

# Dynamic cross-frequency couplings of local field potential oscillations in rat striatum and hippocampus during performance of a T-maze task

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Oscillatory rhythms in different frequency ranges mark different behavioral states and are thought to provide distinct temporal windows that coherently bind cooperating neuronal assemblies. However, the rhythms in different bands can also interact with each other, suggesting the possibility of higher-order representations of brain states by such rhythmic activity. To explore this possibility, we analyzed local field potential oscillations recorded simultaneously from the striatum and the hippocampus. As rats performed a task requiring active navigation and decision making, the amplitudes of multiple high-frequency oscillations were dynamically modulated in task-dependent patterns by the phase of cooccurring theta-band oscillations both within and across these structures, particularly during decision-making behavioral epochs. Moreover, the modulation patterns uncovered distinctions among both high- and low-frequency subbands. Cross-frequency coupling of multiple neuronal rhythms could be a general mechanism used by the brain to perform network-level dynamical computations underlying voluntary behavior.

amplitude modulation | gamma | theta

Oscillations in neural population voltage activity are universal phenomena (1). Among brain rhythms, theta oscillations in local field potentials (LFPs) recorded in the hippocampus are prominent during active behaviors (2–5), and these have long been intensively analyzed in the rodent in relation to spatial navigation (6), memory (7), and sleep (8). Theta-band rhythms (4–12 Hz) are now known to occur in other cortical (9–12) and subcortical (12–15) regions, however, including the striatum (14–17), studied here. Gamma oscillations (30–100 Hz) have also received special attention because of their proposed role in functions such as sensory binding (18), selective attention (19–21), transient neuronal assembly formation (22), and information transmission and storage (23–25). The existence of physiologically meaningful neocortical oscillations at even higher frequencies, above the traditional gamma range, has been reported as well (10, 26–28). In rodents, for example, brief sharp-wave associated ripples (120–200 Hz) appear in the hippocampal formation during slow wave sleep, immobility and consummatory behavior, characteristically in the absence of theta waves (2, 29).

The oscillatory activities conventionally assigned to different frequency bands are not completely independent (2–4, 9, 10, 30). In one type of interaction, the phase of low-frequency rhythms modulates the amplitude of higher-frequency oscillations (9, 10, 30). For example, theta phase is known to modulate gamma power in rodent hippocampal and cortical circuits (2–4, 31), and the phase of theta rhythms recorded in the human neocortex can modulate wide-band (60–200 Hz) high-frequency oscillations (10). Such theta–gamma nesting is thought to play a role in sequential memory organization and maintenance of working memory, and more generally in “phase coding” (25, 31). Based on evidence suggesting that theta rhythms in hippocampal and striatal memory circuits are coordinated in rats during learning and performance of a condi-

tional T-maze task (14), we asked whether theta phase modulates cooccurring high-frequency oscillations in the striatum as well as in the hippocampus, and if so whether such cross-frequency effects occur between the 2 structures, and whether the phase–amplitude coupling is related to specific behavioral performance. We demonstrate here that distinct bands of high-frequency oscillations are modulated by ongoing low-frequency rhythms, both within and across the striatum and hippocampus. We further show that the strength of these cross-frequency interactions changes dynamically, and differentially, during different epochs of behavioral performance requiring decision and action. These findings suggest that the cross-frequency interactions reflect behaviorally relevant simultaneous activation of synchronized striatal and hippocampal memory circuits.

## Results

We analyzed the LFP oscillatory activity recorded in the dorsal caudoputamen and the CA1 field of the dorsal hippocampus as rats ( $n = 6$ ) navigated a T-maze in which they turned right or left in response to auditory instruction cues indicating which of the 2 end arms was baited with chocolate (14, 15) (Fig. 1*A*). In both the striatum and the hippocampus, theta power increased as the rats left the start zone, peaked as the animals traversed the maze, and diminished as the rats approached the goal [Figs. 1*B* and *C* and 2*A* and *B* and [supporting information \(SI\) Fig. S1](#)]. By contrast, low gamma power (LG, 30–60 Hz) diminished during the middle of the task, and high gamma (HG, 60–100 Hz) and high-frequency oscillations (HFO, >100 Hz) powers increased throughout the maze runs (Figs. 1*B* and *C* and 2*A* and *B* and [Fig. S1](#)). Notably, these modulations in power had different time courses in the 2 structures (see Figs. 1*B* and *C* and 2*A* and *B* and [Fig. S1](#)).

To determine whether interactions across these frequency ranges occurred, we developed a cross-frequency measure to analyze phase-to-amplitude modulation in limited-time datasets (modulation index, see [SI Text](#)). This method allowed us to examine phase–amplitude modulation for successive event epochs during the maze runs. Phase-to-amplitude comodulograms were constructed by applying this measure to multiple frequency band pairs made up of “phase frequency” and “amplitude frequency” bands stepped through task time (Figs. 1*D* and 2*C* and *D* and [Fig. S2](#)).

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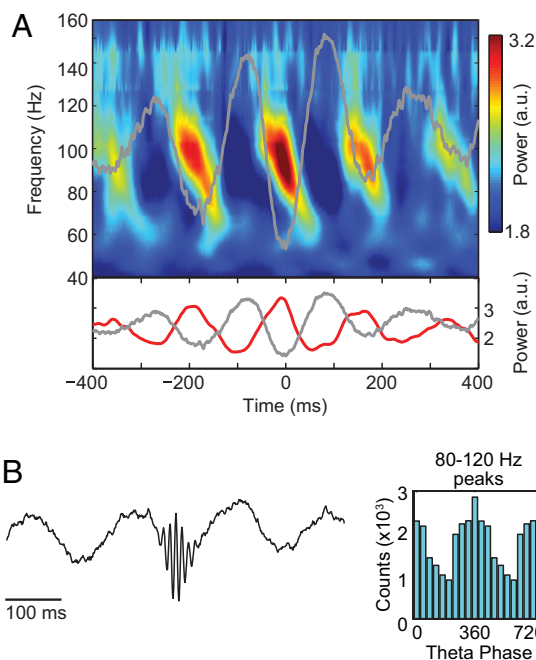
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**Fig. 3.** The amplitude of striatal 80–120 Hz LFP oscillations is maximal at the troughs of cooccurring striatal theta oscillations. (A) (*Upper*) Time–frequency plot of the mean normalized power time-locked to the theta (5–8 Hz) trough. (*Lower*) Plot showing the mean normalized power at 100 Hz (red line). The theta trough-locked averaged raw signal is shown in both *Upper* and *Lower* plots as a gray line. (B) (*Left*) Averaged raw signal obtained by aligning the LFP traces at the peaks of the 80- to 120-Hz oscillation (see *SI Text*). (*Right*) The histogram of the theta phases at which the peaks occurred. Results were obtained from the same animal and experimental session as in Fig. 1.

and the CA1 layer in which the recordings were made. The HG and HFO amplitudes peaked at the trough of the theta oscillation at the deep recording sites (Fig. 4 *A–C Left* and Fig. S5). At the superficial recording sites, the HG power peaked on the rising phase of theta, and the HFO power was maximal near the peak of the theta wave (Fig. 4 *A–C Right* and Fig. S5). The opposite preferred theta phase for the HFO powers recorded at the deep and superficial layers\* likely relates to the well-established phase-reversal of the theta rhythm across the CA1 layers also evident in our recordings (Fig. S5; see also ref. 3). However, this reversal does not account for the differences in preferred phases between the HFO and HG frequency bands in the superficial CA1 layers.

The amplitude modulation of high-frequency rhythms by cooccurring theta was correlated with the power of theta both in the striatum and in the hippocampus, with stronger modulation occurring at greater theta powers (Figs. S6 and S7). The strongest comodulations thus occurred during the middle parts of the maze runs. However, the presence of the theta rhythm per se did not guarantee the existence of the cross-frequency phase-to-amplitude coupling. The peak of theta power in the striatal LFPs did not always match the peak of the cross-frequency modulation observed in the striatum (e.g., Fig. 1 *C* and *D*). In the hippocampal LFPs, clear theta peaks occurred during the pre-trial, warning cue, gate-opening, and goal-reaching periods, when cross-frequency coupling was typically not observed (see Fig. 2 *B–D*). Moreover, comparable levels of hippocampal theta were associated with different modulation index values (e.g., compare the “Gate Opening” and “Tone Onset” events in Fig. 2).

\*Roughly, “superficial” and “deep” CA1 layers correspond to stratum pyramidale and stratum lacunosum-moleculare, respectively; see *SI Text*.

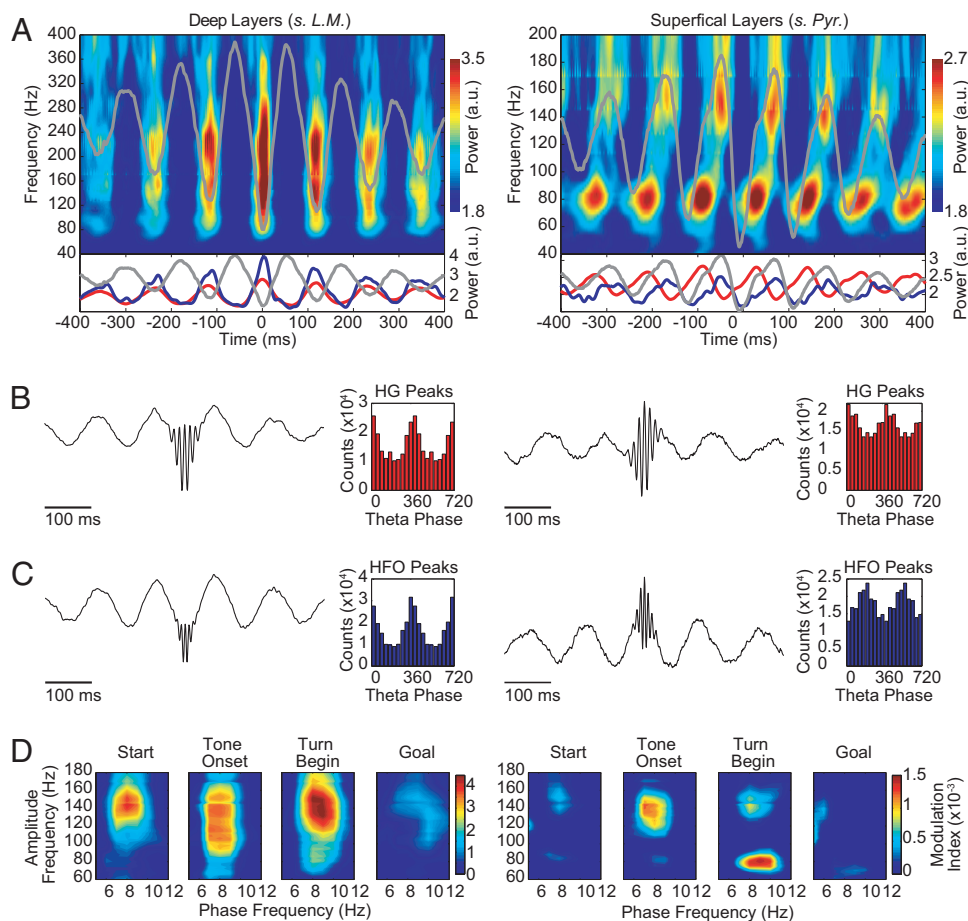
Multiple regression analysis demonstrated that for any given high-frequency rhythm, the amplitude modulation depended partly on its own power and partly on the power of other high-frequency rhythms, in addition to the power of the cooccurring theta rhythm (Fig. S7). Likewise, although the animals’ running speeds increased up to the middle of the maze runs and then decreased toward goal reaching, the relation between the intensity of the cross-frequency coupling and the animals’ speed was not a straightforward one: Speed-controlled analyses demonstrated that changes in speed alone cannot account for the distinct levels of modulation among the task events (Fig. S8).

The presence of phase-amplitude coupling during the midrun period suggested that the coupling might be related to the presence of heightened coherence between the striatal and the hippocampal rhythms, which also tends to occur during this epoch (14). As shown in Fig. 5 for the “Tone Onset” period, cross-structure coupling did occur. The phase–amplitude couplings between the striatal theta phase and the amplitude of the hippocampal fast oscillations were very prominent (Fig. 5*A*, third image from the left). The hippocampal theta modulation of striatal 80- to 120-Hz oscillations was much weaker (Fig. 5*A*, second image from the left). Notably, the striatal–hippocampal cross-structure coupling was strongest at the high theta-band frequencies (8–12 Hz), frequencies that within the hippocampus modulated hippocampal gamma and HFO rhythms, and frequencies at which the striatal and hippocampal theta rhythms were most highly coherent (Fig. 5*C*, see also ref. 14). By contrast, it was the low-frequency striatal theta band (3–8 Hz) that modulated the striatal 80- to 120-Hz oscillations, frequencies at which the striatal and hippocampal theta rhythms were less coherent (Fig. 5*C*). The cross-structure coupling patterns were thus consistent with the patterns of coherence between the theta rhythms in the striatum and hippocampus. Cross-structure phase–amplitude interactions could therefore occur, but they were constrained by subbands within the traditional theta range. It is striking that the frequency constraints for intrastriatal phase–amplitude coupling are different from the constraints for striatal–hippocampal coupling.

A relation between behavioral learning and patterns of striatal–hippocampal theta coherence has been suggested because high levels of cross-structure theta coherence were found in rats that learned the T-maze task used here but not in rats that failed to learn the task (14). In our analysis, we found clear examples of correlations between the phase-amplitude modulation and learning scores (Fig. S9). Our dataset was inappropriate to analyze fully the relationship between the modulation index and the percentage correct performance of all of the rats (see Fig. S9 legend). However, this initial analysis suggests that the phase–amplitude coupling we detected may be related to learning state as well as to active on-line behavioral state.

## Discussion

Our findings were unequivocal in suggesting that phase–amplitude coupling is a prominent feature of the oscillatory LFP activity both in the striatum and in the hippocampus under conditions of active, goal-oriented behavior. These dynamic phase–amplitude modulations were distinct for different high-frequency bands modulated by theta phase and for different subbands within the theta range and thus suggested previously undescribed, behaviorally relevant frequency ranges for both striatal and hippocampal oscillations. Moreover, the phase of striatal theta could modulate high-frequency oscillations not only in the striatum but also in the hippocampus, and hippocampal–striatal modulation also was present. Adjustments in phase–amplitude coupling thus occurred not only within but also across striatal and hippocampal circuits during active behavior. The strongest phase–amplitude coupling tended to occur during behavioral epochs involving decision and behavioral choice, suggesting that the couplings relate, at least in part, to ongoing cognitive demands. These findings suggest that dynamic, frequency-

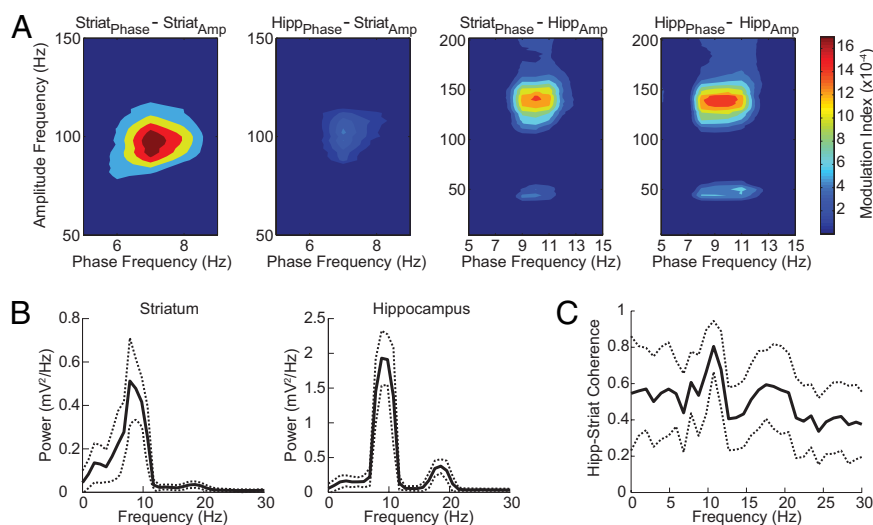


**Fig. 4.** The theta phase modulation of high-frequency hippocampal LFP oscillations differs for rhythms in different frequency bands and layers in the CA1 region of the dorsal hippocampus. (A) (Upper) Time–frequency plots of the mean normalized power time-locked to the theta (7–12 Hz) trough for the deep (Left) and superficial (Right) CA1 layers recordings. (Lower) Plots showing the mean normalized power at 80 Hz (HG, red line) and at 160 Hz (HFO, blue line). The theta trough-locked averaged raw signal is shown in gray in all plots. (B and C) Averaged raw signal obtained by centering the LFP traces at the peaks of the HG (B) or HFO (C) and the corresponding histograms of the theta phases at which the peaks occurred. (D) Phase-to-amplitude comodulograms showing differential theta modulations of HG and HFO rhythms. Results are shown for simultaneous recordings from 1 deep (left column) and 1 superficial (right column) CA1 layer tetrode in a representative rat.

specific phase–amplitude coupling may be a key feature coordinating the activity of striatal and hippocampal learning circuits during sequential voluntary behavior.

**Multiple High-Frequency Bands Are Modulated by Theta Phase.** The striatal high-frequency range for which we found amplitude modulation by striatal theta phase was  $\approx 80$ –120 Hz. It is striking that we did not observe phase–amplitude coupling for the low-gamma (30–60 Hz) range, which is the main gamma band so far analyzed in LFP recording experiments in the rodent striatum (14–17, 32,

33). Furthermore, the theta frequencies for which we found the modulation tended to be in the low theta range ( $\approx 3$ –8 Hz), despite the cooccurrence of strong theta oscillations at higher frequencies within the theta band ( $\approx 8$ –12 Hz). Oscillatory activity in the striatal LFPs likely reflect rhythms in striatal inputs both from distant sources such as the thalamus and neocortex and from local sources, particularly the pallidum, itself part of a subthalamo–pallidal oscillatory circuit (34, 35). Interneurons in the striatum have also been found to exhibit oscillatory activity, and although some of their oscillatory activity has been linked to that of the neocortex, some



**Fig. 5.** Phase-amplitude couplings occur between simultaneously recorded striatal and hippocampal oscillations. (A) Phase-to-amplitude comodulograms obtained during a 1-s interval around the Tone Onset task event. Results are shown for all phase–amplitude combinations as labeled. Note that the theta phase in each structure modulates the amplitude of oscillations in the other structure. (B) Mean power spectrum (solid line) of the LFPs recorded in each brain region during the same task period (Tone Onset), showing a peak in the theta band in both regions. Dashed lines represent  $\pm$ SD. (C) Coherence spectrum (solid line) between the striatal and the hippocampal oscillations during the same task period showing a peak of coherence at  $\approx 10$  Hz. Results were obtained from a representative animal during a session (different rat than in Fig. 1).



enced the appearance of the phase–amplitude couplings both within the striatum and the hippocampus and across these forebrain regions. If so, this decision phase may be one that particularly calls for multiple frequency-band coordination of striatal and hippocampal activity. This behavioral epoch also appears to be the time at which network coherence within the theta band is enhanced across hippocampal, prefrontal, and striatal circuits (14, 50). These findings suggest that phase–amplitude coupling may reflect the engagement across different time scales of network activity related to active cognitive processing.

## Materials and Methods

Behavioral training and electrophysiology recording methods were approved by the Committee on Animal Care of Massachusetts Institute of Technology and are described in detail in refs. 14 and 15. Briefly, 6 male Sprague–Dawley rats were implanted with head stages containing 12 tetrodes, with 6 tetrodes targeting the dorsomedial caudoputamen (AP: +1.7 mm, ML: 1.8 mm, DV: 3.6–4.6 mm) and 6 tetrodes targeting the dorsal CA1 region of the hippocampus (AP: –3.3 mm, ML: 2.2 mm, DV: 2.4–2.8 mm). Tetrodes were lowered to their target depths during

a 1-week postsurgical recovery period. Rats then received daily training sessions (usually 40 trials) on an auditory tone-cued T-maze task. Rats were trained to turn right or left at the choice point of the maze as instructed by 1- and 8-kHz tone cues. A click warning cue preceded the opening of a start gate. Rats were rewarded with chocolate sprinkles if the baited goal was correctly approached. Throughout training, LFPs were amplified (gain: 1,000), filtered (1–475 Hz) and continuously sampled at 1 kHz by using a Cheeetah recording system (Neuralynx). In the hippocampus, the definition of “deep” and “superficial” CA1 layers of the dorsal hippocampus was performed based on the phase reversal of the theta wave combined with daily records of tetrode depth. All analyses were done with MATLAB 7.5 software (MathWorks). Details are given in *SI Text*.

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