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Hexagonal modulation of theta rhythmic attentional sampling of visual space

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Abstract

Spatial attention improves visual perception by selecting behaviorally relevant sensory signals. Traditionally, attention has been conceptualized as a static spotlight, while recent evidence posited that attention operates as a moving spotlight that samples visual space sequentially in discrete snapshots that are clocked by theta rhythms (~3-8 Hz). While theta rhythmic attentional sampling has mainly been observed in fronto-parietal and occipital areas, theta oscillations also hallmark entorhinal-hippocampal grid-cell networks, which encode physical space in hexagonal patterns that guide overt exploration and navigation. We hypothesized that visual attention might rely on the same underlying principles and sample visual space in a hexagonal, grid-like configuration. To test this hypothesis, twenty participants (10 females and 10 males) performed a cue-guided attention task that probed behavioral performance as a function of space and time. Reaction times were assessed as a function of spatial location and varying cue-target intervals, which displayed spatially-structured theta rhythms. Specifically, higher theta power occurred at spatial locations that were aligned to multiples of 60°, consistent with an underlying hexagonal organization. Participants that exhibited stronger hexagonal sampling relied less on the spatial cue to guide their attentional allocation. In sum, these findings suggest that covert visual attention is organized in a hexagonal pattern that might be consistent with the grid-like structure known from the entorhinal-hippocampal system and highlight that theta rhythms could reflect a common organizing principle for spatial cognition.

Significance Statement

Attention prioritizes sensory inputs to optimize behavior. But how does attention sample the environment in space and time? Here, we demonstrate that attentional sampling of visual space is not uniform, but might preferentially explore locations that are oriented along a hexagonal pattern, reminiscent of the spatial configuration of entorhinal-hippocampal grid cells. Moreover, covert attentional sampling exhibited oscillatory theta signatures (3-8 Hz). In sum, these findings suggest that spatial attention and navigation may share a common organizing principle, and indicate that theta rhythms may orchestrate sampling behaviors in space and time as a unifying principle underlying spatial cognition.

Introduction

Spatial attention prioritizes and selects behaviorally-relevant sensory signals to optimize visual perception that guides goal-directed behavior (Buschman & Kastner, 2015). Traditionally, spatial attention has been conceptualized as a *static* spotlight that constantly amplifies visual input at a cued location. However, more recent theories suggest that attention might operate as a *moving* spotlight that samples and explores visual space sequentially (Fiebelkorn et al., 2013; Landau & Fries, 2012; VanRullen, 2016). Critically, the sequential sampling of visual space does not occur randomly but is clocked by rhythmic brain activity. Converging evidence from behavior, (non-)invasive human and non-human primate electrophysiology studies jointly suggests that theta rhythms in the frontoparietal attention network and visual cortex orchestrate the rhythmic sampling of visual space (Fiebelkorn et al., 2018; Helfrich et al., 2018; Kienitz et al., 2018). Specifically, it had been proposed that alternating phases of theta oscillations provide distinct time windows to sample a spatial location and then shift attention to the next relevant location; hence, explaining why attention-guided visual perception is not static over time, but fluctuates as a function of the endogenous theta rhythms (Fiebelkorn & Kastner, 2019; Kienitz et al., 2022). However, theta rhythmic behaviors are not confined to visual attention, but have been described in a variety of other sensory and cognitive modalities (Canolty & Knight, 2010; Colgin, 2013; Fries, 2023; Herweg et al., 2020; Lisman & Jensen, 2013). Theta oscillations are the most prominent electrophysiological signatures in the entorhinal-hippocampal system (Buzsáki, 2002, 2005) where their activity coordinates the firing of grid and place cells (Colgin, 2013; Moser et al., 2008). It has been firmly established that these cells represent the surrounding physical space and define a grid-like hexagonal pattern that facilitates orientation and navigation (Hafting et al., 2005; Moser et al., 2008). Similar to the theta rhythmic attentional sampling of the visual space, hippocampal theta sweeps might explore the surrounding physical space to identify the next navigational target to plan future movement trajectories (Vollan et al., 2024). In humans, such grid-like coding is typically inferred from its hexadirectional signature—a six-fold modulation of a dependent measure as a function of direction, specific to 60° rather than other geometries (Constantinescu et al., 2016; Doeller et al., 2010).

Here we hypothesized that theta rhythmic attentional sampling might also sample space non-uniformly and preferentially explore locations that are oriented along an underlying spatial grid-like pattern that resembles the hippocampal-entorhinal organization. Such a sampling process could either entail a rhythmic modulation of the mean RT or the RT variance over time. However, these do not constitute mutually exclusive scenarios and might overlap. Given the

high degree of similarity between theta-dependent behaviors in covert and overt exploration of space, we specifically tested if attention samples the visual environment in a grid-like, hexagonally-oriented pattern.

Materials and Methods

Participants

20 adults (26.15 ± 4.07 years; mean $\pm$ SD; 10 females) participated in the study. The study and analyses were approved by the IRB board at the University Medical Center Tübingen (protocol number 049/2020BO2) in accordance with the Declaration of Helsinki. All participants provided informed written consent to participate in the study.

Experimental design and procedures

Each trial began with the presentation of a central fixation point (0.7° visual angle) displayed for 500 ms to maintain participants' visual attention. Following the fixation, a central bar, subtending 5° of visual angle, appeared for another 500 ms. The orientation of the bar was randomly chosen from 12 primary directions, equally spaced around a circle (e.g., 0° , 30° , 60° , ..., 330°). After the bar presentation, a brief peripheral spatial cue, 0.7° in visual angle, was displayed for 100 ms to indicate the location where the target was most likely to appear (cue-validity of 90%). After the cue, a variable cue-target interval (500–1500 ms; CTI) was introduced. This interval was divided into 25 equal bins, with the target appearing randomly in one of these bins within each trial. The target, which subtended 0.7° of visual angle, was presented as a brief flash lasting only 17 ms, which corresponds to one screen presentation at 60 Hz. Participants were instructed to respond as quickly as possible to the target by pressing a designated key, with a response deadline of 1 second after target presentation. Responses made prematurely during the cue-target interval were recorded but marked as invalid. On 5% of trials (catch trials), no target was presented to ensure participants remained attentive to the task. Thus, 10% of the trials were invalidly cued, 90% were validly (85% with a target, 5% catch trials).

The experiment was conducted over two sessions on separate days, with each session comprising 1,500 trials, divided into 15 blocks of 100 trials each. Thus, each subject performed

3,000 trials, which is a substantially larger number of trials as in previous experiments (Fiebelkorn et al., 2013; Helfrich et al., 2018; Landau & Fries, 2012).

Each of the 12 bar orientations was presented equally across trials, ensuring balanced sampling. Stimuli were generated using MATLAB (The MathWorks, Natick, MA) and the Psychophysics Toolbox and were presented on a calibrated display at an approximate viewing distance of 70 cm. Visual angles were computed based on screen dimensions and viewing distance.

Eye movements were monitored using an SR EyeLink 1000 Plus with binocular tracking.

A synthetic hexagonal grid pattern was generated for visualization purposes (Figure 1B, left panel) by summing three cosine components arranged at 60° offsets, producing a canonical hexagonal lattice. The pattern was normalized, spatially modulated by random amplitude variations, and combined with Gaussian noise, followed by Gaussian smoothing to yield smoothly varying grid-like blobs. To approximate a gradual transition into background activity, an exponential radial fade was applied before visualization.

Cue Validity Effect on Reaction Times

To evaluate the influence of cue validity on reaction times, behavioral data were preprocessed to exclude outliers identified using Cook's distance (Cook's distance threshold of $2.5 \times$ the mean Cook's distance). Reaction times for valid (cue predicted target location) and invalid (cue did not predict target location) trials were averaged across participants. A Wilcoxon signed-rank test was employed to determine statistical differences between valid and invalid conditions, testing the hypothesis that valid cues yield faster reaction times.

Reaction Time Across Target Angles

The relationship between reaction times and target angles was assessed by grouping trials based on bar orientation angles. For each participant, outliers (determined using Cook's distance) and trials with invalid cues were excluded. Reaction times were averaged for each angle, including the angle's counter-angle (e.g., 0° and 180°). A repeated-measures analysis of variance (RM-ANOVA) tested whether reaction times differed significantly across target angles.

Extraction of the behavioral reaction time trace

To investigate temporal dynamics of attentional sampling, reaction time traces were computed for each participant across experimental conditions. Outliers were identified using Cook's distance and removed alongside trials with invalid cues. For each participant, trials were grouped based on bar orientation angles, where each angle was paired with its counter-angle (e.g., 0° and 180°). Time-resolved behavioral traces were derived using a 50 ms sliding window moving in 1 ms steps, smoothed with a 25 ms window to interpolate any remaining values that resulted from the limited temporal sampling, and were aligned to the cue-target interval (Helfrich et al., 2018; Raposo et al., 2023). The resulting traces were demeaned and detrended (second-order polynomial; variance explained: median $R^2 = 0.76$ vs. 0.95 for a first- vs. second-order fit, $p < 0.001$, Wilcoxon signed-rank test), and the time axis was converted to seconds for subsequent analyses (Fiebelkorn et al., 2013; Helfrich et al., 2018; Kienitz et al., 2018, 2022; Landau et al., 2015; Landau & Fries, 2012). Condition-specific traces were computed for each bar orientation.

Analyses were performed on raw reaction times. Control analyses confirmed that z-scoring reaction times within each session left the aligned-versus-non-aligned modulation unchanged (Cohen's $d = 0.28$ vs. 0.24 for raw RTs), whereas log-transformation preserved the direction of the effect but reduced its magnitude ($d = 0.15$), consistent with the compression of longer reaction times that may carry part of the rhythmic variance.

Spectral analysis of reaction time traces

To explore rhythmic components in reaction time data, behavioral traces were transformed into the frequency domain (Fiebelkorn et al., 2013; Landau & Fries, 2012). To this end, we applied the Fast Fourier Transform (FFT) on preprocessed RT traces from all participants and conditions to compute power spectra for each condition and participant (Fiebelkorn et al., 2013; Helfrich et al., 2018; Kienitz et al., 2018, 2022; Landau et al., 2015; Landau & Fries, 2012). Power spectra were calculated separately for all bar orientations and aggregated across trials. To correct for the aperiodic component in the power spectra, a first-degree polynomial function was fitted to the frequency distribution of each spectrum, and the 1/f fit subtracted to remove background activity (Donoghue et al., 2020, 2021). Hence, power values are expressed as deviations relative to the estimated broadband background. In this framework, a test against zero indicates that the deviation in a given frequency range does or does not reliably exceed the 1/f distribution. Following spectral decomposition, grand-averaged power spectra were computed for each condition.

To investigate theta rhythmic dynamics of attentional sampling, peak frequencies and corresponding power values were extracted from the frequency-domain reaction time data. For each orientation, local maxima in the power spectrum were identified within the theta range (2.5 – 8 Hz) to determine the peak frequency and its associated power (Helfrich et al., 2018). A local maximum was found for all subject $\times$ condition spectra. To ensure that ϕ reflects orientation-specific modulation rather than an overall gradient in power, theta power across the six orientations was linearly detrended before identifying ϕ . Note that this detrending operates across orientations and is thus distinct from the 1/f correction, which removes the aperiodic background across frequency within each power spectrum.

Non-uniformity of power values across angles was quantified using the Kullback–Leibler (KL) divergence between each subject's observed power distribution and a uniform reference distribution. Statistical significance was assessed using a single-trial permutation test: for each of 10,000 permutations, orientation labels were randomly permuted across trials (preserving the number of trials per orientation), the orientation-specific reaction-time traces and power spectra were reconstructed, and the resulting KL divergence was added to a null distribution. Observed KL divergences were then compared against this null distribution using a right-tailed test to determine whether spatial structure exceeded that expected by chance. As the aligned/non-aligned assignment is periodic every 60° and the preferred orientation varies across participants, the group-level result is independent of the exact range of shift offsets used.

Each participant's preferred orientation was defined as the angle with the highest detrended theta power (ϕ). Power and frequency values for all other orientations were then realigned relative to ϕ . Mean peak frequencies were calculated for each bar orientation, and a one-way analysis of variance (ANOVA) was conducted to test whether peak frequencies differed significantly across orientations.

ϕ was estimated empirically following standard practice in the field (Constantinescu et al., 2016; Doeller et al., 2010) and excluded from all further testing. As ϕ is individual and cannot be transferred across participants, nor reliably estimated on a within-participant data split, the permutation test described above accounts for the dependence introduced by alignment and helps to separate estimation and testing.

For example, if the identified bin was the 60° (preferred) bin, then we aligned the remainder of the bins relative to that (90° - 120° - 150° - 0° - 30°), which reflected a sequence of bins that were binarized (non-preferred – preferred – non-preferred ...) relative to the 'preferred' bin (Busch et al., 2009; Busch & VanRullen, 2010; Doeller et al., 2010; Nau, Navarro Schröder, et al., 2018). After alignment to the largest theta peak, we then removed the 'preferred' bin

from the subsequent statistical analysis as this selection step biases the results (i.e., the preferred bin will necessarily have the largest theta peak) (Busch et al., 2009; Busch & VanRullen, 2010; Helfrich et al., 2019).

To examine the spatial organization of theta rhythmicity in attentional sampling, power spectra were compared between bar orientations aligned and non-aligned to ϕ . Aligned and non-aligned angles were grouped according to a 6-fold modulation pattern (spaced by 60°), reflecting the hypothesized hexagonal organization of attentional sampling. For each participant, power spectra were averaged across aligned and non-aligned orientations, respectively. The preferred angle ϕ was excluded to reduce bias and number of angles was matched to avoid sampling bias. Power differences between aligned and non-aligned orientations were calculated around the prominent peak in theta frequency range (4–6 Hz, **Figure 3A**). Control analyses examined the specificity of the observed 6-fold modulation by comparing it with a 4-fold modulation pattern (spaced by 90°).

Relative to each participant's preferred orientation ϕ (excluded from testing; example for $\phi = 0^\circ$), the six-fold analysis contrasted aligned (60° , 120°) with non-aligned (90° , 150°) orientations, matching group size (30° not used to avoid sampling bias). The four-fold analysis contrasted the single aligned orientation (90°) with the mean of the non-aligned 30° and 60° orientations (a "virtual" 45° reference); it therefore comprises only one aligned bin and is inherently noisier.

A Wilcoxon signed-rank test was used to assess statistical differences in theta power between aligned and non-aligned conditions.

To test the hexagonal modulation against chance while controlling for the data-driven alignment, we used a circular-shift permutation approach (10,000 permutations). In each permutation, the ϕ -aligned orientation-wise power profile of each participant was circularly shifted by a random, non-zero offset (one to five bins), so that all six orientations were retained but their alignment to ϕ was disrupted, while the angular spacing and spectral content of each orientation were preserved. The aligned-minus-non-aligned theta-power difference was then recomputed using the identical peak-bin exclusion and aligned/non-aligned definitions as in the observed analysis. The preferred orientation ϕ was not re-estimated across permutations, as it corresponds to the maximum of each participant's power distribution and is invariant to a reordering. The observed modulation was compared against the resulting null distribution using a right-tailed test.

To examine how hexagonal modulation relates to attentional performance, we computed the attention modulation index (Fries et al., 2001), which quantifies the behavioral benefit of valid versus invalid cues. The attention index was calculated as:

$$attention\ index = \frac{RT_{invalid} - RT_{valid}}{RT_{invalid} + RT_{valid}}$$

where RT_{valid} and $RT_{invalid}$ represent the mean reaction times (RTs) for valid and invalid cues, respectively. A higher attention index reflects stronger attentional benefits, as it corresponds to a greater reduction in RTs for validly cued trials relative to invalidly cued trials. Hexagonal modulation was defined as the difference in theta power between aligned and non-aligned orientations (in a 6-fold modulation pattern) in the 4-6 Hz frequency range (cf. **Figure 3A**). We applied robust linear regression to assess the relationship between these two measures, identifying and excluding outliers using Cook's distance (2 participants).

Eye-tracking analysis

The eye data were analyzed with RStudio (v. 2025.05.1+513) and Matlab. We extracted the x- and y-position time series from the continuous signal per eye and averaged both eyes into a composite signal. We epoched the data relative to trial start (-0.5 to +4s). We then flagged all trials that contained artifacts, eye-blinks or when the participant broke fixation during the cue-target-interval (cue onset at +1.5s). Next, we performed saccade detection during the cue-target interval to flag trials where participants made saccades that were larger than 2° visual angle from the screen midpoint using established algorithms (for detailed methods, see (Engbert & Kliegl, 2003; Nyström & Holmqvist, 2010; Otero-Millan et al., 2014; Pastukhov, 2023)). Our conservative criterion was that at least two out of the three detection algorithms had to agree on saccade occurrence. Furthermore, the baseline criteria were set such that the minimal duration of a saccade had to be at least 10 ms, there had to be at least 20 ms between subsequent saccades, and the velocity function used to detect saccades utilized the difference method of the Engbert & Kliegl (2003) algorithm.

We statistically tested whether fixation before target onset changed systematically as a function of target orientation angle. Thus, on a per subject level, we performed circular-linear correlations between target orientation and x- and y-positions (Berens, 2009). We repeated

295 the correlations 1000x after randomly shuffling the condition labels (orientations) to obtain a
296 surrogate distribution per subject for the x- and y-dimension. We z-scored the observed
297 correlation value relative to the surrogate distribution to obtain a metric that indicates how
298 strongly the fixation position along the x- and y-axis varied as a function of the target position.

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Results

To probe whether the rhythmic attentional sampling of visual space follows a hexagonal modulation pattern, twenty participants performed a variant of a classic spatial attention task (Buschman & Kastner, 2015; Posner et al., 1980). On every trial, participants were presented with a bar that was oriented in one of six different directions (0-150° in steps of 30°; **Figure 1A**). After a delay, a spatial cue (90% validity) indicated the likely target position. The target stimulus was presented above perceptual threshold after a variable cue-target-interval (500-1500 ms). We employed eye-tracking to monitor eye position and ensure fixation. This design enabled resolving reaction times of target detection performance as a function of space and time. We predicted a hexagonal modulation of the resulting theta rhythmic sampling behavior with stronger sampling along the preferred cardinal axis φ as well as at directions φ plus integer multiples of 60° (**Figure 1B**). In contrast, we expected lower theta rhythmic sampling along non-aligned orientations, e.g., $\varphi + 30^\circ$.

As hypothesized, we observed a behavioral benefit at the cued location with significantly faster reaction times for cued than uncued targets ($p = 0.03$, Wilcoxon ranked sum test; 294.9 ± 8.1 ms vs. 307.9 ± 7.3 ms, mean $\pm$ SEM, **Figure S1**). Grand-average reaction times did not differ significantly across the six different bar orientations ($p = 0.99$, RM-ANOVA, **Figure S1**). To resolve behavior as a function of space and time, we employed a moving window approach (window size: 50ms, step size: 1ms) to obtain a time-resolved estimate of reaction times. This approach was repeated for every bar orientation separately (**Figure 1C**). Subsequently, time-resolved behavioral estimates were spectrally decomposed after applying a Fast Fourier Transform (FFT). To assess theta power as a function of bar orientation, we initially detected the individual theta peak in a broad theta range from 2.5-8 Hz on the 1/f-corrected power spectra for all bar directions separately (**Figure 1D**). We observed an average theta peak frequency of 4.6 ± 0.1 Hz across all participants (mean $\pm$ SEM). The peak frequency did not differ significantly across the different bar orientations ($p = 0.11$, one-way ANOVA). Thus, for subsequent analyses, we employed a narrower window (4-6 Hz). To demonstrate frequency specificity, we performed the same analysis in the alpha-range (8-12 Hz), but failed to observe a distinct peak that was modulated as a function of hexagonal alignment (**Figure S2**).

Our main hypothesis predicted that theta power should be modulated as a function of the precise bar orientation. Given that the preferred direction φ (i.e. direction with maximum theta power) differed across participants, we re-aligned the remaining orientations with respect to the preferred direction φ for each participant (analogous to (Doeller et al., 2010; Nau, Navarro Schröder, et al., 2018; Staudigl et al., 2018)). Relative to φ , the remaining orientations

were grouped into *aligned* (φ plus multiples of 60°) and *non-aligned* directions. Note that we excluded φ from all subsequent analyses of *aligned* directions as the highest theta power defined φ and therefore, would have biased the subsequent results. We then collapsed behavioral estimates along the aligned and non-aligned orientations (**Figure 2A**).

Single subject observations implied a non-uniform distribution of theta peak power with higher power at φ plus multiples of 60° (**Figure 2B/C**), which was further substantiated at group level as outlined below (**Figure 3**).

We also ensured that participants fixated and that fixation did not systematically change as a function of the stimulus presentation angle (**Figure S4**).

To quantify this observation at the group level, we repeated this analysis and alignment procedure for all participants. Across subjects, power values were non-uniformly distributed across angles (right-tailed permutation test, $p = 0.001$). In the frequency domain, a theta peak for both the *aligned* and *non-aligned* conditions was observed (**Figure 3A**). The theta peak was still evident when controlling for the eye position (**Figure S4**). Yet, theta peak power significantly differed between both conditions ($p = 0.030$, Wilcoxon signed rank test; **Figure 3B**), while peak frequency did not differ between both conditions ($p = 0.856$, Wilcoxon signed rank test). This modulation was comparable in effect size when using a fixed theta-band definition as a control (4–6 Hz, Cohen's $d = 0.22$ vs. 0.24 for peak frequency power vs. average theta-band power, respectively). The effect was likewise stable across moving-window widths (25–100 ms), with a comparable effect size throughout (Cohen's $d = 0.30, 0.24, 0.22, 0.28$), reaching statistical significance for the shorter windows (25 ms: $p = 0.027$; 50 ms: $p = 0.008$) and exhibiting the same direction at the longer windows (75 ms: $p = 0.056$; 100 ms: $p = 0.11$), consistent with the reduced sensitivity expected from stronger temporal smoothing. The theta power modulation was statistically significantly different from the $1/f$ -component at the conventional 5% threshold for the aligned ($p = 0.021$) condition, but not for the non-aligned condition ($p = 0.057$). However, the statistically non-significant result for the non-aligned condition does not signal the absence of a theta rhythmic modulation. Conceptually, it is conceivable that theta rhythms also hallmark sampling at non-preferred locations (Fiebelkorn et al., 2013). Here, the critical observation is that the behavioral theta sampling in the aligned and non-aligned conditions differs. Thus, these results are in accordance with the idea that theta rhythmic sampling explored visual space non-uniformly with a preference for hexagonally oriented spatial locations.

As a control, we further tested if the observed effects were specific to a hexagonal (6-fold) modulation. Hence, we repeated the analysis on surrogate data that assumed a 4-fold modulation (**Figure 3C** and **Figure S3; Methods**). Note that the aligned condition in the 4-fold analysis comprises a single orientation bin, whereas the 6-fold aligned condition averages over two. The 4-fold aligned analysis is therefore based on fewer trials, with the variance therefore likely differing between the two analyses. We observed a significantly stronger modulation in the 6-fold than 4-fold scenario ($p = 0.043$, Wilcoxon signed rank test). Critically, a significant modulation (as compared to 0) was observed for a 6-fold configuration ($p = 0.008$), but not for the 4-fold configuration ($p = 0.977$). Lastly, we implemented a permutation-based null model using random circular shifts of the orientation grid within each participant. This procedure preserves the spectral and angular structure of the data while disrupting the true hexagonal alignment. The circular-shift test thus provides a direct assessment of hexagonal structure, evaluating the 6-fold modulation against random alignment independently of other n -fold modulations. Across 10,000 permutations, the observed aligned-minus-non-aligned theta-band modulation exceeded the null distribution significantly (right-tailed permutation test, $p = 0.0031$), further confirming that the hexagonal modulation in the theta band is significantly stronger than expected under random alignment.

To further illustrate the spatial structure of theta modulation, we visualized peak theta power across all angular bins and subjects after alignment to each participant's preferred direction. This analysis demonstrated a 6-fold modulation pattern across the group (see **Figure S3**).

In contrast to this power modulation between aligned and non-aligned conditions, we did not find any significant phase difference ($p = 0.87$, Rayleigh test).

Finally, in an exploratory analysis, we assessed whether hexagonal modulation mediates a behavioral advantage during allocation of spatial attention. Given that the hexagonal modulation provides a spatial framework for integrating information across visual space, we tested how individual hexagonal modulation of theta rhythmic sampling relates to attentional benefits of the spatial cue. While stronger sampling might be expected to amplify attentional benefits, it is also plausible that broader spatial exploration (in a hexagonal manner) could dilute the focal effects of external cues. The latter would be consistent with prior work in non-human primates showing reduced attentional effects during periods of stronger theta rhythmicity (Spyropoulos et al., 2018). Hence, we quantified the attention index as an established measure of attentional allocation (Fries et al., 2001) and assessed its relationship with the hexagonal modulation (difference in theta power between aligned and non-aligned

orientations, cf. **Figure 3A**). Robust linear regression revealed a significant *negative* association between the attention index and hexagonal modulation (**Figure 4**, $\beta = -7.76$, $p = 0.0379$, $R^2 = 0.24$; linear correlation $r = -0.49$), indicating that stronger hexagonal modulation is linked to a less pronounced benefit of spatial cue. This relationship was observed across participants. Within participants, by contrast, the cueing benefit did not differ between aligned and non-aligned orientations (attention index: 0.026 vs. 0.028, $p = 0.33$; raw benefit: 15.4 vs. 16.9 ms, $p = 0.39$; Wilcoxon signed-rank tests), indicating that the association reflects stable individual differences in sampling strategy rather than a within-participant modulation of cue reliance across orientations.

Collectively, these results suggest that attention-guided theta-rhythmic visual target detection preferentially operates along a possibly underlying hexagonal configuration that is oriented in 60° steps. This observation is reminiscent of an underlying grid-like layout akin to hippocampal place field orientations. Interestingly, rather than enhancing attentional benefits, stronger hexagonal modulation was associated with a reduced cueing effect, suggesting that individuals showing strong hexagonal sampling may sample visual space more extensively, and hence, rely less on a spatial attention cue.

Discussion

Here we demonstrate that *covert* attentional sampling of visual space is not uniformly organized, but follows an underlying hexagonal structure, reminiscent of the structure that defines the *overt* exploration of physical space known from entorhinal-hippocampal spatial coding. Analogous to the theta-dependent exploration of the environment, we observed theta rhythmic attentional sampling of visual space that was differentially modulated across different orientations adhering to a 6-fold hexagonal structure. These results demonstrate how attention might sample the visual environment in space and time and provide a perspective how covert and overt behaviors might be linked through theta rhythmic interactions.

Theta rhythms and attentional sampling

Theta oscillations have been widely implicated in rhythmic attentional sampling, facilitating the sequential covert exploration of visual space (Fiebelkorn et al., 2013; Landau & Fries, 2012). This phenomenon spans multiple scales, from localized oscillatory activity (Kienitz et al., 2018) to large-scale network interactions in non-human primates and humans (Fiebelkorn et al., 2018; Helfrich et al., 2018). Consistent with this body of evidence, our results revealed theta rhythmicity in behavioral traces, evident as spectral peaks in the theta range in 1/f-corrected power spectra.

In the case of overt spatial exploration, it had been shown that entorhinal theta oscillations encode space in hexagonal pattern (Maidenbaum et al., 2018). These findings were recently extended by reports that overt exploration of *visual* space also show hexagonal modulations in humans (Staudigl et al., 2018).—Hence, we predicted that theta oscillations might subserve a domain-general organizing principle of spatial and temporal cognition. In line with this prediction, our results revealed a non-uniform, hexagonal modulation of attentional sampling. This modulation of attentional sampling—a covert and cue-guided version of spatial exploration—is reminiscent of mechanisms that govern *overt* spatial exploration.

While spatial exploration has been studied in primates (Jutras et al., 2013; Killian et al., 2012) and humans (Doeller et al., 2010; Nau, Navarro Schröder, et al., 2018; Staudigl et al., 2018), much of the foundational work has been conducted in rodents, where place and grid cells in the entorhinal-hippocampal system orchestrate navigational processes that are clocked by theta rhythms (Moser et al., 2008; O'Keefe, 1976). Moreover, recent studies in non-human primates and humans have demonstrated that grid-like signals in the entorhinal cortex can be triggered by covert spatial attention, independent of physical movement (Giari et al., 2023; Wilming et al., 2018). Our findings further substantiate this line of inquiry and suggest that

rhythmic attentional sampling – a core principle of spatial attention – is modulated by an underlying hexagonal structure, potentially relying on the same organizing principles that govern spatial exploration and navigation. Mechanistically, we hypothesize that sampling along the grid axes would recruit grid cells and theta modulation more strongly than off-axis sampling, manifesting as a stronger hexagonal sampling pattern in attentional behavior. In addition, our findings further imply that the observed hexagonal modulation is not a mere byproduct of rhythmic attentional sampling but may play an active role in shaping behavior. However, rather than enhancing attentional cueing benefits, stronger hexagonal modulation was associated with a reduced cueing effect, suggesting that individuals with more pronounced *intrinsic* hexagonal sampling may rely less on *extrinsic* spatial cues. This is in line with previous reports in non-human primates that demonstrated reduced neural theta oscillations in the visual cortex during focused attention (Spyropoulos et al., 2018). This raises the possibility that hexagonal modulation may reflect an intrinsic spatial sampling mechanism that complements top-down attentional control. It should be noted, however, that this association is observed across participants and thus most likely reflects stable individual differences in intrinsic sampling strategy; a mechanistic within-participant link remains to be tested directly in future studies.

Given that theta rhythmicity has recently been observed in external (visual attention-guided detection) and internal (working memory) sampling, it is conceivable that both rely on a shared theta-rhythmic sampling process that rhythmically reweights the need to allocate attention to external or internal representations (Balestrieri et al., 2022; Ede & Nobre, 2023; Gresch et al., 2024; Han et al., 2026).

Yet, our behavioral results could not resolve if, and how, different (grid) cells with different preferred hexagonal structures might contribute to the behavioral sampling. Dedicated experiments involving single unit recordings in the hippocampus will have to determine the precise cellular substrates of the observed sampling behavior.

While we did not record any neural activity in the present study, our behavioral results make predictions for future combined neural and behavioral studies. Specifically, a testable hypothesis arising from our behavioral observations is that RTs might be locked to different neural theta cycles (as derived from LFP or EEG recordings) across the six spatial positions. In fact, this hypothesis is supported by a recent non-human primate study that showed sequential spatial sampling during working memory operations, where phase determined RT (Han et al., 2026).

A common neural basis for covert and overt behavior?

It had long been speculated that attentional sampling relies on the same circuitry as overt behaviors as exemplified by the premotor theory (PMT) of attention (Rizzolatti et al., 1987). In line with a frontal origin, theta-dependent covert sampling has been observed in the frontal eye fields (FEF) as well as in adjacent frontal areas (Fiebelkorn et al., 2018; Helfrich et al., 2018; Raposo et al., 2023). Moreover, Gaillard et al. reported that saccadic eye movements are paced by a theta rhythm in FEF and explore space rhythmically (Gaillard et al., 2020). Given the prevalence of theta oscillations across fronto-parietal, occipital, and entorhinal-hippocampal networks, it is conceivable that covert and overt sampling rely on shared neural mechanisms.

To date, it remains unresolved whether the same mechanisms give rise to theta activity in archi- and neocortex. However, there is evidence that frontal and other regions' activity phase-lock to hippocampal theta rhythms during cognitive engagement (Hyman et al., 2005; Knudsen & Wallis, 2020; Sirota et al., 2008), thus, underscoring the notion that both are related.

Our results now provide additional behavioral evidence for a common neural basis. While theta rhythms likely originate from anatomically-distinct regions—such as the prefrontal and parietal attention network, occipital sensory areas and the entorhinal-hippocampal circuitry—they appear relevant for exploratory behaviors. Moreover, theta rhythms in different regions share several common features, such as phase coding (Kunz et al., 2019; Qasim et al., 2021; Smith et al., 2019), theta-gamma cross-frequency coupling (Canolty et al., 2006; Helfrich et al., 2018; Kienitz et al., 2021; Tort et al., 2009; Weber et al., 2024) or frequency modulation (Axmacher et al., 2010; Johnson et al., 2022) and are often reciprocally coupled (Daume et al., 2024; Johnson et al., 2023; Tamura et al., 2017). Hence, it is conceivable that theta-coupled behaviors constitute a unifying framework for spatial cognition. This consideration entails that the geometric hexagonal organization might not only subserve spatial maps, but could potentially also structure cognitive maps (Constantinescu et al., 2016; Epstein et al., 2017; Nau, Julian, et al., 2018), thus, reflecting a core principle underlying human cognition.

Limitations and Future Directions

In the present study, we observed theta rhythmic sampling behavior, modulated as a function of space. Yet, despite providing behavioral evidence for hexagonal modulation of covert attentional sampling, several limitations need to be acknowledged. First, only behavioral data was acquired, thus, we cannot resolve the neuroanatomical origins of the observed rhythms. It is likely that an interplay between frontoparietal networks, visual areas and hippocampal-

prefrontal networks forms the basis for theta rhythmic sampling (Fiebelkorn & Kastner, 2019; Kienitz et al., 2022). However, previous work also implicated the thalamus in orchestrating theta-dependent network (Fiebelkorn et al., 2019; Griffiths et al., 2022; Sweeney-Reed et al., 2015). Hence, future studies that employ simultaneous, high spatiotemporal recordings from the different network nodes, ideally by means of intracranial electroencephalography (Parvizi & Kastner, 2018), need to determine whether covert and overt sampling behaviors indeed rely on the same underlying mechanisms.

Secondly, theta rhythmicity has been contested recently. Especially, potentially inappropriate surrogate testing can disrupt inherent signal autocorrelations (Brookshire, 2022; Fiebelkorn, 2022; Re et al., 2022; Tosato et al., 2022). Here, we did not employ time-shuffled surrogate testing, but instead employed within-subject comparisons across different sampling orientations. We observed that spectral differences between aligned and non-aligned conditions in the theta range (see also Figure S2). This is in line with recent lesion work demonstrating that a focal disruption of the frontoparietal attention network alters theta rhythmic attentional sampling (Raposo et al., 2023).

Third, the employed paradigm was designed to test a specific hypothesis and thus, focused specifically on a 6-fold modulation and testing it against a 4-fold modulation pattern. Although the results support a hexagonal organization, other spatial configurations cannot be entirely ruled out. While we recorded a high trial count per participant (3000 trials across two sessions, exceeding typically reported trial numbers, cf. (Fiebelkorn et al., 2013; Helfrich et al., 2018; Landau & Fries, 2012)) to detect subtle rhythmic effects, incorporating additional trials and spatial orientations proved challenging, since it rendered the experiment unacceptably long (> 3-4h).

Yet, the high trial count is suited to yield reliable single-participant estimates despite a cohort of 20 subjects, and all key inferences rely on non-parametric statistics and permutation-based null models that make no distributional assumptions.

Fourth, we used a 50 ms moving window with 1 ms steps to construct behavioral reaction time traces. While this could potentially induce a bias, the impact on the signal autocorrelation was recently tested in detail (Raposo et al., 2025) with the very same parameters, demonstrating a negligible impact of the precise window parameters on the theta rhythmic sampling.

Fifth, several of our analysis choices, including the identification of individual theta peaks, were data-driven. We consider this principled rather than a limitation: individually resolving peak frequencies increases sensitivity to spectral effects and accounts for well-documented inter-individual variability in theta frequency, in line with current parameterization approaches (e.g.,

Donoghue et al., 2020). Importantly, the peak bin used for alignment was excluded from all subsequent testing to reduce a potential bias regarding the reported contrasts.

Lastly, following common practice (Doeller et al., 2010; Nau, Navarro Schröder, et al., 2018; Staudigl et al., 2018), we excluded the optimal direction ϕ from our 'aligned' condition and equated the number of angles across conditions to mitigate sampling bias. While this might potentially reduce effect size, it ensures that the statistical contrast is not driven by the selection step itself.

Furthermore, we equated the number of angles for the 'aligned' and 'non-aligned' conditions to mitigate any sampling bias. While this is considered best practice, it needs to be stressed that omitting the optimal phase also attenuates the overall effect size.

Conclusion

Collectively, our findings demonstrate that visual attention samples visual space consistent with an underlying hexagonal grid-like layout. This non-uniform sampling of visual space exhibited theta rhythmic signatures. Hence, these results provide a perspective how the brain might employ similar mechanisms to support both, covert and overt exploratory behaviors, and extends known spatio-temporal coding mechanisms during spatial exploration to covert attentional processing. In sum, this study demonstrates how the brain samples the visual environment in space and time, with theta oscillations possibly reflecting a unifying principle underlying spatial cognition.

References

- Axmacher, N., Henseler, M. M., Jensen, O., Weinreich, I., Elger, C. E., & Fell, J. (2010). Cross-frequency coupling supports multi-item working memory in the human hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, 107(7), 3228–3233. <https://doi.org/10.1073/pnas.0911531107>
- Balestrieri, E., Ronconi, L., & Melcher, D. (2022). Shared resources between visual attention and visual working memory are allocated through rhythmic sampling. *European Journal of Neuroscience*, 55(11–12), 3040–3053. <https://doi.org/10.1111/ejn.15264>
- Berens, P. (2009). CircStat: A MATLAB Toolbox for Circular Statistics. *Journal of Statistical Software*, 31(10). <https://doi.org/10.18637/jss.v031.i10>
- Brookshire, G. (2022). Putative rhythms in attentional switching can be explained by aperiodic temporal structure. *Nature Human Behaviour*, 6(9), 1280–1291. <https://doi.org/10.1038/s41562-022-01364-0>
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 29(24), 7869–7876. <https://doi.org/10.1523/JNEUROSCI.0113-09.2009>
- Busch, N. A., & VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proceedings of the National Academy of Sciences of the United States of America*, 107(37), 16048–16053. <https://doi.org/10.1073/pnas.1004801107>
- Buschman, T. J., & Kastner, S. (2015). From Behavior to Neural Dynamics: An Integrated Theory of Attention. *Neuron*, 88(1), 127–144. <https://doi.org/10.1016/j.neuron.2015.09.017>
- Buzsáki, G. (2002). Theta oscillations in the hippocampus. *Neuron*, 33(3), 325–340. [https://doi.org/10.1016/S0896-6273\(02\)00586-X](https://doi.org/10.1016/S0896-6273(02)00586-X)
- Buzsáki, G. (2005). Theta rhythm of navigation: Link between path integration and landmark navigation, episodic and semantic memory. *Hippocampus*, 15(7), 827–840. <https://doi.org/10.1002/hipo.20113>
- Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2006). High gamma power is phase-locked to theta oscillations in human neocortex. *Science (New York, N.Y.)*, 313, 1626–1628. <https://doi.org/10.1126/science.1128115>
- Canolty, R. T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. *Trends in Cognitive Sciences*, 14(11), 506–515. <https://doi.org/10.1016/j.tics.2010.09.001>
- Colgin, L. L. (2013). Mechanisms and functions of theta rhythms. *Annual Review of Neuroscience*, 36, 295–312. <https://doi.org/10.1146/annurev-neuro-062012-170330>
- Constantinescu, A. O., O'Reilly, J. X., & Behrens, T. E. J. (2016). Organizing conceptual knowledge in humans with a gridlike code. *Science*, 352(6292). <https://doi.org/10.1126/science.aaf0941>
- Daume, J., Kamiński, J., Schjetnan, A. G. P., Salimpour, Y., Khan, U., Kyzar, M., Reed, C. M., Anderson, W. S., Valiante, T. A., Mamelak, A. N., & Rutishauser, U. (2024). Control of working memory by phase–amplitude coupling of human hippocampal neurons. *Nature*, 629(8011), 393–401. <https://doi.org/10.1038/s41586-024-07309-z>
- Doeller, C. F., Barry, C., & Burgess, N. (2010). Evidence for grid cells in a human memory network. *Nature*, 463(7281), 657–661. <https://doi.org/10.1038/nature08704>
- Donoghue, T., Haller, M., Peterson, E. J., Varma, P., Sebastian, P., Gao, R., Noto, T., Lara, A. H., Wallis, J. D., Knight, R. T., Shestyuk, A., & Voytek, B. (2020). Parameterizing neural power spectra into periodic and aperiodic components. *Nature Neuroscience*, 23(12), 1655–1665. <https://doi.org/10.1038/s41593-020-00744-x>

622 Donoghue, T., Schaworonkow, N., & Voytek, B. (2021). Methodological considerations for studying
623 neural oscillations. *European Journal of Neuroscience*, (January), 1–43.
624 <https://doi.org/10.1111/ejn.15361>

625 Ede, F. van, & Nobre, A. C. (2023). Turning Attention Inside Out: How Working Memory Serves
626 Behavior. *Annual Review of Psychology*, 74(Volume 74, 2023), 137–165.
627 <https://doi.org/10.1146/annurev-psych-021422-041757>

628 Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision*
629 *Research*, 43(9), 1035–1045. [https://doi.org/10.1016/S0042-6989\(03\)00084-1](https://doi.org/10.1016/S0042-6989(03)00084-1)

630 Epstein, R. A., Patai, E. Z., Julian, J. B., & Spiers, H. J. (2017). The cognitive map in humans: Spatial
631 navigation and beyond. *Nature Neuroscience*, 20(11), 1504–1513.
632 <https://doi.org/10.1038/nn.4656>

633 Fiebelkorn, I. C. (2022). There Is More Evidence of Rhythmic Attention than Can Be Found in
634 Behavioral Studies: Perspective on Brookshire, 2022. *Journal of Cognitive Neuroscience*,
635 35(1), 128–134. https://doi.org/10.1162/jocn_a_01936

636 Fiebelkorn, I. C., & Kastner, S. (2019). A Rhythmic Theory of Attention. *Trends in Cognitive Sciences*,
637 23(2), 87–101. <https://doi.org/10.1016/j.tics.2018.11.009>

638 Fiebelkorn, I. C., Pinsk, M. A., & Kastner, S. (2018). A Dynamic Interplay within the Frontoparietal
639 Network Underlies Rhythmic Spatial Attention. *Neuron*, 99(4), 842-853.e8.
640 <https://doi.org/10.1016/j.neuron.2018.07.038>

641 Fiebelkorn, I. C., Pinsk, M. A., & Kastner, S. (2019). The mediodorsal pulvinar coordinates the
642 macaque fronto-parietal network during rhythmic spatial attention. *Nature Communications*,
643 10(1), 215.

644 Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic sampling within and between
645 objects despite sustained attention at a cued location. *Current Biology : CB*, 23(24), 2553–
646 2558. <https://doi.org/10.1016/j.cub.2013.10.063>

647 Fries, P. (2023). Rhythmic attentional scanning. *Neuron*, 111(7), 954–970.
648 <https://doi.org/10.1016/j.neuron.2023.02.015>

649 Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal
650 synchronization by selective visual attention. *Science (New York, N.Y.)*, 291(5508), 1560–
651 1563. <https://doi.org/10.1126/science.291.5508.1560>

652 Gaillard, C., Ben Hadj Hassen, S., Di Bello, F., Bihan-Poudec, Y., VanRullen, R., & Ben Hamed, S.
653 (2020). Prefrontal attentional saccades explore space rhythmically. *Nature Communications*,
654 11(1), 1–13. <https://doi.org/10.1038/s41467-020-14649-7>

655 Giari, G., Vignali, L., Xu, Y., & Bottini, R. (2023). MEG frequency tagging reveals a grid-like code
656 during covert attentional movements. *Cell Reports*.
657 <https://doi.org/10.1016/j.celrep.2023.113209>

658 Gresch, D., Boettcher, S. E. P., Gohil, C., van Ede, F., & Nobre, A. C. (2024). Neural dynamics of
659 shifting attention between perception and working-memory contents. *Proceedings of the*
660 *National Academy of Sciences*, 121(47), e2406061121.
661 <https://doi.org/10.1073/pnas.2406061121>

662 Griffiths, B. J., Zaehle, T., Repplinger, S., Schmitt, F. C., Voges, J., Hanslmayr, S., & Staudigl, T.
663 (2022). Rhythmic interactions between the mediodorsal thalamus and prefrontal cortex
664 precede human visual perception. *Nature Communications*, 13(1), 3736.
665 <https://doi.org/10.1038/s41467-022-31407-z>

666 Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map
667 in the entorhinal cortex. *Nature*, 436(7052), 801–806. <https://doi.org/10.1038/nature03721>

668 Han, H.-B., Brincat, S. L., Buschman, T. J., & Miller, E. K. (2026). Working memory readout varies
669 with frontal theta rhythms. *Neuron*, 114(1), 159-166.e2.
670 <https://doi.org/10.1016/j.neuron.2025.09.031>

671 Helfrich, R. F., Fiebelkorn, I. C., Szczepanski, S. M., Lin, J. J., Parvizi, J., Knight, R. T., & Kastner, S.
672 (2018). Neural Mechanisms of Sustained Attention Are Rhythmic. *Neuron*, 99(4), 854–865.
673 <https://doi.org/10.1016/j.neuron.2018.07.032>

674 Helfrich, R. F., Lendner, J. D., Mander, B. A., Guillen, H., Paff, M., Mnatsakanyan, L., Vadera, S.,
675 Walker, M. P., Lin, J. J., & Knight, R. T. (2019). Bidirectional prefrontal-hippocampal dynamics
676 organize information transfer during sleep in humans. *Nature Communications*, 10(1), 3572.
677 <https://doi.org/10.1038/s41467-019-11444-x>

678 Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta Oscillations in Human Memory. *Trends*
679 *in Cognitive Sciences*, 24(3), 208–227. <https://doi.org/10.1016/j.tics.2019.12.006>

680 Hyman, J. M., Zilli, E. A., Paley, A. M., & Hasselmo, M. E. (2005). Medial prefrontal cortex cells show
681 dynamic modulation with the hippocampal theta rhythm dependent on behavior.
682 *Hippocampus*, 15(6), 739–749. <https://doi.org/10.1002/hipo.20106>

683 Johnson, E. L., Lin, J. J., King-Stephens, D., Weber, P. B., Laxer, K. D., Saez, I., Girgis, F.,
684 D'Esposito, M., Knight, R. T., & Badre, D. (2023). A rapid theta network mechanism for
685 flexible information encoding. *Nature Communications*, 14(1), 2872.
686 <https://doi.org/10.1038/s41467-023-38574-7>

687 Johnson, E. L., Yin, Q., O'Hara, N. B., Tang, L., Jeong, J.-W., Asano, E., & Ofen, N. (2022).
688 Dissociable oscillatory theta signatures of memory formation in the developing brain. *Current*
689 *Biology*, 32(7), 1457-1469.e4. <https://doi.org/10.1016/j.cub.2022.01.053>

690 Jutras, M. J., Fries, P., & Buffalo, E. a. (2013). Oscillatory activity in the monkey hippocampus during
691 visual exploration and memory formation. *Proceedings of the National Academy of Sciences*,
692 110(32), 13144–13149. <https://doi.org/10.1073/pnas.1302351110> /
693 DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1302351110

694 Kienitz, R., Cox, M. A., Dougherty, K., Saunders, R. C., Schmiedt, J. T., Leopold, D. A., Maier, A., &
695 Schmid, M. C. (2021). Theta, but Not Gamma Oscillations in Area V4 Depend on Input from
696 Primary Visual Cortex. *Current Biology*, 31(3), 635-642.e3.
697 <https://doi.org/10.1016/j.cub.2020.10.091>

698 Kienitz, R., Schmid, M. C., & Dugué, L. (2022). Rhythmic sampling revisited: Experimental paradigms
699 and neural mechanisms. *European Journal of Neuroscience*, 1–15.
700 <https://doi.org/10.1111/ejn.15489>

701 Kienitz, R., Schmiedt, J. T., Shapcott, K. A., Kouroupaki, K., Saunders, R. C., & Schmid, M. C. (2018).
702 Theta Rhythmic Neuronal Activity and Reaction Times Arising from Cortical Receptive Field
703 Interactions during Distributed Attention. *Current Biology*, 1–11.
704 <https://doi.org/10.1016/j.cub.2018.05.086>

705 Killian, N. J., Jutras, M. J., & Buffalo, E. a. (2012). A map of visual space in the primate entorhinal
706 cortex. *Nature*, 491(7426), 761–764. <https://doi.org/10.1038/nature11587>

707 Knudsen, E. B., & Wallis, J. D. (2020). Closed-Loop Theta Stimulation in the Orbitofrontal Cortex
708 Prevents Reward-Based Learning. *Neuron*, 106(3), 537-547.e4.
709 <https://doi.org/10.1016/j.neuron.2020.02.003>

710 Kunz, L., Wang, L., Lachner-Piza, D., Zhang, H., Brandt, A., Dümpelmann, M., Reinacher, P. C.,
711 Coenen, V. A., Chen, D., Wang, W.-X., Zhou, W., Liang, S., Grewe, P., Bien, C. G.,
712 Bierbrauer, A., Navarro Schröder, T., Schulze-Bonhage, A., & Axmacher, N. (2019).
713 Hippocampal theta phases organize the reactivation of large-scale electrophysiological
714 representations during goal-directed navigation. *Science Advances*, 5(7), eaav8192.
715 <https://doi.org/10.1126/sciadv.aav8192>

Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology : CB*, 22(11), 1000–1004. <https://doi.org/10.1016/j.cub.2012.03.054>

Landau, A. N., Schreyer, H. M., van Pelt, S., & Fries, P. (2015). Distributed Attention Is Implemented through Theta-Rhythmic Gamma Modulation. *Current Biology*, 25, 2332–2337. <https://doi.org/10.1016/j.cub.2015.07.048>

Lisman, J. E., & Jensen, O. (2013). The Theta-Gamma neural code. *Neuron*, 77(6), 1002–1016. <https://doi.org/10.1016/j.neuron.2013.03.007>

Maidenbaum, S., Miller, J., Stein, J. M., & Jacobs, J. (2018). Grid-like hexadirectional modulation of human entorhinal theta oscillations. *Proceedings of the National Academy of Sciences*, 201805007. <https://doi.org/10.1073/pnas.1805007115>

Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience*, 31, 69–89. <https://doi.org/10.1146/annurev.neuro.31.061307.090723>

Nau, M., Julian, J. B., & Doeller, C. F. (2018). How the Brain's Navigation System Shapes Our Visual Experience. *Trends in Cognitive Sciences*, 22(9), 810–825. <https://doi.org/10.1016/j.tics.2018.06.008>

Nau, M., Navarro Schröder, T., Bellmund, J. L. S., & Doeller, C. F. (2018). Hexadirectional coding of visual space in human entorhinal cortex. *Nature Neuroscience*, 21(2), 188–190. <https://doi.org/10.1038/s41593-017-0050-8>

Nyström, M., & Holmqvist, K. (2010). An adaptive algorithm for fixation, saccade, and glissade detection in eyetracking data. *Behavior Research Methods*, 42(1), 188–204. <https://doi.org/10.3758/BRM.42.1.188>

O'Keefe, J. (1976). Place units in the hippocampus of the freely moving rat. *Experimental Neurology*, 51(1), 78–109. [https://doi.org/10.1016/0014-4886\(76\)90055-8](https://doi.org/10.1016/0014-4886(76)90055-8)

Otero-Millan, J., Castro, J. L. A., Macknik, S. L., & Martinez-Conde, S. (2014). Unsupervised clustering method to detect microsaccades. *Journal of Vision*, 14, 1–17. <https://doi.org/10.1167/14.2.18>

Parvizi, J., & Kastner, S. (2018). Promises and limitations of human intracranial electroencephalography. *Nature Neuroscience*, 21(April). <https://doi.org/10.1038/s41593-018-0108-2>

Pastukhov, A. (2023). *saccadr: Extract Saccades via an Ensemble of Methods Approach* (Version 0.1.3) [Computer software]. <https://cran.r-project.org/web/packages/saccadr/index.html>

Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109(2), 160–174. <https://doi.org/10.1111/j.1755-6724.1986.mp60004004.x>

Qasim, S. E., Fried, I., & Jacobs, J. (2021). Phase precession in the human hippocampus and entorhinal cortex. *Cell*, 184(12), 3242–3255.e10. <https://doi.org/10.1016/j.cell.2021.04.017>

Raposo, I., Fiebelkorn, I. C., Lin, J. J., Parvizi, J., Kastner, S., Knight, R. T., Breska, A., & Helfrich, R. F. (2025). Human attention-guided visual perception is governed by rhythmic oscillations and aperiodic timescales. *PLOS Biology*, 23(6), e3003232. <https://doi.org/10.1371/journal.pbio.3003232>

Raposo, I., Szczepanski, S. M., Haaland, K., Endestad, T., Solbakk, A.-K., Knight, R. T., & Helfrich, R. F. (2023). Periodic attention deficits after frontoparietal lesions provide causal evidence for rhythmic attentional sampling. *Current Biology*, 33(22), 4893–4904.e3. <https://doi.org/10.1016/j.cub.2023.09.065>

Re, D., Tosato, T., Fries, P., & Landau, A. N. (2022). *Perplexity about periodicity repeats perpetually: A response to Brookshire* (p. 2022.09.26.509017). *bioRxiv*. <https://doi.org/10.1101/2022.09.26.509017>

- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1A), 31–40. [https://doi.org/10.1016/0028-3932\(87\)90041-8](https://doi.org/10.1016/0028-3932(87)90041-8)
- Sirota, A., Montgomery, S., Fujisawa, S., Isomura, Y., Zugaro, M., & Buzsáki, G. (2008). Entrainment of neocortical neurons and gamma oscillations by the hippocampal theta rhythm. *Neuron*, 60(4), 683–697. <https://doi.org/10.1016/j.neuron.2008.09.014>
- Smith, E. H., Horga, G., Yates, M. J., Mikell, C. B., Banks, G. P., Pathak, Y. J., Schevon, C. A., McKhann, G. M., Hayden, B. Y., Botvinick, M. M., & Sheth, S. A. (2019). Widespread temporal coding of cognitive control in the human prefrontal cortex. *Nature Neuroscience*, 22(11), 1883–1891. <https://doi.org/10.1038/s41593-019-0494-0>
- Spyropoulos, G., Bosman, C. A., & Fries, P. (2018). A theta rhythm in macaque visual cortex and its attentional modulation. *Proceedings of the National Academy of Sciences*, 115(24), E5614–E5623. <https://doi.org/10.1073/pnas.1719433115>
- Staudigl, T., Leszczynski, M., Jacobs, J., Sheth, S. A., Schroeder, C. E., Jensen, O., & Doeller, C. F. (2018). Hexadirectional Modulation of High-Frequency Electrophysiological Activity in the Human Anterior Medial Temporal Lobe Maps Visual Space. *Current Biology*, 28(20), 3325–3329.e4. <https://doi.org/10.1016/j.cub.2018.09.035>
- Sweeney-Reed, C. M., Zaehle, T., Voges, J., Schmitt, F. C., Buentjen, L., Kopitzki, K., Hinrichs, H., Heinze, H.-J., Rugg, M. D., Knight, R. T., & Richardson-Klavehn, A. (2015). Thalamic theta phase alignment predicts human memory formation and anterior thalamic cross-frequency coupling. *eLife*, 4, e07578. <https://doi.org/10.7554/eLife.07578>
- Tamura, M., Spellman, T. J., Rosen, A. M., Gogos, J. A., & Gordon, J. A. (2017). Hippocampal-prefrontal theta-gamma coupling during performance of a spatial working memory task. *Nature Communications*, 8(1), 2182. <https://doi.org/10.1038/s41467-017-02108-9>
- Tort, A. B. L., Komorowski, R. W., Manns, J. R., Kopell, N. J., & Eichenbaum, H. (2009). Theta-gamma coupling increases during the learning of item-context associations. *Proceedings of the National Academy of Sciences of the United States of America*, 106(49), 20942–20947. <https://doi.org/10.1073/pnas.0911331106>
- Tosato, T., Rohenkohl, G., Dowdall, J. R., & Fries, P. (2022). Quantifying rhythmicity in perceptual reports. *NeuroImage*, 262, 119561. <https://doi.org/10.1016/j.neuroimage.2022.119561>
- VanRullen, R. (2016). Perceptual Cycles. *Trends in Cognitive Sciences*, 20(10), 723–735. <https://doi.org/10.1016/j.tics.2016.07.006>
- Vollan, A. Z., Gardner, R. J., Moser, M.-B., & Moser, E. I. (2024). *Left-right-alternating theta sweeps in the entorhinal-hippocampal spatial map* (p. 2024.05.16.594473). bioRxiv. <https://doi.org/10.1101/2024.05.16.594473>
- Weber, J., Solbakk, A.-K., Blenkmann, A. O., Llorens, A., Funderud, I., Leske, S., Larsson, P. G., Ivanovic, J., Knight, R. T., Endestad, T., & Helfrich, R. F. (2024). Ramping dynamics and theta oscillations reflect dissociable signatures during rule-guided human behavior. *Nature Communications*, 15(1), 637. <https://doi.org/10.1038/s41467-023-44571-7>
- Wilming, N., König, P., König, S., & Buffalo, E. A. (2018). Entorhinal cortex receptive fields are modulated by spatial attention, even without movement. *eLife*, 7, 1–16. <https://doi.org/10.7554/eLife.31745>

Figure legends

[Figure 1]

Experimental design and approach

(A) Left: Participants performed a spatial attention task where they reacted to high-contrast target indicated an increase in luminance after having received a spatial cue (90 % validity) at either end of a bar. Different cue-target-intervals (CTI) allowed resolving reaction times as a function of time (as outlined in panel C). Right: The bar was randomly displayed at one of 6 possible main directions (right panel), allowing to assess attentional sampling along the 0, 30, 60, 90, 120 and 150° axes.

(B) The experimental design was geared towards assessing a hexagonal modulation of rhythmic attentional sampling. The left panel depicts a simulated entorhinal grid cell map with spiking locations marked in yellow. As entorhinal grid cell organization yields stronger activation in *aligned* directions (i.e., preferred direction φ as well as φ plus multiples of 60°) compared to *non-aligned* directions, we tested if attentional sampling along different directions also exhibits such a hexagonal modulation. We only assessed the theta-modulatory influence along a 5° radius, which yields a comparable modulation as across different directions or angles (red line in Figure1 left panel). (C) Left: Single subject, single trial reaction times (demeaned). Center: Behavioral fluctuations were extracted from trials of a given orientation by binning and detrending reaction times across CTIs. Right: Time-resolved behavior was transformed to the frequency domain and power spectra were obtained per subject and bar orientation.

(D) Left: Individual peaks in the theta range (2.5-8 Hz) were then detected for each subject and angle on the 1/f corrected power spectra. The preferred individual direction φ was defined as the angle that exhibited the maximal theta power. Right: Angles were then re-aligned with respect to φ .

[Figure 2]

Single subject behavior

(A) Average detrended reaction time traces for *aligned* (red) vs. *non-aligned* (orange) angles in one exemplary participant. Note the more pronounced fluctuations of reaction times for aligned angles.

(B) Theta peak power was non-uniformly distributed across the different angles. Higher power was found at the *aligned* (multiples of 60° with regard to φ) compared to the *unaligned* directions, indicating a hexagonal modulation across angles.

(C) 1/f corrected power spectrum of the behavioral traces (*aligned* (red) vs. *non-aligned* (orange) directions. Note the higher power in the theta range for aligned directions. Results for this example subject implied a shift in peak frequency, which however was not present on the group level ($p = 0.856$, Wilcoxon signed rank test).

[Figure 3]

Hexagonal modulation of attentional sampling

846 (A) Left: Grand-average 1/f-corrected power spectra for *aligned* (red) vs. *non-aligned* (orange) angles.
847 Right: Power differences between aligned and non-aligned angles across participants. Note the peak
848 in the theta range indicating higher theta power for aligned directions.

849 (B) Distributions of average theta power (4-6 Hz) for every participant for aligned (red, $p = 0.021$,
850 Wilcoxon signed rank test) and non-aligned (orange, $p = 0.057$, Wilcoxon signed rank test) angles. Note
851 the significantly higher average theta power for aligned angles ($p = 0.030$, Wilcoxon signed rank test).

852 (C) Distributions of modulation strength (*aligned* – *non-aligned* angles) for every participant for a 6-fold
853 vs. 4-fold modulation. A significantly larger modulation was observed for the 6-fold modulation ($p =$
854 0.043 , Wilcoxon signed rank test). Note that only the 6-fold modulation was significantly larger than
855 zero ($p(6\text{fold} > 0) = 0.008$; $p(4\text{fold} > 0) = 0.977$).

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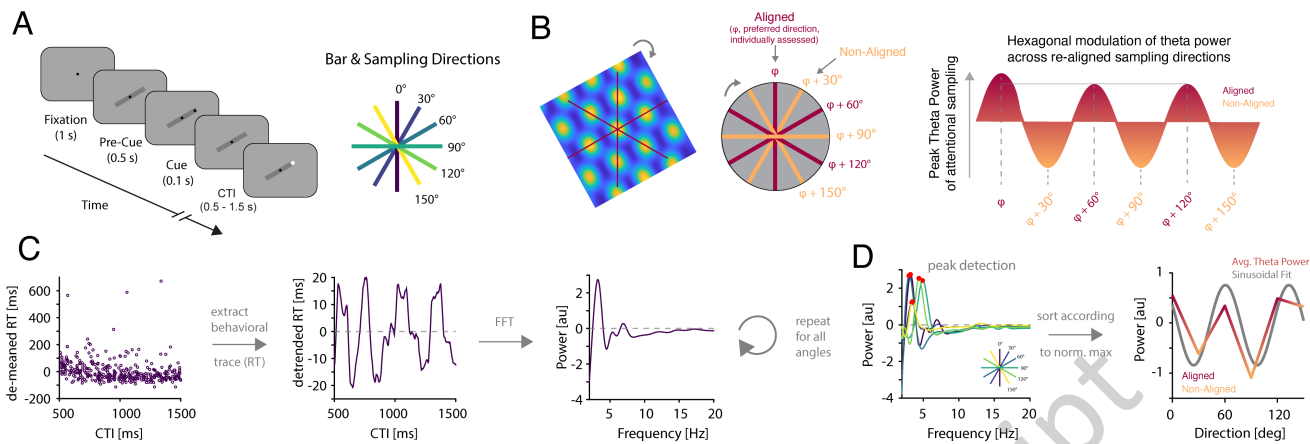
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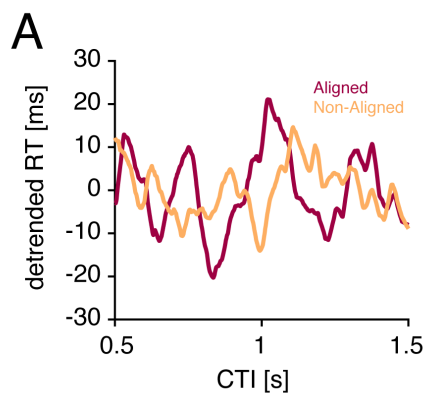
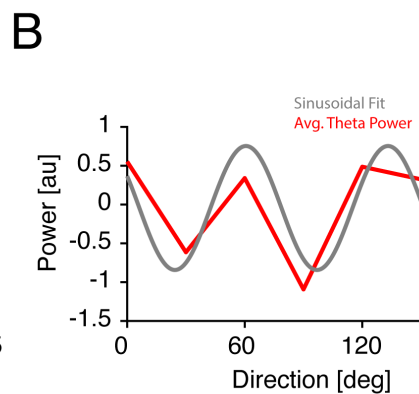
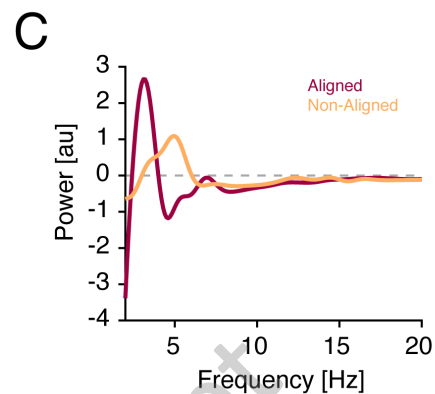
858 **[Figure 4]**

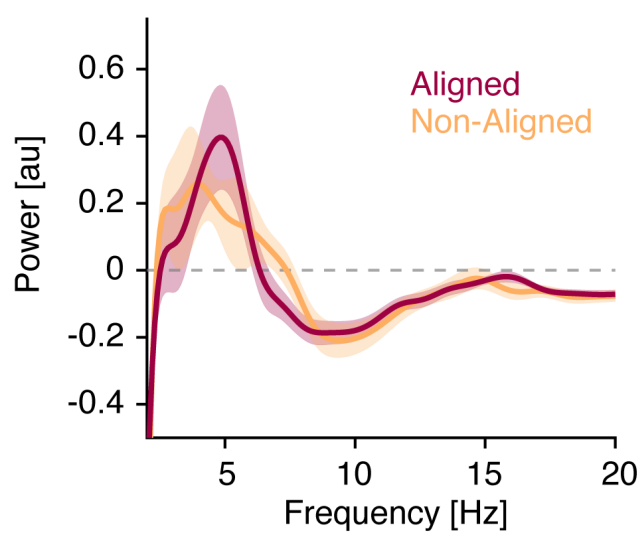
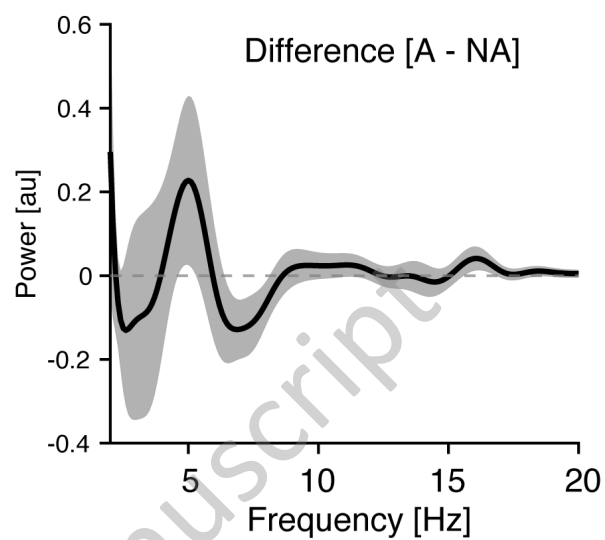
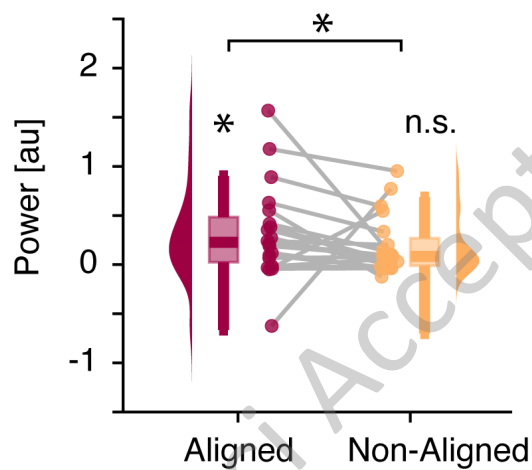
859 **Hexagonal modulation and attentional spatial cueing benefit**

860 Scatter plot illustrating the significant negative correlation ($r = -0.49$) between the attention index (higher
861 values indicate stronger benefits of the spatial attention cue) and hexagonal sampling (higher values
862 indicate stronger hexagonal modulation of sampling).

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