothesis is that active decisions about movement direction and predictions about choice outcomes facilitate learning via reinforcement learning mechanisms. As participants explore their environment, they make predictions about where they are, what objects they will encounter next, and how the paths connect. Decision points may be associated with multiple environmental contexts. For example, turning right at a decision point leads home, while going straight leads to the grocery store. Navigators must disambiguate the contexts to keep track of their goals. Their prediction is reinforced with feedback after they explore a path (‘actually, the bank—not the church—was to the left’). Thus, prediction testing in the environment—and receiving feedback during exploration—is hypothesized to facilitate memory during learning.

From the neuroscience perspective, we theorize that the hippocampus and medial prefrontal cortex (mPFC) work in concert during active navigation and decision-making. The hippocampus binds object information to the context (Davachi, 2006; Eichenbaum et al., 2007; Preston and Eichenbaum, 2013; Ranganath, 2010; Ritchey et al., 2015), while it has been suggested that the mPFC monitors environmental contextual information. This process is supported by decision-making and reinforcement learning mechanisms involving the mPFC, anterior cingulate, and striatum (Hasselmo, 2005; Hyman et al., 2005). Theta oscillations coordinate communication among these regions by synchronizing

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the firing of cell assemblies during active exploration (e.g. Hyman et al., 2005; Zhang et al., 2018). Thus, active decision-making strengthens this *prefrontal-hippocampal-striatal* pathway. Based on this model, theta oscillations within the prefrontal-hippocampal-striatal circuit are critical to new learning. Recent evidence suggests that hippocampal theta oscillations are related to volitional learning (Estefan et al., 2021), providing support for this model. Midfrontal theta oscillations have been linked to reinforcement learning (Cavanagh et al., 2010; Frank et al., 2015), cognitive control mechanisms (Cavanagh and Frank, 2014), and response to uncertainty (Cavanagh and Shackman, 2015) indicating that these oscillations may represent a signature of learning and decision-making. In contrast, an alternative hypothesis is that increased attention underlies the advantage for active decision-making; broadly increased arousal from active decision-making could facilitate improved learning. Increased attention would be expected to have oscillation signatures in the alpha band and would likely be localized to parietal areas (Benedek et al., 2014; Klimesch, 1999; Klimesch et al., 1998; Sauseng et al., 2005). Thus, we can contrast the reinforcement learning and attention hypotheses by testing both the frequency band and location of significant oscillations during learning.

1.2. Contributions of Theta Oscillations to Learning and Memory

The theta rhythm, which oscillates at 4-8 Hz in humans, is a key indicator of brain dynamics during learning and memory (Buzsáki and Moser, 2013; Hasselmo and Stern, 2014; Klimesch, 1999; Nyhus and Curran, 2010). Communication within the prefrontal-hippocampal-striatal circuit is hypothesized to be driven by theta oscillations, but the general role of theta oscillations during navigation is still unknown. Two theories about the role of theta oscillations in navigation have emerged (Ekstrom and Watrous, 2014; Vass et al., 2016). One hypothesis posits a role for theta oscillations in sensorimotor integration, as evidenced by theta oscillations' relationship to running speed and motor movements. Volitional control of movement and planning is associated with increased hippocampal theta rhythm activity in both spatial and non-spatial tasks (Caplan et al., 2003; de Araújo et al., 2002; Ekstrom et al., 2005; Jutras et al., 2013; Kaplan et al., 2012). Theta oscillations are modulated by movement speed in humans and animals (Aghajan et al., 2017; Bohbot et al., 2017; Goyal et al., 2020; Hasselmo and Stern, 2014; Korotkova et al., 2018; McFarland et al., 1975; Monaghan et al., 2017; Sheremet et al., 2016; Snider et al., 2013; Watrous et al., 2011; Wells et al., 2013), acceleration in rodents (Kropff et al., 2021), codes for distance traveled (Kahana et al., 1999; Vass et al., 2016), and increases for longer compared to shorter routes (Kahana et al., 1999). These findings suggest that theta oscillations have a role in self-motion tracking.

The second hypothesis proposes a direct mnemonic role for theta oscillations in coordinating the dynamics of encoding and retrieval (Hasselmo et al., 2002). For example, hippocampal theta oscillations are correlated with accuracy in locating a target relative to boundaries (Cornwell et al., 2008; Kaplan et al., 2012). A recent study (Aghajan et al., 2019) found a relationship between medial temporal lobe theta oscillations and subsequent navigational memory, although they found no increase in theta oscillations when discovering target locations during active exploration compared to being directed to the goal locations. In non-spatial episodic memory, increases in theta and gamma oscillations during encoding predict subsequent recall (Addante et al., 2011; Osipova et al., 2006; Sederberg et al., 2003). Additional work has demonstrated that interventions to increase theta oscillations improve memory, indicating a causal link between theta and memory (Hanslmayr, et al., 2019; Roberts et al., 2018). In monkeys, active eye movements produce a reset of theta oscillations that predicts performance, suggesting that active exploration is important for non-spatial memory encoding (Jutras et al., 2013). In rodents, coherence between mPFC and hippocampal theta oscillatory peaks when learning new rules about reward contingencies, indicating a role for theta oscillations in reinforcement and reward learning (Amarante et al., 2017; Benchenane et al., 2010; Hasselmo et al., 2002; Hyman et al., 2005).

Across the prefrontal-hippocampal-striatal circuit, theta oscillations are theorized to facilitate hippocampal inputs to mPFC during learning (Backus et al., 2016; Colgin, 2016, 2011). For example, coupling of theta oscillations in mPFC and the hippocampus predicts memory integration and associative learning (Backus et al., 2016). Phase coupling between theta oscillations in the hippocampus and mPFC has been observed during spatial recall using MEG (Kaplan et al., 2014), demonstrating the importance of communication between these regions for learning and memory. In a connectivity-based EEG/fMRI study, theta oscillations appear to provide a mechanism binding nodes of the prefrontal-hippocampal-striatal circuit during successful recall (Herweg et al., 2016). Together, these findings demonstrate compelling evidence linking theta oscillations and mnemonic processes across the prefrontal-hippocampal-striatal circuit during learning.

The current study used scalp EEG to test whether theta oscillations in human navigation are related to active exploration. Previous studies have not decoupled movement from exploration, since a continuous exploration session typically involves both movement and active exploration at the same time. Accordingly, in this study, the Free group made unrestricted decisions about where they wanted to move at each intersection during exploration, whereas the Guided group followed paths yoked to the routes travelled by the Free group. Critically, each movement choice was marked by a discrete button press, allowing for precise timing of the decision. Movement speed was equivalent across both groups, and the movement decision was made when stationary, so oscillation differences can only be attributed to active exploration.

2. Methods

2.1. Subjects

Seventy-three people participated in the experiment and were randomly assigned to the Free exploration or Guided exploration groups. Data from 13 subjects were discarded because of motion sickness (n = 1), failure to find all of the objects during exploration (n = 3), failure to complete all experimental trials (n = 2), excessive number of bad channels (n = 2), and experimenter error (n = 5). Of the 60 subjects analyzed, there were 16 male and 14 female subjects ranging from 18-21 years old in the Free exploration group and 15 male and 15 female subjects ranging from 18-22 years old in the Guided exploration group. All subjects were right-handed and fluent English speakers. All participants signed to give informed consent under the approval of the Bowdoin College IRB and all received course credit for their participation.

2.2. Environment

The desktop virtual maze environment (Fig. 1) was adapted from tasks in the literature (Chrastil and Warren, 2015, 2014, 2013) and was designed to produce a wide range of performance. The environment consisted of several main hallways with branch alcoves containing nine target objects. Paintings on the walls of hallways served as landmarks to aid in orientation. Participants pressed arrow keys to move around the environment, with translational movement fixed at 1.0 m/s (virtual meters/second) and rotation speed fixed at 90° per second. Movement was gated such that the button press at each choice point caused visual movement to the next choice point. This was achieved by recording videos of the movement between locations. The correct video would play based on the person's location, facing direction, and the choice they made (left turn, right turn, or straight). A static image of each choice point was created by taking the first image of each video and adding the arrows of the potential choices in Photoshop (Adobe). The maze was created in Blender and rendered in Unity. We recorded videos from Unity and presented the experiment using E-Prime (Psychology Software Tools Inc., Sharpsburg, PA) software. The task was presented on a Dell Optiplex

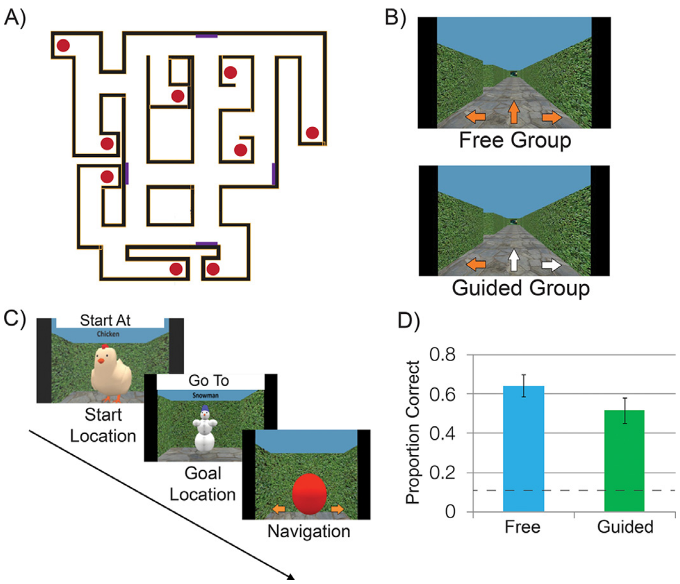

Fig. 1. Experimental task and design. A) Overhead view of the maze, which participants never saw. Red dots indicate the locations of objects. Purple rectangles indicate the location of paintings in the hallways. The maze was the same for all participants. B) During the exploration phase, the Free group was allowed to choose from any of the options at each intersection, making a button press to indicate their choice. The Guided group saw all the options but had to choose the marked (filled) arrow. Each person in the Guided group was yoked to a member the Free group, such that both groups had equal experiences with the environment (n = 30 per group). C) The test phase was the same for both groups. Participants were started at one object, then instructed to navigate to a second object. Once they began navigating, all the objects appeared as red spheres to minimize feedback. D) Behavioral results indicated that the Free group performed marginally better than the Guided group (p = .07, 1-tailed test, Cohen's d = .38). A Wilcoxon signed rank test found significant differences between the groups (Z = -4.29, p < .01). Dashed line indicates chance performance.

7010 PC featuring quad-core 3.40GHz Intel® Core™ i7 processors, 8GB RAM, AMD RADEON™ HD 7570 graphics card, and a 22-inch monitor.

2.3. Task

We designed the Maze Learning Task to assess the ability to learn the graph structure of an environment—the paths and connections between locations (Chrastil and Warren, 2014). A video example of a test trial is available online at https://www.youtube.com/watch?v = LMs-Gpo2Ss7M

Exploration. Participants navigated the virtual environment for 16 minutes, using a button box (a response box with buttons that provides precise reaction time information) (SRBox Serial Model 200a, Psychology Software Tools Inc., Sharpsburg, PA) to make right or left turns or straight movement. All participants were instructed to find all of the objects and learn their locations. During exploration, the Free group was free to make decisions at each intersection. The Guided group followed a path, yoked to the Free group, during exploration. The Guided group saw all available options at each intersection but were required to select the orange arrow (Fig. 1b), which were linked to the choices made by participants in the Free group. Following the yoked path included matching any “looking around”, or turns in place, such that the visual information was exactly the same in the two groups. Participants in the Guided group could not deviate from the path – even if they pressed the incorrect button, the video followed the path of the Free participant. Thus, participants in both groups experienced the same motor movements and visual information. The only difference in the groups was whether they actively chose where to explore.

Test. The test phase was exactly the same for both groups. Acquired spatial knowledge was tested on each trial by starting participants at one object in the maze, and then directing them to travel, via the shortest route, to another object using the hallways of the maze. Participants then used the button box to move through the maze, pressing a button when they thought they reached the target object. Feedback was minimized by changing all of the objects in the maze (including the start and target objects) into red spheres during test (Fig. 1c), although the landmark paintings in the hallway remained. This task tests graph knowledge (Chrastil and Warren, 2014) because it requires knowing the connections of the hallways to reach the target without necessarily knowing the metric distances and angles between locations.

With nine objects in the maze, a full permutation of all start and target pairs yielded 72 possible trials. However, due to time constraints, we tested a subset of 48 trials for each participant. We created three lists of trials, each with 2/3 of the possible trials. Each participant followed one of the lists, and trial lists were matched across the yoked pairs of Free and Guided participants. The trial list was presented in random order for each participant.

2.4. Questionnaires

Following each experimental session, subjects were asked to complete the Santa Barbara Sense of Direction Scale (SBSOD) (Hegarty et al., 2002) and a questionnaire including report of current and past video game use. We note that video game experience has been shown to be a factor in virtual navigation (Richardson et al., 2011).

2.5. Procedure

Participants were greeted in the lab and were given information about the study. They signed forms indicating their informed consent. They were then given instructions about the exploration phase of the task, which differed somewhat for the Free and Guided groups. All participants were instructed to find all the objects and learn their locations. The Free group was informed that they could go wherever they wanted to, while the Guided group was informed that the path they went on would take them around the maze. Participants were shown the controls and given practice with them. Participants were then seated in the EEG testing room and the electrodes and cap were placed on their scalp. The 16-minute exploration phase then began. After the exploration phase, the instructions for the test phase were provided on the computer screen. Participants then completed 48 trials of the test phase, with built-in breaks every 12 trials. After the test phase was complete, the EEG cap was removed and participants could wash their hair. Finally, participants completed the spatial abilities questionnaires.

2.6. EEG Recording & Preprocessing

During the exploration and testing phase of the experiment, scalp voltages were collected with a 64-scalp channel plus two EOG channel actiCHamp system (Brain Products, Munich, Germany). Amplified analog voltages (0.1-100 Hz bandpass) were digitized at 500 Hz. Individual sensors were adjusted until impedances were less than 25kΩ.

EEG was further preprocessed using EEGLab (Delorme and Makeig, 2004). The EEG was downsampled to 250 Hz and digitally high-pass filtered at 1 Hz and low-pass filtered at 100 Hz. Individual bad channels were replaced on a trial-by-trial basis with a spherical spline algorithm (Srinivasan et al., 1996). EEG was measured with respect to a vertex reference (Cz), but an average-reference transformation was used to minimize the effects of reference-site activity and accurately estimate the scalp topography of the measured electrical fields (Dien, 1998). EEG was segmented from 1000 ms before the stimulus onset to 2000 ms after the stimulus onset (e.g. the choice point and the decision response onset) in each condition. Trials were discarded from analysis if there were voltage fluctuations of over 1,000 μV or data was deemed to be mathematically improbable, with this probability threshold set at five standard deviations. Infomax-based independent component analysis (ICA) (Bell and Sejnowski, 1995) was run. Semi-Automated Selection of Independent Components of the electroencephalogram for Artifact correction (SASICA) (Chaumon et al., 2015), along with manual inspection, was used to identify and remove noise components (eye-blink and eye-movement artifact). Data were converted to the time frequency domain in roughly 9 ms steps across 63 log-spaced frequencies from 3 Hz to 125 Hz using a Morlet wavelet transformation from 440 ms before the stimulus onset to 1436 ms after the stimulus onset for each trial. The beginning and ending boundaries of the -1000 to 2000 ms epochs were cut to account for boundary artifacts introduced by wavelet transformation. The length of the wavelets increased from 3 cycles at 3 Hz to 62.5 cycles at 125 Hz.

2.7. *Data Analysis*

Behavioral data. The primary outcome measure for this task was the proportion of trials in which the participant reached the correct object. Correct trials included trials in which the person pressed the button to select the correct location and the much rarer situation in which the person reached the correct object but time ran out before they could press the button to select it.

Behavioral performance in each group was first compared with chance level performance using one-sample t-tests. Because there were 9 objects in the maze, chance was set as 1/9 (.11). The proportion of correct test trails was compared between Free and Guided groups with a 2 × 2 Group (Free, Guided) x Sex (male, female) between-subjects analysis of variance (ANOVA). Follow-up tests were conducted using Wilcoxon signed rank tests to examine whether the differences in performance between the experimental groups was consistent across all levels of ability (Chrastil & Warren, 2015). Questionnaires were also analyzed using the 2 × 2 ANOVA design to test for group differences in spatial abilities that could account for the differences in performance between the groups. Although sex differences were not a primary focus of this study, given that sex differences in navigational ability are a common question (e.g. Nazareth et al., 2019; Yu et al., 2021), we included sex as a variable in our behavioral analyses. We also wanted to determine whether sex interacted with the experimental conditions.

EEG analysis. EEG analysis was conducted using the EEGLab toolbox for Matlab. Analysis was separated into the exploration phase and the test phase. Average spectral power changes relative to baseline in frontal and parietal channels were compared across conditions.

Exploration phase. Exploration consisted primarily of participants moving around the maze. This movement alternated between stationary standing at the choice points (intersections with arrows showing the possibilities) and movement to the next choice point. Note that movement to the next choice point could also include a turn in place to face a new direction. On average, participants made 300.53 (±25.95 SD) of these decisions during the exploration phase. We were primarily interested in the EEG recordings surrounding the choice point.

For exploration, we analyzed the arrival at the choice point and the decision made at the choice point. Previous research has shown that “pre-stimulus” theta is associated with increased encoding (Addante et al., 2011; Gruber et al., 2013; Hseih & Ranganath, 2014), therefore we included both the choice itself and the approach to the choice point. Including both time windows also allows us to capture more possible times during which the Free group could be making decisions. For these two analysis timepoints, we designated time 0 as the time they arrived at the choice point and as the moment they pressed the button to make their choice of where to travel next, respectively. We analyzed 300 ms prior to the arrival at the choice point and prior to the decision at the choice point (-300-0 ms) to determine whether there were differences between the Free and Guided groups as the decision became imminent. The 300 ms time window prior to arrival at the choice point matches that of our analysis at the choice point (see below) and guarantees that the time window only contains movement and does not include any time at the previous choice point. Once participants arrived at the choice point, they stayed for a variable amount of time while deliberating over their next move. Preliminary analysis of the time between arrival at the choice point and the button press indicated that the decision occurred, on average, after 620.57 ms (±158.27SD) with a median of 380.72 ms for the Free group. The Guided group had a mean of 757.94 ms (±215.56SD) with a median of 574.65 ms. The faster response time for the Free group can likely be attributed to these participants planning their next movement prior to the choice point, whereas the Guided group had to wait for visual instruction to guide their next move. We examined the time period 300 ms prior to making the decision (button press). Although there is a possibility that this time window includes some movement prior to arriving at the choice point, the majority (81.77%) of trials fell within this range to only reflect the time when making the decision. For the analysis of 300 ms prior to arrival at the choice point, all trials for both groups have the same amount of movement, so they are completely equated for that timepoint.

Based on previous research describing theta oscillatory effects related to reinforcement learning (Cavanagh et al., 2010), our primary *a priori* analysis for the exploration phase focused on the theta frequency (4-8 Hz) in the -300-0 ms range prior to arrival at the choice point and prior to the decision at the choice point over midfrontal channels. To test the alternative hypothesis that attentional processing makes a significant contribution to active learning, we examined alpha oscillations (8-12 Hz) over parietal channels (Benedek et al., 2014) in the -300-0 ms range prior to arrival at the choice point and prior to the decision at the choice point. We additionally examined EEG effects from -300-0 ms in other frequencies, including beta (12-20 Hz), and gamma (25-50 Hz), and in other channels. Exploratory analyses were corrected for multiple comparisons using false discovery rate (FDR) correction.

Test phase. For the test phase, we first analyzed the processes involved when recalling the location of the target object and when processing the relationship between the start and target objects. We examined the time frame just after the target object was presented, with time 0 being the onset of the presentation of the target object. Based on *a priori* hypotheses, we analyzed theta frequency (4-8 Hz) from 0-500 ms, 500-1000 ms, and 1000-1500 ms once the target was presented over left parietal channels, according to previous research showing event-related potential (ERP) and theta oscillatory effects during memory retrieval in parietal channels (Medrano et al., 2017; Nyhus et al., 2019; Nyhus and Badre, 2015; Ross et al., 2018, 2015). Participants were not moving during this time but were simply viewing the target object picture. We compared trials in which the participant correctly reached the target object vs. trials in which the participant did not reach the target (correct vs. incorrect contrast). The number of trials varied for each participant, but on average 57.78% of the 48 test trials were correct across all groups.

We also examined whether oscillations were related to the spatial properties of the maze itself. For this analysis, we tested both the Euclidean (straight-line) distance and path length (vis-à-vis the number of virtual units of the shortest path) distance between the start and target objects. The maze was designed so that these two values were somewhat—but not perfectly—correlated ($r^2 = .31$), making these two tests relatively independent of each other. We split the trials in half for both types of distance, and then compared short vs. long Euclidean distance and short vs. long path length distance. To make a more focused examination on this question, we only tested the areas where we found effects in the correct vs. incorrect contrast (left parietal channels) and only tested the 0-500 ms time window.

For both test phase analyses, we focused primarily on the theta frequency. We also conducted an exploratory analysis of EEG effects in other frequencies that have been related to memory, including alpha, beta, and gamma, and in other channels. Exploratory analyses were corrected for multiple comparisons using FDR correction.

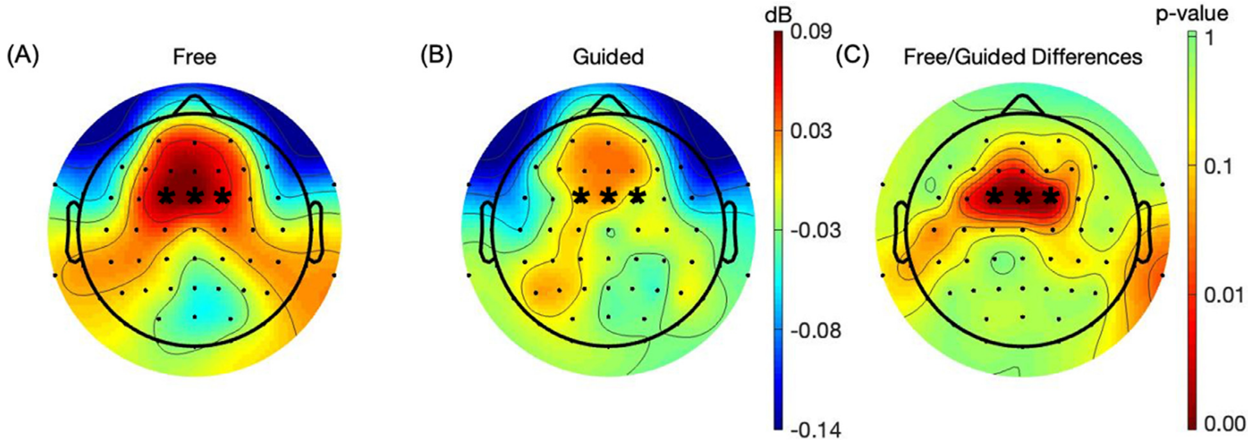

Fig. 2. Theta power for the (A) Free and (B) Guided group just prior to arrival at the choice point during exploration. Theta power across all channels from -300-0 ms. Black * indicates analyzed channels in midfrontal regions. Color scale: decibel change from baseline. (C) Differences between Free and Guided groups. Theta power in midfrontal channels was greater for the Free group than the Guided group ($t(58) = 4.15$, $MSE = .02$, $p < .01$). Color scale: p-value of Free compared to Guided group differences.

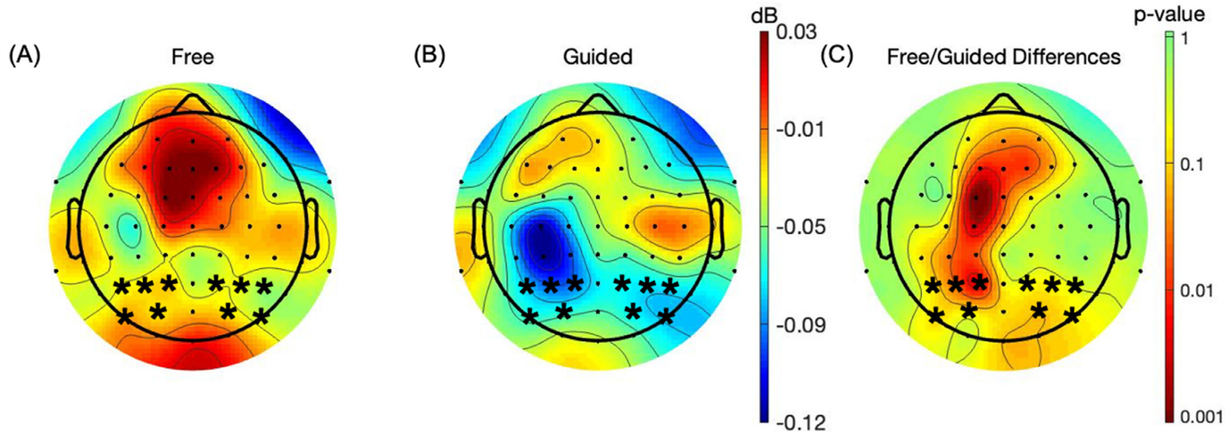

Fig. 3. Alpha power for the (A) Free and (B) Guided group just prior to arrival at the choice point during exploration. Alpha power across all channels from -300-0 ms. Black * indicates analyzed channels in left and right parietal regions. Color scale: decibel change from baseline. (C) Differences between Free and Guided groups. Alpha power in parietal channels was greater for the Free group than the Guided group ($F(1,58)=5.84$, $MSE=.01$, $p=.02$). Color scale: p-value of Free compared to Guided group differences.

3. Results

3.1. Behavior

Navigation. The proportion of correct test trials was analyzed with a one-sample t-test relative to chance performance (.11). Subjects in both the Free ($t(29) = 9.23$, $MSE = .06$, $p < .01$) and the Guided group ($t(29) = 6.41$, $MSE = .06$, $p < .01$) performed significantly above chance, indicating that subjects successfully learned the spatial layout of the maze (Fig. 1d).

The proportion of correct test trials was compared between Free and Guided groups with a Group x Sex between-subjects ANOVA. The Free group performed marginally better than the Guided group ($F(1,56) = 2.16$, $MSE = .09$, $p = .07$, 1-tailed), and males performed better than females ($F(1,56) = 14.00$, $MSE = .09$, $p < .01$), but there was no interaction between group and sex. Cohen's d for the Free vs. Guided contrast was .38. A Wilcoxon signed rank test evaluated the rankings of the proportion correct in the two groups and found that the rankings were significantly different (Z = -4.29, $p < .01$), indicating that the Free group performed better overall than the Guided group. These results suggests that, while there were floor and ceiling effects at the low and high ends of the spectrum, active decision-making increased learning by 10% to 20% (by one or two objects) in the broad midrange of spatial performance.

Questionnaires. To rule out between-subject differences in the Free and Guided groups that could drive discrepancies in performance on the spatial learning task, SBSOD scores and video game use were compared between Free and Guided groups with a Group x Sex between-subjects ANOVA. SBSOD scores were higher for males than females ($F(1,54) = 14.48$, $MSE = 1.25$, $p < .01$), but there was no main effect of group nor interaction between group and sex. Video game use ($F(1,54) = 10.90$, $MSE = .15$, $p < .01$) and current video game use ($F(1,53) = 16.81$, $MSE = .37$, $p < .01$) was higher for males than females, but there was no main effect of group or interaction between group and sex. Therefore, the Free and Guided groups were well-matched on pre-experimental spatial ability and video game experience. Accordingly, these factors cannot account for group differences in performance on the spatial learning task, but sex differences in spatial ability and video game experience could account for sex differences in test trial performance.

3.2. EEG Recordings

3.2.1. Exploration phase

The regions of interest (ROI) were a midfrontal channel group (see Fig. 2 and 4) and left and right parietal channel group (see Fig. 3 and 5);

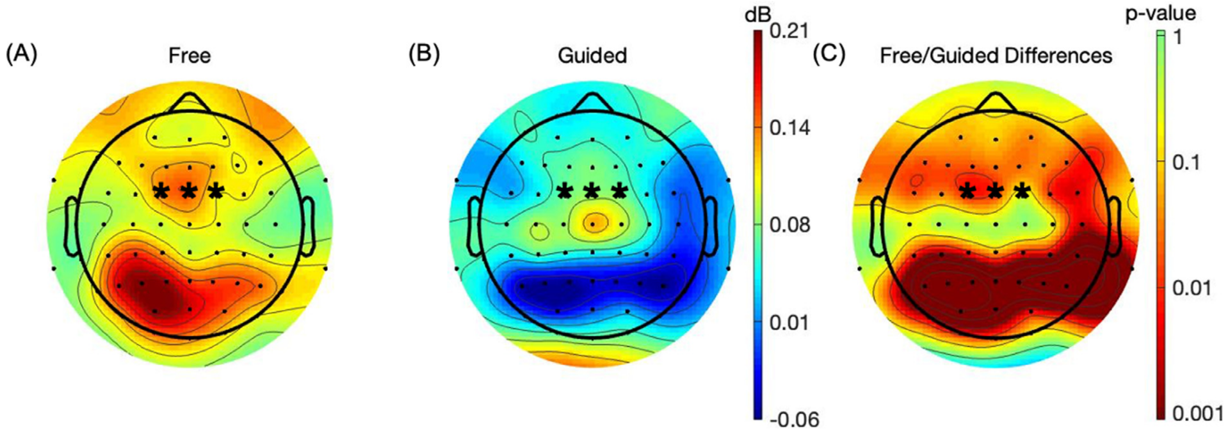

Fig. 4. Theta power for the (A) Free and (B) Guided group just prior to the decision at the choice point during exploration. Theta power across all channels from -300-0 ms. Black * indicates analyzed channels in midfrontal regions. Color scale: decibel change from baseline. (C) Differences between Free and Guided groups. Theta power in midfrontal channels was marginally greater for the Free group than the Guided group ($t(58) = 1.81$, $MSE = .03$, $p = .08$). Exploratory analysis showed increased theta power in the Free group in parietal channels. Color scale: p-value of Free compared to Guided group differences.

mean theta (4-8 Hz) and alpha (8-12 Hz) power from -300-0 ms prior to the choice point was computed by averaging the channels within each region for each condition/subject. Topographic plots of theta and alpha power across all channels from -300-0 ms prior to arrival at the choice point and differences between Free and Guided groups are shown in Fig.s 2 and 3. Midfrontal theta power was compared between Free and Guided groups with an unpaired t-test. Theta power in midfrontal channels was greater for the Free group than the Guided group ($t(58) = 4.15$, $MSE = .02$, $p < .01$). Parietal alpha power was compared between Free and Guided groups and left and right parietal channels with a Group x Hemisphere (left, right) mixed ANOVA. Alpha power in parietal channels was greater for the Free than the Guided group ($F(1,58) = 5.84$, $MSE = .01$, $p = .02$). There was no main effect of hemisphere ($F(1,58) = .06$, $MSE = .01$, $p = .80$), nor was there a group x hemisphere interaction ($F(1,58) = .50$, $MSE = .01$, $p = .48$).

In addition, we examined midfrontal theta and parietal alpha power from -300-0 ms prior to the decision at the choice point. Theta power in midfrontal channels was marginally greater for the Free than the Guided group ($t(58) = 1.81$, $MSE = .03$, $p = .08$) (see Fig. 4). To decrease the chance that movement contributed to theta power effects, additional analyses were performed between -200-0 ms and -100-0 ms. The pattern of results was similar to -300-0 ms, theta power in midfrontal channels was greater for the Free group than the Guided group. Alpha power in parietal channels was greater for the Free than the Guided group ($F(1,58) = 22.80$, $MSE = .02$, $p < .01$) (see Fig. 5).

We additionally conducted exploratory analyses where we examined EEG effects from -300-0 ms prior to arrival at the choice point and prior to the decision at the choice point in other frequencies, including beta (12-20 Hz), and gamma (25-50 Hz), and in other channels. Beta power in right frontal and left parietal channels was greater for the Free group than the Guided group prior to arrival at the choice point (FDR corrected $p < .05$). Theta power in parietal channels was greater for the Free group than the Guided group prior to the decision at the choice point (FDR corrected $p < .05$, Fig. 4) .

3.3. *Test phase*

The ROI was a left parietal channel group (see Fig. 6 and 7); mean theta (4-8 Hz) power from 0-500 ms, 500-1000 ms, and 1000-1500 ms was computed by averaging the channels within each region for each condition/subject. Topographic plots of theta power across all channels from 0-500 ms and differences between correct and incorrect targets are shown in Fig. 6. Left parietal theta power was analyzed first with a Group x Accuracy (correct, incorrect) mixed ANOVA. Theta power in left parietal channels from 0-500 ms was greater for correct than incorrect targets ($F(1,46) = 5.98$, $MSE = 2.20$, $p = .02$). We did not find any significant theta power effects in the 500-1000 ms or 1000-1500 ms time windows.

Using the same spatiotemporal ROI defined by the contrast of correct to incorrect targets, we also examined differences between short and long Euclidean and path length distances with a Group x Distance (short, long) mixed ANOVA. Theta power was marginally greater for long than short path length distances ($F(1,58) = 2.86$, $MSE = .44$, $p = .10$) (see Fig. 7), but no trend was seen for Euclidean distance ($F(1,58) = .04$, $MSE = .46$, $p = .85$). In addition, we examined the correlation between path length and single trial theta power across trials and subjects for each path length. There was a marginal positive correlation between theta power and path length ($r = .38$, $n = 25$, $p = .06$, two-tailed).

Additionally, we examined EEG effects from 0-500 ms, 500-1000 ms, and 1000-1500 ms in other frequencies related to memory, including alpha, beta, and gamma, and channels. Right parietal beta power was greater for correct than incorrect targets (FDR corrected $p < .05$).

4. Discussion

This study examined the role of theta oscillations in active learning and tested hypotheses about memory-related exploration and theta-band contributions to human spatial navigation. Participants who actively decided where to explore (Free group) tended to have better navigation performance during test compared to those who were guided (Guided group). Compared to the Guided group, the Free group exhibited significantly increased midfrontal theta oscillatory power immediately preceding arrival at a choice point and marginally increased theta oscillations just prior to making the decision to make movement. Critically, this difference emerged even though motor responses and movement speed were matched across Free and Guided conditions, suggesting that theta oscillations' role in navigation is related to exploration and learning, and is not exclusively tied to movement speed. We also hypothesized that theta oscillations were related to reinforcement learning processes during active learning. The current study supports this hypothesis, because the observed theta oscillations were localized primarily in midfrontal channels, which are associated with reinforcement learning mechanisms. In addition, we found evidence of attentional processing at alpha frequency just prior to both the arrival at the choice point and the decision. Together, these results suggest that theta oscillations play a fundamental role in navigation through active learning and decision-making.

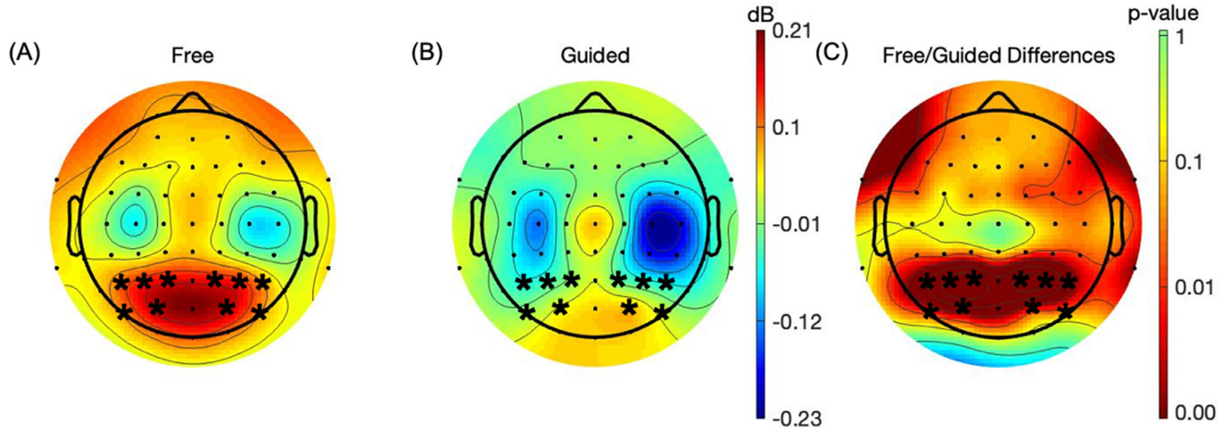

Fig. 5. Alpha power for the (A) Free and (B) Guided group just prior to the decision at the choice point during exploration. Alpha power across all channels from -300-0 ms. Black * indicates analyzed channels in left and right parietal regions. Color scale: decibel change from baseline. (C) Differences between Free and Guided groups. Alpha power in parietal channels was greater for the Free group than the Guided group ($F(1,58)=22.80$, $MSE=.02$, $p < .01$). Color scale: *p*-value of Free compared to Guided group differences.

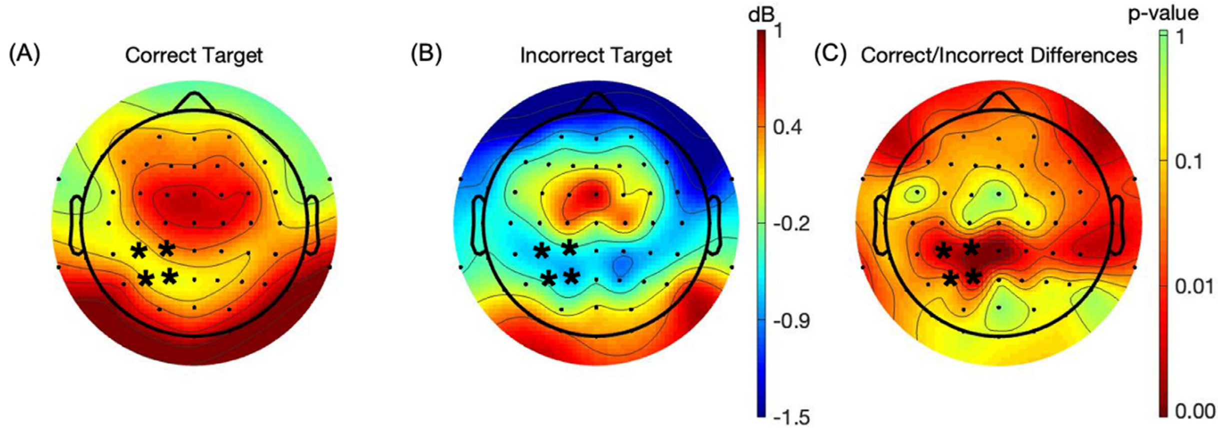

Fig. 6. Theta power for correct (A) vs. incorrect (B) targets during test. Theta power across all channels from 0-500 ms.. Black * indicates analyzed channels in left parietal regions. Color scale: decibel change from baseline. (C) Differences between correct and incorrect trials. Theta power in left parietal channels from 0-500 ms was greater for correct than incorrect targets ($F(1,46) = 5.98$, $MSE = 2.20$, $p = .02$). Color scale: *p*-value of correct compared to incorrect trial differences.

4.1. The Role of Theta Oscillations in Navigation

Our results support the theory that theta oscillations are related to memory encoding processes, particularly during active exploration. During exploration, we identified increased midfrontal theta power in active decision-makers in the time window just prior to the choice point and a trend prior to making each decision. Critically, guided participants moved at the same speed as the active group, and all decisions were made when stationary, controlling for potential effects of speed or movement. Together with these factors, our results are consistent with the exploration and memory theory.

The case for a mnemonic role for theta oscillations is strengthened by our observation of increased theta power during correct trials compared to incorrect trials during the test phase. The theta oscillations during retrieval were localized over left parietal channels, just after the target locations were presented. Parietal channels have been observed to be important for memory processes in non-spatial tasks along similar time scales (Medrano et al., 2017; Nyhus et al., 2019; Nyhus and Badre, 2015; Ross et al., 2018, 2015). We also observed a strong effect of active exploration for theta oscillations in parietal channels just prior to making the decision, suggesting that theta oscillations in parietal regions could be important for encoding. Furthermore, we found choice-point-related beta oscillations during exploration in right frontal and left parietal channels, and during correct trials of the test phase in a right parietal channel. Beta oscillations are also known to play a role in memory encoding and retrieval processes (Düzel et al., 2003; Fell et al., 2008; Hanslmayr et al., 2012, 2011, 2009; Ketz et al., 2014; Khader and Rösler, 2011; Sederberg et al., 2003; Spitzer et al., 2009; Waldhauser et al., 2012, 2015; Weiss and Rappelsberger, 2000), further supporting the importance of memory for this task. A recent study identified a similar role for memory retrieval for theta oscillations during navigation, but did not find the same advantage for active exploration (Aghajan et al., 2019). However, our study incorporated precise timing for each decision point of active exploration, making the decision about how to explore a discrete choice, rather than a continuous movement. The ability to separate the decision from other movement processes in our study eliminates the confound between movement and exploration.

Our results are not wholly incompatible with the possibility that movement and spatial processing could be an additional factor for theta oscillations. We saw promising signs that theta oscillations are related to spatial information, with a trend for increased theta power in trials where the path between the start and target objects was long, although we found no such trend for Euclidean distances. This finding is consistent with previous studies showing that theta oscillations code for distances traveled (Kahana et al., 1999; Vass et al., 2016). None of our participants were physically moving, so it is possible that the addition of physical movement (e.g. Aghajan et al., 2017; Bohbot et al., 2017) would also lead to increased theta oscillations or amplify the present re-

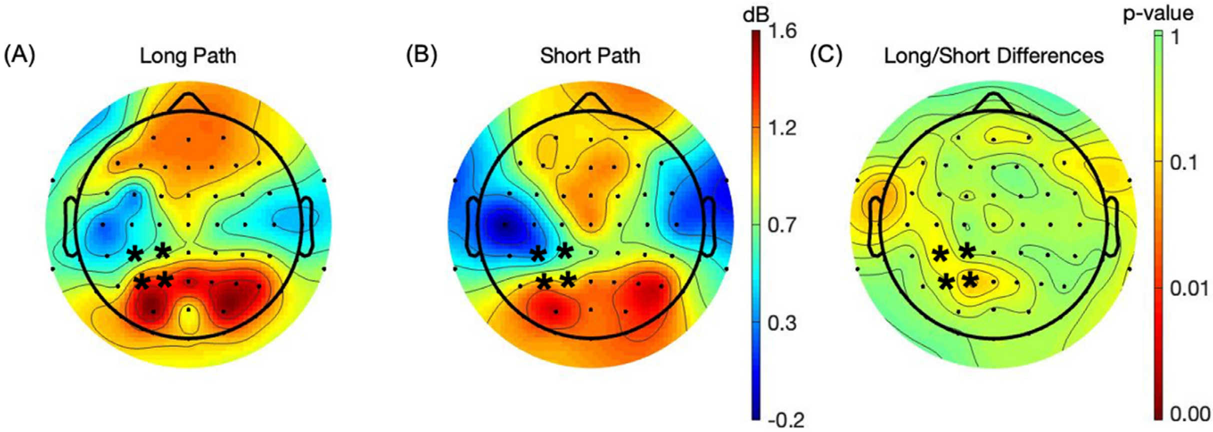

Fig. 7. Theta power for long (A) vs. short (B) path length distances during test. Theta power across all channels from 0-500 ms. Black * indicates analyzed channels in left parietal regions. Color scale: decibel change from baseline. (C) Differences between short and long paths. Theta power was marginally greater for long than short path length distances (($F(1,58) = 2.86$, $MSE = .44$, $p = .10$). Color scale: *p*-value of long compared to short trial differences.

sults. We also used scalp EEG, whereas many previous studies on human theta oscillations used intracranial recordings directly on the medial temporal lobe, and so the recording method could also limit our ability to detect movement-related theta oscillations. In addition, it is possible that the different roles for high (~8 Hz) and low (~3 Hz) theta oscillations in spatial processing and speed (Goyal et al., 2020; Miller et al., 2018) could be a factor in our results. Although the rodent literature suggests a relationship between hippocampal theta rhythms and movement speed (e.g. McFarland et al., 1975), it is possible that rodent navigation processes differ from those in human navigation. In addition, the recent finding that rodent theta oscillations are linked to acceleration rather than speed (Kropff et al., 2021, but see Kennedy et al., 2022) suggests that future studies might observe larger differences in theta oscillations if acceleration was systematically varied. Although all of these considerations suggest ways in which we could find stronger or additional differences in theta oscillations between our conditions, they do not contradict our findings that support a role for theta oscillations in active exploration. Thus, we cannot rule out the possibility that theta oscillations are also related to movement. However, our results indicate that in human navigation, theta rhythms are not exclusively linked to movement speed and are associated with memory-related exploration processes.

4.2. Active Decision-Making and Reinforcement Learning

In addition to the broader role of theta oscillations during human spatial navigation, we were interested in understanding more about the neural correlates of active learning during navigation. Active compared to passive learning is related to increased theta oscillations in the human hippocampus (Estefan et al., 2021), suggesting that they are important for volitional learning. Previous studies of volitional attention suggest that activity in frontal and central parietal regions is associated with cues related to active attentional decisions (Bengson et al, 2015; Liu et al., 2016). Additional work suggests that increased frontal theta power is associated with volitional attentional decision-making (Rajan et al., 2019) and memory encoding and retrieval (Addante et al., 2011; Hseih & Ranganath, 2014).

We found increased theta oscillations in midfrontal channels during learning for active navigators compared to passive navigators. Our results support the hypothesis that active learning is related to learning mechanisms. This theory is based on the idea that theta oscillations facilitate functional communication among medial prefrontal, hippocampal, and striatal systems (prefrontal-hippocampal-striatal circuit) during learning. When actively learning a complex environment, navigators make small predictions at each decision point about what they expect to find and subsequently receive feedback on that prediction when they move. We theorize that this process is supported by reinforcement learning mechanisms. We focused specifically on the prediction and decision side of this process, rather than the feedback (and there was no explicit reward), so it is possible that other learning mechanisms are involved that are not captured here. Although we also do not know for sure exactly when participants in the Free group were thinking of their next decision, both the time window when approaching and when at the decision point show similar results. Midfrontal theta oscillations have been related to reinforcement learning (Cavanagh et al., 2010), cognitive control mechanisms (Cavanagh and Frank, 2014), response to uncertainty (Cavanagh and Shackman, 2015), and reward expectancy and memory encoding (Gruber et al., 2013). Theta oscillations observed during the exploration phase of this study were localized to midfrontal channels, consistent with the medial prefrontal cortex being involved in coordinating learning mechanisms.

In addition, we saw increased alpha band activity for active navigators compared to the guided group. One possible explanation for better performance in active navigators is that active navigators were simply attending to the task more than guided navigators. Since alpha oscillations are typically associated with attentional processes (Klimesch et al., 1998; Sauseng et al., 2005), including volitional attention (Bengson et al., 2014), our results are also consistent with an attentional explanation. Furthermore, we saw alpha oscillations in parietal channels during learning, which are typical locations for attentional processes (Benedek et al., 2014). Additional work is needed to understand the relationship between the contributions of theta and alpha oscillations during active navigational learning. In sum, we also observed evidence for a volitional attentional explanation underlying the advantage for active learning.

It is important to note that this study used scalp EEG, which presents a challenge for the precise localization of the origin of the theta oscillatory signal observed in the midfrontal channels. Scalp EEG also hinders the direct recording of signal from the hippocampal or striatal regions, due to their depth in the brain. Therefore, this study paves the way for future experiments using intracranial EEG (iEEG) methods to further test the prefrontal-hippocampal-striatal circuit learning theory. However, given the strong connections between mPFC and hippocampal processing during learning (Brown et al., 2012; Brown & Stern, 2014; Ito, 2017; Kirchhoff et al., 2000), the previous evidence for midfrontal theta oscillations being involved in reinforcement learning and cognitive control processes (Cavanagh et al., 2010; Frank et al., 2015), and our observation of theta power in midfrontal channels during exploration, our results further support the theory that theta rhythms represent learning mechanisms within the prefrontal-hippocampal-striatal circuit.

In conclusion, we found evidence that theta oscillations support active navigational learning, with neural signatures suggesting reinforcement learning mechanisms. Furthermore, our results indicate that theta oscillations are related to memory encoding and retrieval processes and are not exclusive to movement speed. These findings provide evidence for the memory encoding theory about the nature of theta oscillations in human navigation. We also found evidence for alpha oscillations, suggesting that the volitional control of attention could also be an important factor in active learning. Our findings suggest that exploratory behavior during spatial learning is important for utilizing feedback about where items are located and how paths connect. Theta oscillations facilitate the learning dynamics of this process. We also found some signatures of spatial processing during the test phase related to path distance required to reach the target. Overall, our results implicate a mnemonic role for theta oscillations during navigational learning.

5. Data Code Availability

Data for this study were newly acquired for the study. Data will be made openly available in an open science repository upon publication of the manuscript.

Analysis code will also be available in an open repository upon publication of the manuscript.

Data availability

Data will be made available on request.

Acknowledgments

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