

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

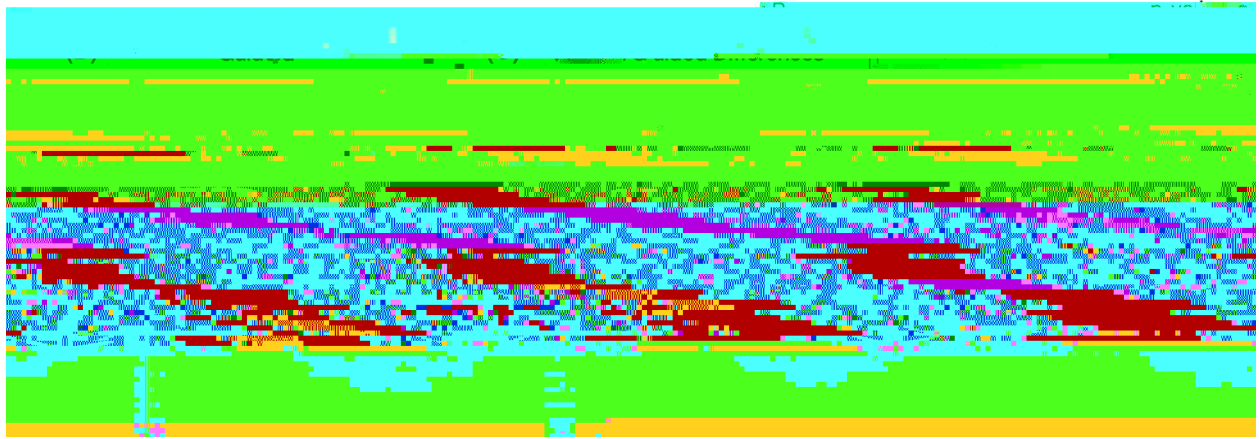


Fig. 2. Theta power for the (A) Free and (B) Guided group just prior to arrival at the choice point during exploration. Theta power across all chan25 0 TD .0007 Tc (M.)Tj

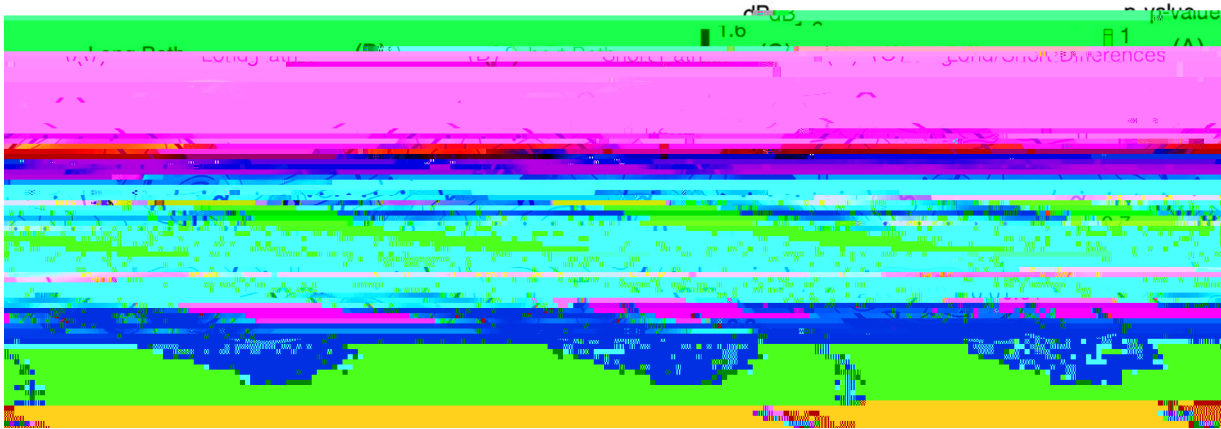


Fig. 7. Theta power for long (A) vs. short (B) path length distances during test. Theta power across all channels from 0-500 ms. Black indicates analyzed channels in left parietal regions. Color scale: decibel change from baseline. (C) Differences between short and long paths. Theta power was marginally 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 (Kropf 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; Hsieh & Ranganath, 2014).

We found increased theta oscillations in midfrontal for navigators. /F2 1 Tf 6.3761 0 0 6.3761 143.931897431345 7m .0Tc ()Tj /F1 1 Tf 7.9701 0 0 7.9701 63148

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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