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RESEARCH REPORT

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Theta oscillatory power decreases in humans are associated with spatial learning in a virtual water maze task

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Abstract

Theta oscillations (4–8 Hz) in humans play a role in navigation processes, including spatial encoding, retrieval and sensorimotor integration. Increased theta power at frontal and parietal midline regions is known to contribute to successful navigation. However, the dynamics of cortical theta and its role in spatial learning are not fully understood. This study aimed to investigate theta oscillations via electroencephalogram (EEG) during spatial learning in a virtual water maze. Participants were separated into a learning group ($n = 25$) who learned the location of a hidden goal across 12 trials, or a time-matched non-learning group ($n = 25$) who were required to simply navigate the same arena, but without a goal. We compared all trials, at two phases of learning, the trial start and the goal approach. We also compared the first six trials with the last six trials within-groups. The learning group showed reduced low-frequency theta power at the frontal and parietal midline during the start phase and largely reduced theta combined with a short increase at both midlines during the goal-approach phase. These patterns were not found in the non-learning group, who instead displayed extensive increases in low-frequency oscillations at both regions during the trial start and at the parietal midline during goal approach. Our results support the theory that theta plays a crucial role in spatial encoding during exploration, as opposed to sensorimotor integration. We suggest our findings provide evidence for a link between learning and a reduction of theta oscillations in humans.

KEYWORDS
efficiency, learning, navigation, spatial memory, theta oscillations

1 | INTRODUCTION

Navigation is an essential everyday skill that allows us to get to and from important locations. Spatial cognition involves combining acquired knowledge of our environment and its features, to help us plan and move through space with both ease and efficiency (Ekstrom et al., 2003; Epstein, 2008; Epstein et al., 2017). In humans, it is thought that theta oscillations (4–8 Hz) may support successful spatial exploration and sensorimotor integration during navigation (Burgess & O'Keefe, 2011; Colgin, 2020). For example, speed of travel and path

distance have been shown to be related to increased theta power in both animals and humans (Bush et al., 2017; Kennedy et al., 2022; Yassa, 2018). Furthermore, bursts in theta power have been observed during navigational direction-changes (Do et al., 2021). According to Ekstrom et al. (2005), theta power changes observed in the human hippocampus are related to movement and not to learning. However, there is also support for theta oscillations playing an important role in learning, particularly in spatial or episodic memory encoding and retrieval. This link has been found in several intracranial electroencephalogram (iEEG) and scalp EEG studies with humans (Bohbot et al., 2017; Buzsáki, 2005; Chrastil et al., 2022; Ekstrom et al., 2005; Kahana et al., 1999; Lega et al., 2012; Lin et al., 2017; Pastötter & Bäuml, 2014). For example, Lega et al. (2012), Kerrén et al. (2018), and Vivekananda et al. (2021) all report increases in low-frequency theta power that are related to successful spatial memory encoding (but see Bohbot et al., 2017). Most recently, Chrastil et al. (2022) found theta power increases relate to encoding, specifically during a decision-making phase of active exploration.

In a recent review, Herweg et al. (2020) explored the dynamics of these theta changes, with iEEG studies reporting theta power reductions related to successful memory encoding, whereas scalp EEG studies demonstrated increases in theta power. EEG studies focusing on navigation have also reported increased theta power oscillations during active learning, recall and decision-making (Chrastil et al., 2022; Lin et al., 2022; Vivekananda et al., 2021). However, decreases in theta power have also been noted during associative learning and episodic recall (Greenberg et al., 2015). For example, decreases in human hippocampal theta power have been shown to be related to improved navigation performance and successful spatial encoding (Cornwell et al., 2012; Crespo-García et al., 2016). Spatial memory formation during real-world navigation has also recently been linked to theta power decreases in humans (Griffiths et al., 2016).

Connectivity models suggest that low-frequency oscillations from the hippocampus, retrosplenial cortex and posterior parietal cortex contribute to spatial navigation and may be reflected by cortical theta (Ekstrom et al., 2003, 2017). Therefore, studies have generally focused on theta changes in two key cortical regions, the frontal and parietal midline (Chrastil et al., 2022; Kane et al., 2019; Kaplan et al., 2014; Liang et al., 2018, 2021; Lin et al., 2022; Meltzer et al., 2009). These areas are known to display synchrony during encoding and retrieval of information (Fell & Axmacher, 2011). There is also supporting evidence for communication between the two regions for spatial working memory and goal directed attention via the frontoparietal network (Fellrath et al., 2016; Sauseng et al., 2005). Frontal theta increases have also been observed during recall of successful spatial information (Kaplan et al., 2014; Roberts et al., 2013) and on approach to decision-points during active exploration at the frontal midline (Chrastil et al., 2022). Chrastil et al. also found increases at the parietal midline during spatial decision-making.

Navigation is dynamic and trying to capture sub-second neural changes during environment exploration and encoding is extremely difficult. As such, it is important to break navigation into its component parts and investigate each separately. One good place to start is the review by Nyberg et al. (2022) that suggests evidence for three essential phases of navigation behaviour: (1) planning and route initiation, (2) travel and (3) goal approach. Importantly, each phase has evidence of related neural networks as well as behaviours that are relatively easy to identify. With the use of this approach, we focused on two phases, route initiation and goal approach, in an attempt to understand the role of frontal and parietal theta oscillations (specifically 4–8 Hz) in spatial learning (De Araújo et al., 2002; Kunz et al., 2019; Sosa & Giocomo, 2021) using a virtual navigation task. As noted above, there is evidence of theta changes in both encoding (e.g., associative learning, episodic memory retrieval) and searching behaviours (e.g., speed and sensorimotor integration) during navigation. In an attempt to resolve this issue and examine whether theta changes (across frontal and parietal sites) are specifically related to learning, we focused on the difference between two groups of trials—the first six (learning) and last six (learned). In addition, we used a time-matched non-learning (control) group that simply had to navigate an arena without a goal present; that is, this group was exposed to the same environment for the same number of trials and time but did not learn a specific location. Furthermore, we controlled for speed of movement in both learning and non-learning groups. In addition, both groups started in the same location of the arena for each trial in an attempt to control for directionality. Therefore, we hypothesised that if the contribution of theta power is related to learning during exploration, we should demonstrate theta power differences between the non-learning and learning groups following completion of the task. However, if it is related to active sensorimotor integration, we should show no differences between the groups. Furthermore, we hypothesised that theta power would increase in the learning group and not in the non-learning group at both ROIs, based on previous findings. We hypothesised this would occur within-groups, as the task is eventually learned.

2 | MATERIALS AND METHODS

2.1 | Participants

Fifty young adults (36 females, 14 males) aged between 18 and 45 ($M = 21.7$, $SEM = \pm 0.637$) were recruited via Maynooth University Department of Psychology and externally using personal connections, flyers and social media. The required sample size was estimated using the '*pwr*' package available in R. On the basis of typical sample sizes in similar EEG studies and their power, we calculated the minimum number of participants required with a Cohen's d of 0.8 and a power of 80% at an alpha level of 0.05. The sample size estimated for the non-learning and learning groups was 25.5/group. All participants gave informed consent prior to starting the project and were given a full briefing of the experiment, along with the exclusion criteria. Some participants from Maynooth University received course credit for participation.

Due to technical failure (2) or low recording quality resulting in excessive noise (1), the EEG epochs of 3 participants (learning group) were excluded from the associated analyses (trial 12 epoch only). This project and the use of human subjects with EEG were approved by the Maynooth University ethics committee (BSRESC-2021-2453422). A sample of participants ($n = 30$) was tested using several neuropsychological control tasks to ensure that both learning ($n = 7$) and non-learning ($n = 25$) groups were cognitively matched. The first task was the National Adults Reading Test (NART; Nelson & Willison, 1991). Responses were recorded as being correct or incorrect, and the number of errors (out of 50) was used to score verbal IQ. Secondly, the Trail Making Test (TMT; Army Individual Test Battery, 1944; Reitan & Wolfson, 1992) was used to examine visuospatial ability, motor functioning and overall executive control (see Sánchez-Cubillo et al., 2009). Finally, participants were given the Montreal Cognitive Assessment (MoCA) to examine executive functioning, memory and attention in one short sitting (Nasreddine et al., 2005).

2.2 | Spatial navigation task

After the electrophysiological preparation (see next section for details), participants were seated 50 cm from the LCD computer screen on their own in a darkened, electrically shielded and sound-attenuated testing cubicle (150 × 180 cm) with access to a joystick for navigating. The spatial navigation task used was NavWell (see Commins et al., 2020 for in-depth details). In brief, the virtual maze consisted of a medium circular environment (taking 15.75 s to traverse the arena, calculated at 22.05 Vm). Two cues were used and were located on the wall of the arena: a yellow square (northeast quadrant wall) and a light of 50% luminance (Figure 1a). A square goal was hidden in the middle of the northeast quadrant and was 15% of the total arena size and consisted of a bright blue square that only became visible when the participant crossed it (northwest quadrant wall, see Figure 1b).

All participants underwent 12 trials from pseudorandom starting positions around the arena (N, S, E and W), with a maximum of 60 s/trial to locate the goal. Participants were transported to the location of the goal if they failed to locate it. There was a 10-s inter-trial interval between each trial. The goal remained in the same location throughout (centre of NE quadrant). Participants were randomly assigned to either a learning group (who were required to learn the location of a hidden target across 12 trials, $n = 25$, 8 males and 17 females) or a non-learning group (who were required to move around the same arena for 12 trials, but without the presence of a goal; each trial was time-matched to the average latency of the learning group, $n = 25$, 6 males and 19 females). Latency (time taken to locate target or complete trial; measured in seconds), path length (distance travelled in virtual metres [Vm]) and percentage time spent in goal quadrant are typical measures of water maze performance (see Vorhees & Williams, 2014). These were recorded for each participant during each trial by NavWell (see also Commins et al., 2020).

2.3 | EEG recording

EEG data were acquired using a BioSemi ActiveTwo system (BioSemi B.V., Amsterdam, Netherlands) providing 32 Ag/AgCl electrodes positioned according to the 10/20 system during NavWell. Analogue event signals were sent manually by the researcher during three time-points of each trial: (1) when participants began their trial, (2) when they reached the goal and (3) when their Inter Trial Interval (ITI) ended. BioSemi designed caps using the 32-electrode international 10–20 layout were also used. The recording system was stored in the same room, and participants were seated during navigation and data were recorded continuously. A PC running the ActiView software (version 7.05) was positioned in the room adjacent to the experimental cubicle, for constant monitoring of the EEG recording. Participants were instructed to relax and move as little as possible. Four electrodes (EXG1–EXG4) were positioned on the face to monitor eye movements and blinks. Raw EEG data were sampled at 1024 Hz but were down-sampled offline to 512 Hz.

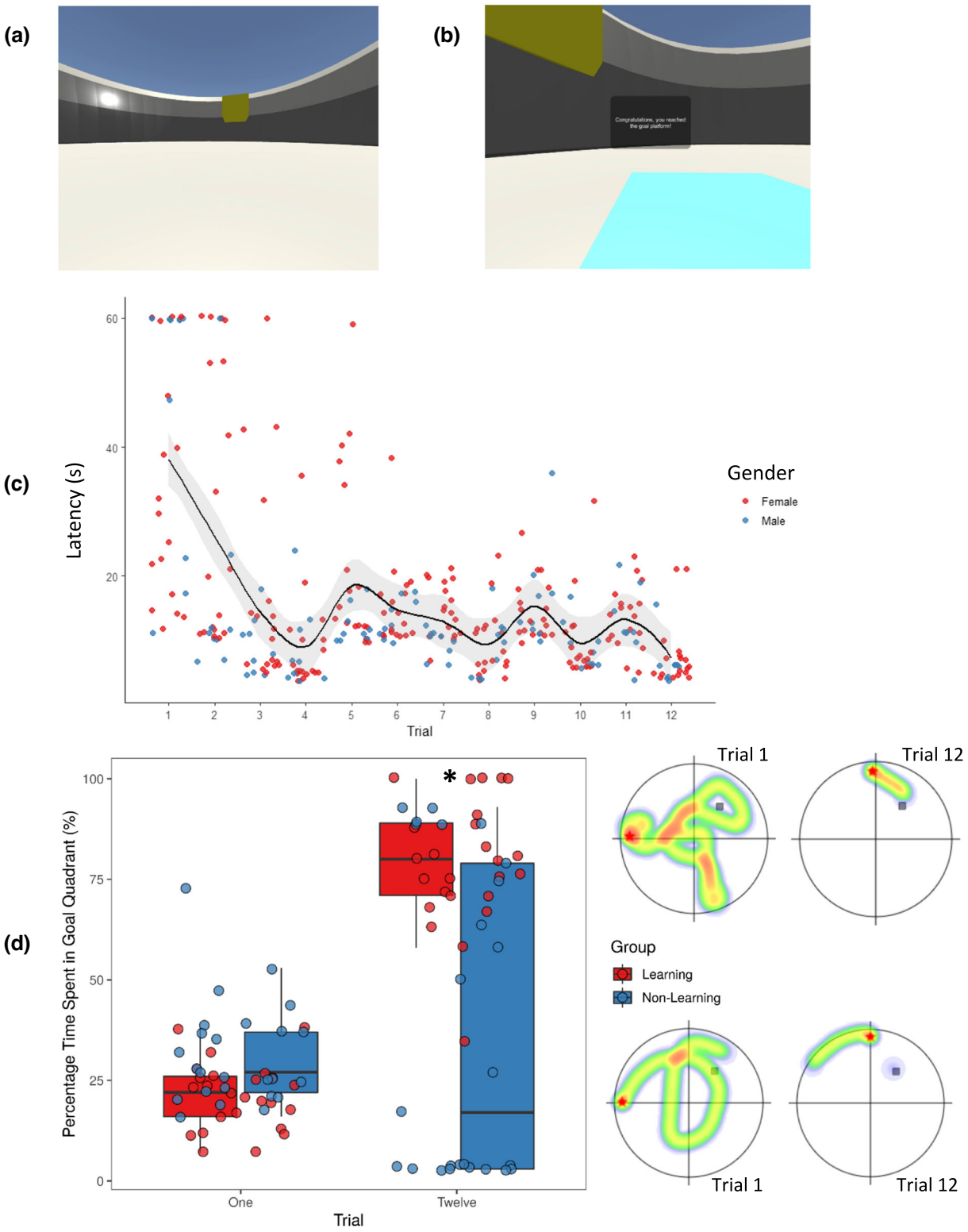

FIGURE 1 (a) Screenshot of the NavWell environment used in this experiment, with light and square cues on the wall of the environment. (b) NavWell goal becomes illuminated when a participant walks over it, 'congratulations, you reached the goal platform!' message displayed. (c) Plot of task latencies (in seconds) across the 12 trials for learning group, split by gender. The mean time for each trial is denoted by the line along with standard error denoted by the shaded region around the line. (d) Box plots and individual data points for each learning group participants percentage time spent searching in the target quadrant for Trials 1 and 12. Diagrams of the water maze arena on the right side demonstrate heat maps of where participants (Learning: upper, Non-Learning: lower) spend most of their search time, during Trials 1 and 12.

2.4 | EEG pre-processing

Continuously recorded EEG data were analysed offline in MATLAB R2021B using scripts within the Brainstorm package (Tadel et al., 2011). A 1-Hz high-pass filter and a 40-Hz low-pass filter were applied. Data were visually inspected for bad segments and bad electrodes, which were then removed. Independent component analysis (ICA) was performed to remove and correct artefacts, namely, eye movements, blinks and muscle artefacts. We used the EEGLAB infomax algorithm callable via brainstorm using the *runica* function. Bad electrodes that originated from pre-defined regions of interest (ROIs) were interpolated (1), if possible, using Brainstorm after ICA. EEG data were then referenced to the average of the 32 electrodes.

2.5 | EEG frequency band analysis

Artefact-free data were then epoched around each analogue trigger for all 12 trials for all 50 participants. For analysis of the trial start, we used −500 ms and +2000 ms. We then used −2000 ms before and +500 ms marker for the goal trigger. We chose these epoch times as we believe it was sufficient to perform a good estimation of the overall power spectrum and avoid edge-effect estimation contaminations near important behaviours. Additionally, we also used −1000 ms to -500 ms before the start of the trial as a baseline. During this time, participants were sitting still waiting to start their next trial. To not contaminate our baseline with edge-effects, the full time epoched at the trial start was −1500 ms to +2000 ms. The initial 500 ms was to adjust for edge-effect contamination (see Gyurkovics et al., 2021 for the importance of doing this), the baseline was then calculated for the following 500 ms, then we examined the remaining −500 ms before the trigger, which was included in the analysis to allow for some error/time-lag in the temporal accuracy for behaviours. The same baseline was used to standardise each participant's goal-approach epoch as well (see the Supporting Information for further information).

Each participant starts epoch, and goal approach epoch was extracted from all 12 trials in each condition. This provided a total of near 600 epochs per condition, 300 per phase. We used a Morlet wavelet time-frequency analysis, with a central frequency of 1 Hz and a full width half maximum time resolution of 3 s alongside a linear frequency definition from 1 to 30 Hz (1:1:30). A 1/f normalisation was not applied here. Instead, power was then standardised via baseline normalisation and converted to dB for each individual participant. This normalisation is done independently for each participant and electrode site. For statistical analysis outside of brainstorm, we averaged the power within each frequency band across time (using the underlying MATLAB Fast Fourier Transform defaults available via our linear frequency definition), then extracted these data for our ROIs for each individual participant. We examined the power at our ROIs, the frontal midline (Fz, F3, F4) and the parietal midline (Pz, P3, P4) to capture activity from both the anterior and posterior parts of the scalp. Mean theta power for each participant was calculated by averaging the channels across this time from each ROI, for each subject in each group.

2.6 | Statistical analysis

Statistical analyses and visualisation of the behavioural data were performed using a combination of JASP (version 0.15) and R software version 4.0.2 with the tidyverse and ggplot2 package. Statistical exploration of the EEG data was initially run using Brainstorm in MATLAB 2021b, mainly comprising of two-tailed independent or paired parametric *t* tests with a *p* threshold of 0.05. We corrected for multiple comparisons in EEG data using an false discovery rate (FDR) correction. This was chosen as it is more detrimental to report an effect that is not there (type I error), as opposed to missing one that is (type II error; see Jabès et al., 2021 for similar EEG study with the same statistical power). However, statistics were then performed again on mean power of the oscillatory bands across time in JASP. For the frequency bands, theta was defined as 4–8 Hz, based on current literature discussed above. For statistical analysis in JASP, the power of the time-frequency calculations was used (μV^2) and normalised using a dB (decibel) standardisation (10 * log10(x/μ). Topographies and time-frequency plots are displayed as change of dB converted magnitude (or amplitude: √power) in this paper to provide clarity and more interpretable plots when using statistical comparisons, as has been encouraged by other researchers (Burgess, 2019). There was no effect of reported gender nor age in our sample, and therefore, all data were combined for EEG analysis.

3 | RESULTS

3.1 | Behavioural results

Initially, we compared both groups' scores on a variety of cognitive tests to ensure that both groups were cognitively matched. There were no significant differences between the two groups on the number of NART errors (*t*

(30) = 0.36, $p = 0.721$), total time taken to complete the TMT ($t(30) = 0.448$, $p = 0.657$) and scores on the MOCA ($t(30) = -0.445$, $p = 0.659$). In addition, both groups were well matched for age ($t(48) = -0.845$, $p = 0.402$). Gender differences were not the focus of this study, but there are some known gender differences in both navigation performance and theta power (Astur et al., 1998; Pu et al., 2020). Although, the NavWell software seems to eliminate this effect (see Commins et al., 2020). However, just to confirm this, gender was included in the below analyses of behaviour and EEG.

We next analysed performance of the learning group on the virtual water maze task. The task latency of participants during the acquisition phase was analysed using a 2 (Gender) × 12 (Trials) mixed-factorial analysis of variance (ANOVA). Mauchly's test of sphericity indicated that the assumption of sphericity was violated ($p < 0.05$); therefore, a Greenhouse–Geisser sphericity correction was applied to the model. Latency was defined by the amount of time it takes a participant to find the target (with a maximum of 60 s). There was an overall significant decrease in latency across all participants for the 12 trials ($F_{4.15,\ 95.46} = 14.933$, $p < 0.001$, $\eta^2 = 0.338$). Bonferroni-corrected t tests revealed that participants were significantly ($p < 0.001$) faster at locating the target on Trial 12 ($M = 7.44$ s, SEM = ±0.96 s) compared with Trial 1 ($M = 36.88$ s, SEM = ±3.95 s) and Trial 2 ($M = 27.32$ s, SEM = ±4.22 s). All participants in the learning group successfully learned the task, reducing their times across trials (see Figure 1c). There was no difference in latency between gender ($F_{1,\ 23} = 1.78$, $p = 0.195$, $\eta^2 = 0.007$). Likewise, no trial × gender interaction effect ($F_{4.15,\ 95.46} = 1.98$, $p = 0.101$, $\eta^2 = 0.045$) was reported. Note, latency was not analysed for the non-learning group, as they were time matched to the learning group in order to have comparable EEG trial lengths.

The percentage of time spent in the goal quadrant of the circular environment was also used as a measure of spatial learning (Barnhart et al., 2015; Vorhees & Williams, 2006). We investigate differences from Trial 1 to Trial 12 across groups. Trial 1 should capture searching in both groups, and Trial 12 should capture goal-directed searching in our learning group. We ran a 2 (Group) × 2 (Gender) × 2 (Trial) mixed-factorial ANOVA to investigate this. We report a main effect of Trial ($F_{1,\ 96} = 91.205$, $p < 0.001$, $\eta^2 = 0.231$). We also report a significant between-subjects difference in percentage time for Group ($F_{1,\ 96} = 22.254$, $p < 0.001$, $\eta^2 = 0.067$) but not Gender ($F_{1,\ 96} = 0.124$, $p = 0.246$). As expected, we also reported an interaction effect for Trial × Group ($F_{1,\ 96} = 65.134$, $p < 0.001$, $\eta^2 = 0.165$) but no Trial × Gender effect ($F_{1,\ 96} = 0.005$, $p = 0.943$) nor a three-way interaction effect between Trial × Group × Gender ($F_{1,\ 96} = 0.739$, $p = 0.392$). Independent samples t tests reveal that following learning of the task (Trial 12), the learning group displays significantly ($t(48) = 4.95$, $p < 0.001$) higher percentage time searching in the goal quadrant ($M = 0.792$, SEM ± 0.031) compared with the non-learning group ($M = 0.381$, SEM ± 0.077).

Although the non-learning group was matched to the learning group in terms of the number of trials and the duration of each trial, the path length may have differed between the two groups. As such, the path length of participants during learning was analysed using a 2 (Group) × 2 (Gender) × 12 (Trials) mixed-factorial ANOVA. Mauchly's test of sphericity also indicated that the assumption of sphericity was violated ($p < 0.05$); therefore, a Greenhouse–Geisser sphericity correction was applied to the model. There was significant main effect for path length across all participants for the 12 trials ($F_{3.5,\ 336.1} = 148.694$, $p < 0.001$, $\eta^2 = 0.492$). We also reported a significant difference between the two groups on path length ($F_{1,\ 96} = 150.431$, $p < 0.001$, $\eta^2 = 0.093$) but not between Genders ($F_{1,\ 96} = 0.418$, $p = 0.519$). Additionally, we report a significant Trial × Group interaction effect ($F_{3.5,\ 336.1} = 5.347$, $p < 0.001$, $\eta^2 = 0.018$) and a significant Trial × Gender interaction effect ($F_{3.5,\ 336.1} = 3.526$, $p = 0.011$, $\eta^2 = 0.012$). We did not report a significant three-way interaction effect for Trial × Group × Gender ($F_{3.5,\ 336.1} = 2.306$, $p = 0.067$, $\eta^2 = 0.008$). Tukey-corrected t tests reveal that the groups did not differ in path length at Trial 1 ($t = -1.769$, $p = 0.983$) but began to differ in later trials such as Trials 6, 9 and 11 (all $p < 0.001$; mean difference = −54.329, −54.904 and −54.848 Vm, respectively). The non-learning group demonstrates longer path lengths than the learning group. Examining our Trial × Gender interaction effect, females had shorter path lengths than males on Trial 1 ($t = -3.785$, $p = 0.031$, mean difference = −27.856 Vm) but then do not differ on any other trial after that (all $p > 0.199$). Considering the fact there is more females than males distributed in each group, and that we do not find a between-subjects effect for gender, nor a three-way interaction effect, we can assume gender did not having any major impact on spatial learning.

3.2 | EEG results

We first examined between-group effects, by averaging across trial epochs ($n = 12$ per phase) and participants

($n = 25$) and comparing the differences between conditions (Learning and Non-Learning). This resulted in 297 (3 bad) trials for the learning condition and 300 trials for the non-learning condition, per navigation phase (Trial Start/Trial End) per ROI (Frontal Midline/Parietal Midline). We also computed dB standardised time-frequency plots (see baseline correction used in Appendix 1) based on Morlet wavelet calculated magnitudes (1–30 Hz) during each phase and condition, at each ROI. The resulting time-frequency plots and group differences can be found in Figure 2 (Route Initiation/Start Phase) and Figure 3 (Goal Approach/End Phase). We then ran FDR-corrected permutation *t* tests focusing only on mean Theta (4–8 Hz) across the mean phase time, across all 32-channels. Furthermore, an overall 2×12 mixed-factorial ANOVA was used to compare relative mean Theta power (4–8 Hz) from each trial, across Gender, Condition and Phase. This design was run for each ROI and are reported below.

3.3 | Trial start (route initiation phase)

Focusing on our two ROIs and mean relative theta power at each trial, we employed a 2 (Condition) × 2 (Gender) × 12 (Trial) mixed-factorial ANOVA to compare theta between groups (Non-Learning and Learning) across the full epoch (−500 ms before and 2000 ms after participants started the trial) for each ROI. The data did not violate the assumptions of homogeneity, nor did they violate sphericity assumptions; therefore, no correction was applied. For the **frontal midline**, there was no main effect for Trial ($F_{1,\ 11} = 1.005$, $p = 0.170$, $\eta^2 = 0.017$). There were no significant between-subjects effects for group or gender ($F_{1,\ 11} = 0.185$, $p = 0.669$, $F_{1,\ 11} = 0.612$, $p = 0.438$, respectively). However, there was a significant Trial × Group interaction effect ($F_{1,\ 11} = 2.086$, $p = 0.020$, $\eta^2 = 0.025$). There was also a significant Trial × Gender interaction effect ($F_{1,\ 11} = 2.636$, $p = 0.003$, $\eta^2 = 0.032$). Tukey corrected *t* tests revealed

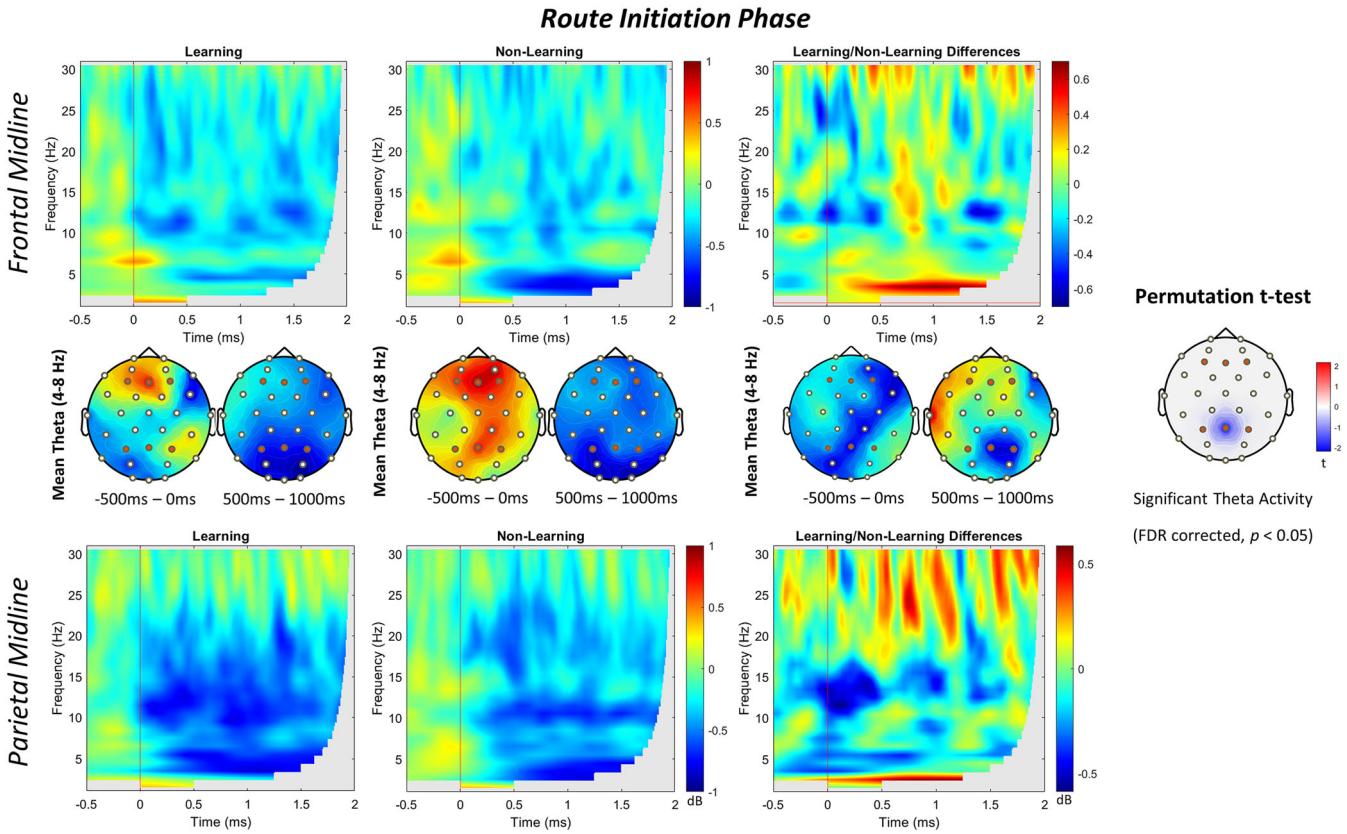

FIGURE 2 Time-frequency plots showing oscillatory power (1–30 Hz) differences between each group at each region of interest (ROI). Displayed as baseline-normalised dB change. The line at 0 ms marks when the trial started. The grey area after 1.5 s is removed due to edge-effect. Average theta power (4–8 Hz) topography during both phases is shown beneath the plots, scaled to the same as the time-frequency plots. Permutation *t*-test results are displayed on a topography for average theta power (4-8 Hz) across time, FDR-corrected for signal dimensions.

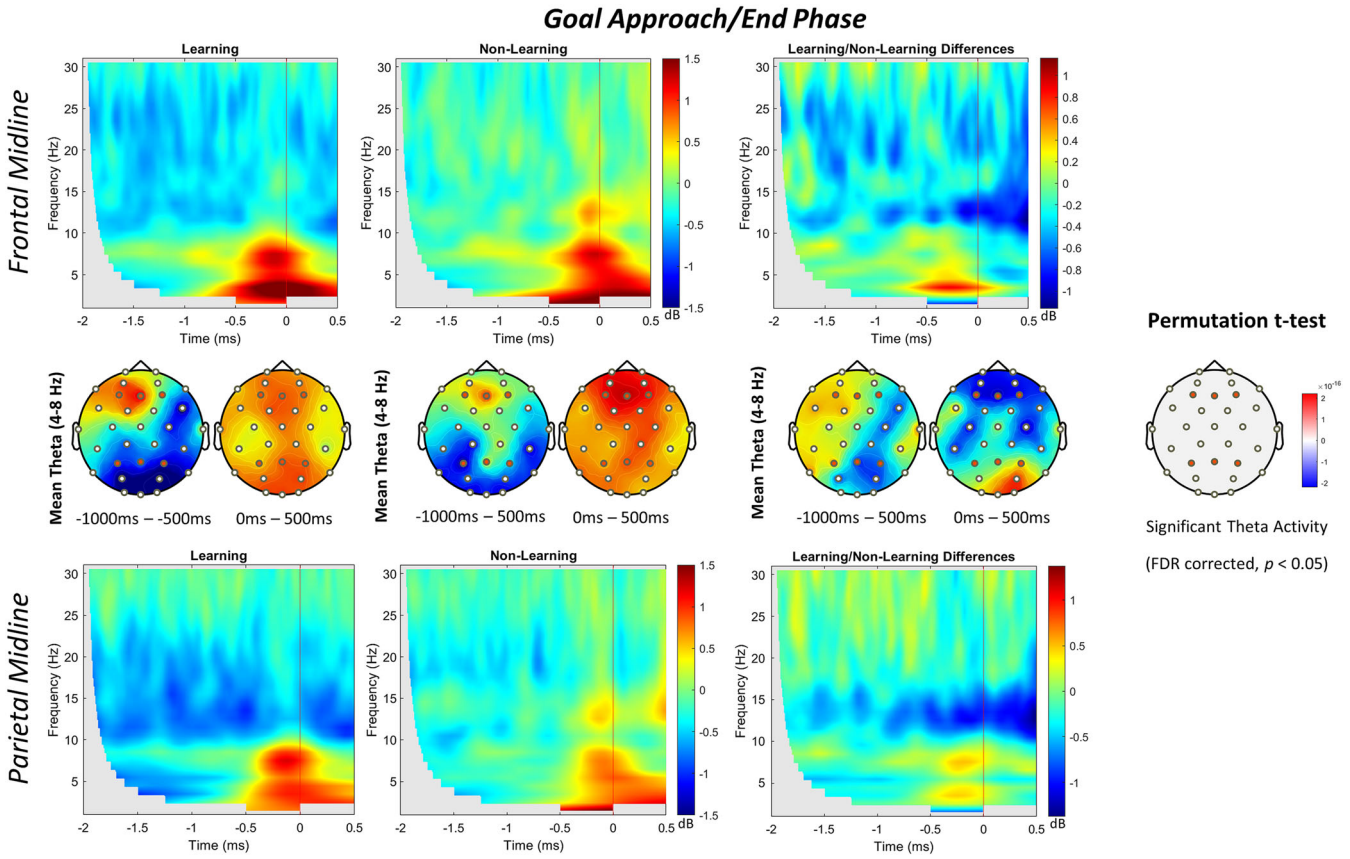

FIGURE 3 Time-frequency plots showing oscillatory power (1–30 Hz) differences between each group at each region of interest (ROI). Displayed as baseline-normalised dB change. The line at 0 ms marks when the trial ended, or the goal was found. The grey area before 1.5 s is removed due to edge-effect contamination. Average theta power (4–8 Hz) topography during both phases is shown beneath the plots, scaled to the range of 4-8 Hz in the time-frequency plots. Permutation *t*-test results are displayed on a topography for average theta power (4-8 Hz) across time, FDR-corrected for signal dimensions.

no group differences at any of the trials. However, they did reveal that Males had significantly reduced theta power on Trial 12 compared with Trial 1 ($t = -2.001$, $p = 0.015$, mean difference $= -0.056$). For the **parietal midline**, there was no significant main effect of Trial ($F_{1,\ 11} = 0.998$, $p = 0.447$). Interestingly, there was no significant difference in parietal midline theta between Genders ($F_{1,\ 11} = 3.890$, $p = 0.055$) nor Groups ($F_{1,\ 11} = 2.258$, $p = 0.140$). Additionally, there was no significant interaction effect for Trial × Group ($p = 0.457$) nor Trial × Gender ($p = 0.189$).

Further examination using time-frequency maps (Figure 3) to investigate the specificity of theta power reveals that frontal midline theta decreases observed appear greater in the non-learning group compared with the learning group, particularly at the lower frequencies (Figure 3, upper). The observed burst in theta power around the trial start (0 ms) appears weaker in the learning compared with the non-learning group. In contrast, there is also a more notable decrease of parietal midline theta in the learning group compared with the non-learning group throughout this phase. This decrease reached statistical significance at the Pz site (Figure 2). These results suggest that a greater reduction in theta at the parietal midline may be associated with spatial learning, with lesser reductions at the frontal midline also important for setting off on a planned route or goal-directed orientation.

3.4 | Trial end (goal approach phase)

We next explored the same ROI as above, the frontal (Fz, F3, F4) and parietal (Pz, P3, P4) midlines, but for the goal approach. A 2 × 2 × 12 mixed-factorial ANOVA was used to compare learning between groups (Non-Learning and Learning) across the full epoch (2000 ms before and 500 ms after participants reached the goal). The data did not violate the assumptions of homogeneity nor sphericity assumptions; therefore, no corrections were applied. Again, at the **frontal midline**, there was no main effect of Trial ($F_{1,\ 11} = 1.162$, $p = 0.311$). There were no

significant between-subjects differences reported for Gender ($F_{1,\ 11} = 0.001$, $p = 0.97$) nor Group ($F_{1,\ 11} = 0.019$, $p = 0.891$). There was also no significant interaction between Trial × Group ($F_{1,\ 11} = 0.404$, $p = 0.954$) nor Trial × Gender ($F_{1,\ 11} = 0.915$, $p = 0.525$). However, there was a significant Trial × Group × Gender interaction effect ($F_{1,\ 11} = 2.214$, $p = 0.013$, $\eta^2 = 0.031$). However, post hoc Tukey corrected *t* tests revealed no significant differences at any measure (all $p > 0.9$). For the **parietal midline** ROI, there was no main effect of Trial ($F_{1,\ 11} = 1.794$, $p = 0.052$, $\eta^2 = 0.025$). There were no significant between-subjects differences reported for Gender ($F_{1,\ 11} = 1.912$, $p = 0.174$) or Group ($F_{1,\ 11} = 0.974$, $p = 0.329$). Additionally, there was no Trial × Group ($F_{1,\ 11} = 1.101$, $p = 0.358$) nor Trial × Gender ($F_{1,\ 11} = 1.101$, $p = 0.449$) interaction effects.

However, from our time-frequency analysis (Figure 3), we see the learning group showed sustained decreases in both frontal and parietal midline theta as participants approached the goal location. This is followed by a greater burst of theta at the goal across a range of frequencies, especially at lower frequencies (4 Hz). This pattern is not observed for the non-learning group, where we see a continuous increase in parietal midline theta and also across other frequency bands such as alpha and beta. No site reached statistical significance across mean theta and mean epoch time.

3.5 | Learning theta: Exploratory within-subjects analysis

Learning is a demanding and dynamic process; everyone does not learn at the same rate, and this is particularly true for spatial cognition and navigation tasks (Commins et al., 2022). A second method was used, to capture learning, where we examined the within-groups differences [$(T_{7–12}) – (T_{1–6})$] from the first and last 6 trials. Frequency estimation variance across time stabilises after approximately five trials on a memory task (Hanslmayr et al., 2009). This is also half-way through our task, in which almost all of those in the learning group, will have

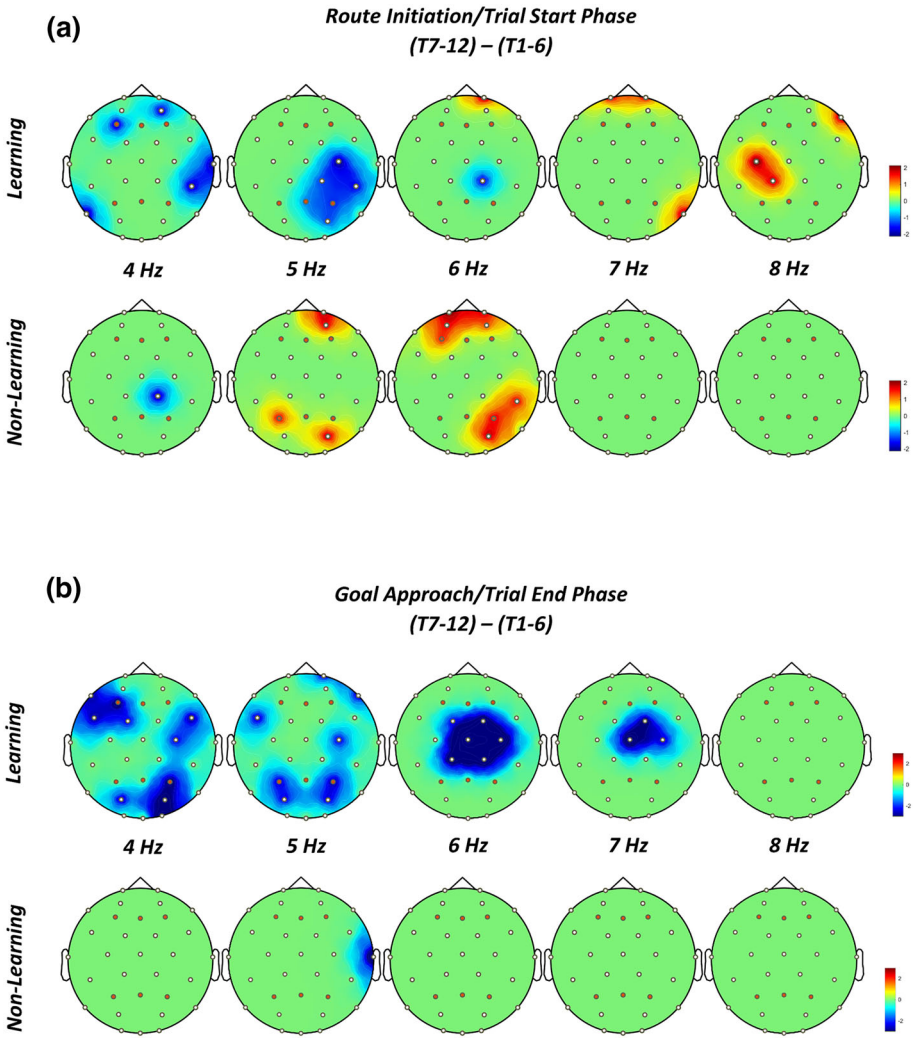

FIGURE 4 (a) Topography plots displaying within-group differences between the last and first 6 trials at the route initiation/trial start phase. Differences were calculated using a paired t-test for each group [$(T_{7–12}) – (T_{1–6})$]. Changes are displayed as *t* values, averaged across time with an alpha level of 0.05, FDR-corrected across signal and frequency dimensions. (b) Topography plots displaying within-group differences between the last and first 6 trials at the goal approach/trial end phase. Differences were calculated using a paired *t* test for each group [$(T_{7–12}) – (T_{1–6})$]. Changes are displayed as *t* values, averaged across time with an alpha level of 0.05, FDR-corrected across signal and frequency dimensions.

successfully learned and subsequently recalled the goal location, albeit at different rates (see Figure 1c). This analysis should provide an insight into the contributions of theta oscillations throughout the process of spatial learning. We examine the start and end phases again, this time examining the entire frequency band in a linear frequency definition from 4:1:8 with a frequency resolution of 1 Hz. We produced an approximate total of 300 trials per group, with approx. 150 per group, in each navigation phase. We used an FDR-corrected paired permutation *t* test with 1000 permutations to evaluate the difference between late and early trials within each group (Figure 4).

With the assumption that these are differences displayed after the task has been learned, we see that the learning group displays significant decreases across 4 and 5 Hz, compared with the non-learning group, who demonstrate significant increases at 5 Hz. These 5-Hz changes mainly occur at one electrode site of the three in our parietal ROI but can be seen across the scalp. There are significant increases in the 7- and 8-Hz range, with no differences displayed in the control group at these frequencies. A reduction in theta power at lower frequencies may illustrate that the task has been learned, and route initiation or initial orientation towards the goal now requires significantly less theta power. Theta increases as trials progress in our non-learning group. We see significant decreases across a range of frequencies in our learning group for the goal approach phase, particularly at our parietal ROI (reported previously). It is possible that theta power needed for successful goal recall and/or goal-directed navigation reduces once the location is learned. Theta power seemingly remains constant during searching behaviour.

4 | DISCUSSION

This study aimed to examine the changes in the brain's electrical activity during spatial learning in a virtual environment. We focused on two stages of learning: the route initiation phase and the goal-approaching phase. We had hypothesised that if theta power was related to learning, we should see theta power differences between the non-learning and learning groups following completion of the task. However, if theta power was related to active sensorimotor integration, we would find no differences between the groups. Having controlled for trial time, starting position, path length and speed, we observed changes in theta for our learning group at both start and goal phases that were different to the non-learning group, suggesting that theta is related to learning rather than sensorimotor integration. The key difference between the two groups was that one group had learnt a specific goal location, whereas the other continued to navigate the environment.

Contrary to our hypothesis however, the learning group displayed significant *decreases* in power of both frontal and parietal theta overall *and* after learning in both navigation phases. Such decreases may indicate a more efficient use of neural resources. Once a task has been learned and the location is known, there may be little need for further exploration or encoding of the environment. As such, there may be no need to expend further neural energy on the task—both behaviour and neural activity have become efficient (see Commins, 2018). Alternatively, low-frequency decreases have been associated with directed attention in both spatial memory and non-memory related tasks (Harris et al., 2017; Park et al., 2019). Decreases in theta power are suggested to be responsible for the communication between areas involved in the successful formation of memories for spatial locations (Griffiths et al., 2016). As participants in the learning group would have directed all attention to the goal location and/or an associated stimulus (e.g., landmarks—see Delaux et al., 2021), theta decreases may be explained by a shift to a more direct spatial attention and memory formation process.

Embedded within the general decreases in theta, both groups also showed a burst of increased theta, at the parietal and frontal midline, at the goal location/trial end. Interestingly, a similar rapid increase in theta (around 8 Hz) is also observed around the immediate start of the trial for the two ROIs, with the learning group having greater theta power early on. Such increases may be related to the processing of stimuli (such as landmarks) to facilitate route and goal recall (Cheng et al., 2022). For example, Chrastil et al. (2022) reported a similar increase in theta, approx. 300 ms prior to participants approaching a chosen location (also see Kerrén et al., 2018). A pre-stimulus increase in parietal theta has been demonstrated to indicate successful encoding and successful recall (Ekstrom et al., 2017; Guderian et al., 2009; Quintana & Fuster, 1993). Alternatively, it may be argued this increase could reflect rapid estimation of goal distance and direction calculation, as has been suggested by other researchers (Liang et al., 2021). However, we believe that the task-related shifts in theta power support the theory that human theta is specific to the encoding/learning, rather than any sensorimotor integration. Thus, the learning groups' larger theta power may reflect a shift to a cortically effortful recall of spatial information, possibly in response to landmarks or route planning at the beginning of trials (Jaiswal et al., 2010).

The non-learning group, which did not have a specific goal, and instead showed significantly *increased*

theta within-group differences at 5–6 Hz during route initiation. This is consistent with previous research indicating that the parietal cortex, which covers the parahippocampal and retrosplenial regions, is involved in the encoding of spatial information and memory retrieval (Heimrath et al., 2012; Rodriguez, 2010; Sestieri et al., 2017). This ongoing increase may indicate that the non-learning group was attempting to encode their environment or recalling and combining features and/or previously explored places in order to develop new search strategies, which may place greater demand on theta rhythms (Caplan & Glaholt, 2007; Chrastil et al., 2022; Kahana et al., 1999; Kaplan et al., 2012). These findings align with previous research in the field that has linked theta *increases* to exploratory behaviour and suggests that theta may play a larger role in the encoding of spatial information, rather than movement speed or integration of sensory information, which we controlled for here (Buzsáki, 2005; Buzsáki & Moser, 2013; Goyal et al., 2020; Lega et al., 2012; Lin et al., 2017, 2022).

It is important to note that we did not control for frustration or motivation in the non-learning group, which could be responsible for some of the EEG dynamics during the task. However, in general, there is increased (Figure 4a) or stabilised (Figure 4b) task-related theta in the non-learning group, particularly in frontal regions. The groups' alpha power also seems relatively great throughout the task. Therefore, the group may well have been engaged, as increased theta and alpha power have been shown to be related to increased cognitive load and attention (Chattopadhyay et al., 2021; Klimesch, 1999; Mussel et al., 2016). This needs to be further explored, perhaps using more electrode sites and/or frequency bands. Moreover, using 32-channel *scalp* EEG does place limits on the types of analysis we can run. We could also not perform accurate source analysis and reconstruction to explore this possible communication or synchrony between the parietal cortex, hippocampus, retrosplenial cortex and frontal regions (Ekstrom et al., 2017).

Most studies with humans use iEEG when examining virtual navigation, with some demonstrating sensorimotor-related increases in theta (Bohbot et al., 2017; Bush et al., 2017; Cornwell et al., 2012; Ekstrom et al., 2005; Epstein, 2008; Kunz et al., 2019; Lega et al., 2012; Miller et al., 2018). Virtual tasks, including NavWell, do not involve any physical traversal during navigation. The addition of this, alongside scalp EEG, may facilitate more accurate or ecologically valid sensorimotor integration and should be considered in future research investigating theta dynamics (see Bohbot et al., 2017), and see Griffiths et al. (2016).

Focusing on only two of three phases of navigation suggested by Nyberg et al. (2022) may have limited our understanding of the complete dynamics of theta. However, there is a good reason for our selection, as the start and the end phases allowed us to have a standardised time epoch that was shared by all participants. Escape latencies would vary between individuals during travel, but every participant started and ended the task. Additionally, using the average trial time to time-match our non-learning group was perhaps not the most effective method. Instead, matching participants on an individual level as opposed to a group level may have resulted in more accurate understanding of the non-learning groups searching behaviour (see Commins et al., 2022 for the advantages of this). In line with our hypothesis-driven task design and analysis approach, we limit our discussion to the cortical sites and frequency ranges that were initially hypothesised. We recognise the importance of maintaining the integrity of our hypothesis-driven investigation. However, it is noteworthy that our time-frequency explorations revealed changes in other frequency bands within our ROIs that were not initially anticipated. Although these findings are out of the scope of our current discussion, we briefly acknowledge their potential significance to understanding the broader dynamics associated with spatial learning below.

Furthermore, the low number of trials used to estimate oscillatory activity may have reduced the quality of data used to draw some of the above conclusions. However, human spatial learning is a fast and dynamic cognitive process. The attempt to capture this process and the underlying neural correlates is a current work in progress in the literature (see Du et al., 2023). However, averaged time-frequency plots for each participant help improve the signal-to-noise ratio and stability of the oscillatory measures compared to single trial analysis (Cohen, 2014). Morales and Bowers (2022) also claim that fewer trials are needed for reliably estimated oscillatory effects than would be for ERPs. As the number (and age) of participants increases, particularly for between-group analyses, fewer trials are required to produce reliable and less variable oscillatory estimates (Boudewyn et al., 2018; Morales & Bowers, 2022). This is not the first attempt to capture the spatial learning and navigation process using few trials combined with EEG (e.g., 3 trials per environment in the *Audiomaze*: Miyakoshi et al., 2021). Nevertheless, we have taken careful consideration of our limitations, by performing an a priori power calculation to provide a sufficient participant number to produce statistically reliable results (which is rarely done in EEG studies; of 100 reviewed, not a single study reported a sample size calculation; see Larson & Carbine, 2017).

Furthermore, we corrected for multiple comparisons using FDR correction and utilised non-parametric permutation *t* tests so that our data are not relying on asymptotic assumptions of normality as well as only reporting findings we previously hypothesised. Nevertheless, the results here should be interpreted carefully until further work can investigate the fluidity of navigational behaviour and spatial learning.

4.1 | Interactions with other frequency bands & the default mode network (DMN)

Our time-frequency analysis from 1 to 30 Hz reveals several intriguing dynamics in frequency bands that were not initially hypothesised. Specifically, we observed noticeable differences between the groups at Alpha (8–12 Hz) and Beta (13–29 Hz). Reduced alpha activity, particularly at the goal approach, could be attributed to two possible phenomena. Firstly, it may represent cortical activation and/or a release of attentional inhibition (Klimesch, 2012; Peylo et al., 2021). Alternatively, the reduction could be observed in the mu rhythm, which falls between alpha and beta frequencies (12–15 Hz). Power decreases within this rhythm have been associated with goal-directed sensorimotor integration and intention (Harris et al., 2017; Pereira et al., 2017). Therefore, it is possible that the substantial reduction in the 12- to 15-Hz range could be linked to the learning group's execution of goal-directed sensorimotor integration and movement. This is particularly prominent in the parietal midline as well as the navigation phase containing a goal-approach behaviour.

Furthermore, our results may also have implications for the emerging literature surrounding the involvement of the DMN in goal-directed behaviours. The observed theta-alpha oscillatory reductions primarily focused on the parietal midline and adjacent areas, which are known to encompass the DMN (Smallwood et al., 2021). Decreased oscillatory activity is associated DMN suppression (Burgess & Gruzelier, 1997; Chen et al., 2008; Scheeringa et al., 2008; Smallwood et al., 2021). Considering that greater reductions were found in the group that are actively navigating towards a goal, these results could support the idea that successful learning suppresses DMN activation. However, it is important to note that the non-learning group was also technically performing a goal-directed task, and although they demonstrate greater overall activation during the same navigation phase, there is insufficient evidence to conclude that their DMN is engaged. Further adjustments to the experimental paradigm would be required to investigate this phenomenon accurately. Additionally, our results would not entirely align with the existing spatial memory and DMN literature (Patai & Spiers, 2021; Pezzulo et al., 2019; Spiers & Maguire, 2008).

5 | CONCLUSIONS

This study found that human theta oscillations (4–8 Hz) are involved in spatial learning in a virtual environment. The non-learning group, who navigated without a goal, showed increased low-frequency (5–6 Hz) theta power in the route-initiation/start phase, indicating that increased theta oscillations play a larger role in encoding spatial information. The learning group, who learned to navigate to a goal location, showed decreased theta power in the same phase, including when the goal location had been learned. This suggests that as the task becomes more familiar, the integration of theta power in the learning process becomes reduced, particularly during route initiation and initial orientation. Active learning, however, leads to some task-dependent increases in theta power. These findings give us a deeper understanding of the neural mechanisms involved in spatial learning in virtual environments and the dynamics of theta oscillations in this process. Our results support previous research that suggests theta oscillations play a role in learning-related exploration and spatial encoding. Our findings also provide preliminary evidence of a reduction in neural resources or shift in theta activity from an encoding role to a more direct-attention and on-demand retrieval role when learning has taken place. However, further research is needed to fully investigate its link to the neural efficiency hypothesis. Our interpretation of this evidence during spatial learning in a virtual water maze is novel, and future studies should be carefully controlled to confirm our findings.

AUTHOR CONTRIBUTIONS

Conor Thornberry: Conceptualization; formal analysis; investigation; methodology; visualization; writing—original draft. **Michelle Caffrey:** Investigation; resources; writing—review and editing. **Sean Commins:** Conceptualization; methodology; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors report no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data used for statistical analyses, pre-processing scripts and the *R* code used to run power analyses and create plots have been made available via OSF (https://osf.io/vgwcd/).

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