

# Plasticity in oscillatory coupling between hippocampus and cortex

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Neural oscillations observed in local field potentials (LFP) represent gross cellular activity near the recording electrode. Coupling of oscillations in distributed brain circuits has been proposed to enhance communication across the circuits, and the plasticity in oscillatory coupling can underlie flexible task learning, but the direct evidence has been lacking. Recently, evidence for plasticity in oscillatory coupling in theta, beta and gamma bands has been obtained in memory circuits consisted of the hippocampus and its connected areas, suggesting importance of oscillatory coupling plasticity in memory processing. I hypothesize that such plasticity in oscillatory coupling could be a key mechanism for enhancing inter-regional neural communication, especially in the entorhinal-hippocampal and prefrontal-hippocampal memory circuits that underlie formation, control and retrieval of memory.

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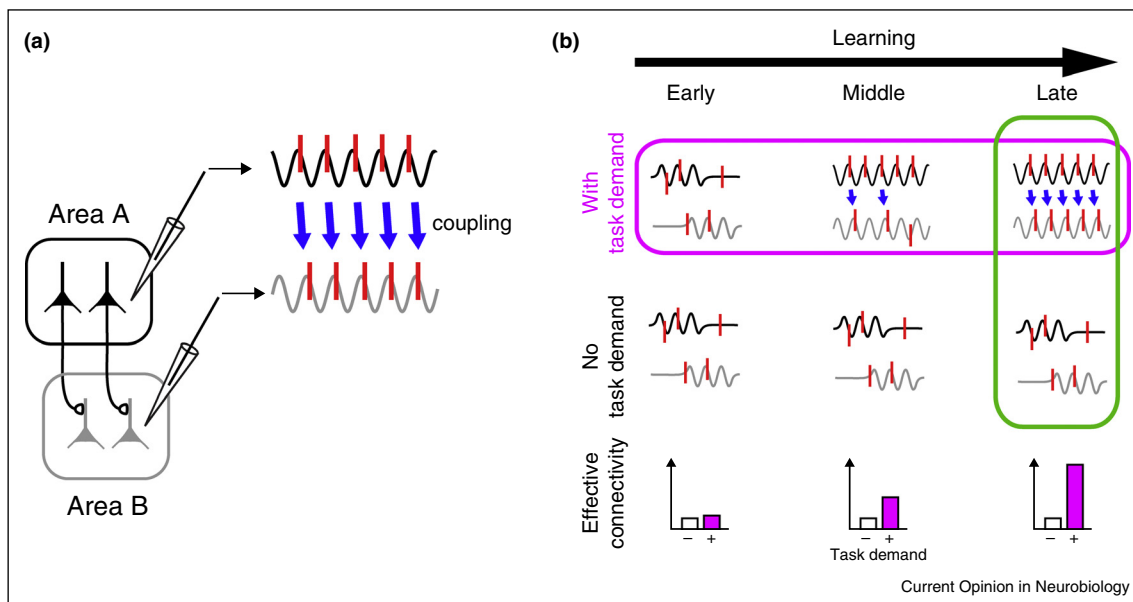
## Introduction

Neural oscillations are one of the prominent features of brain activities [1]. These oscillations can be recorded by placing an extracellular recording electrode in a brain area and filtering out local field potential (LFP) activities (<500 Hz) from spike activities (>1 kHz). The LFP activities derive from transmembrane current of a population of neurons that are periodically synchronized [2,3], and typically include theta (~5–10 Hz) [4,5], beta (~15–25 Hz) [6], gamma (~25–100 Hz) [7–9] and ripple (~150–300 Hz) [10] oscillations. These oscillations have been observed in various brain regions including the hippocampus, visual cortical areas, and olfactory cortex. In studies using simultaneous recording from multiple brain areas, related network oscillations have been observed across these areas

with a certain delay and are termed as coupled oscillations (Figure 1a). In a broadly accepted model, these coupled oscillations are hypothesized to route flow of information by modulating ‘effective connectivity’ [11,12]. Effective connectivity is an idealized index of connectivity that is functionally effective in a given behavioral period, and it would ultimately describe a degree of spike information flow (Figure 1a and b). During the oscillatory coupling, spikes in the presynaptic area can contribute in generating spike activities in the postsynaptic area because the spikes arrive postsynaptic area at peaks of excitability (Figure 1a). During low oscillatory coupling, spikes will arrive when the postsynaptic neurons are less excitable, and flow of spike information is limited. Thus, oscillatory coupling can modulate effective connectivity beyond the fixed anatomical connectivity between the two areas. Oscillatory coupling is dynamically controlled depending on a demand of the information processing between the two regions, which is presumably dependent on the ongoing task that animals are performing (green box in Figure 1b). Studies of subjects engaging cognitive tasks such as working memory, attentional selection and decision making reported elevated oscillatory coupling emerged when animals were engaging these tasks, but less in the control tasks [13–18].

The studies above strongly suggested the importance of the oscillatory coupling for the task performance. However, these studies typically reported oscillatory coupling from animals that had already learned the tasks. How does the oscillatory coupling sculpt the circuit connectivity during the learning of the task? Does the oscillatory coupling evolve monotonically during the task acquisition, or emerge only when the performance reaches an asymptotic level? To answer this question, several recent studies have examined plasticity in oscillatory coupling during task learning. A technical commonality of these studies is that they used: first, behavioral tasks that animals learned in a certain period of time and second, chronic multiple LFP recordings from brain areas that are required for the performance of the task (magenta box in Figure 1b). Since the hippocampus is required for several types of memory [19] and it is of great interest whether the oscillatory coupling sculpt the learning circuit in the hippocampus, most of these studies employed hippocampus-dependent memory tasks and recordings from the hippocampus and its connected areas. Here, I review these recent reports and discuss their implications and remaining open questions that should be addressed in future studies.

Figure 1



Evolution of oscillatory coupling during learning. **(a)** Oscillatory neural activity (sinusoidal curves) and spike activity (red ticks) are recorded simultaneously from two areas. Similar oscillations recorded with a delay are termed as ‘coupled oscillations’. Spike activity is typically observed at a specific phase of the oscillations. **(b)** Evolution of oscillatory coupling during task learning (magenta box). (Left row) In the early stage of task learning, oscillatory coupling, and thus the effective connectivity, is low at any time. (Middle row) In the middle stage of learning, oscillatory coupling starts to emerge. This coupling may provide coincidence of spikes between presynaptic and postsynaptic neurons with a short delay, resulting in the spike-time-dependent plasticity (arrows). (Right row) The synapses will be further strengthened in the late stage of learning, providing elevated effective connectivity when animals are engaging tasks and efficient information processing between two areas is required. Previous reports have focused this elevated coupling obtained from subjects after learning (green box).

### Plasticity in oscillatory coupling between the hippocampus and entorhinal cortex

One group of recent studies on the plasticity in oscillatory coupling targeted the entorhinal cortex (EC) and the hippocampus. The EC serves as an interface of information to the hippocampus. The hippocampus receives most of the cortical inputs through the direct projection from the EC [20]. In the hippocampus, the CA1 subfield receives entorhinal input via two major routes: directly from layer III EC cells, and indirectly from layer II EC cells via synapses in the dentate gyrus and CA3. Both the hippocampus and EC show theta and gamma oscillations [4,8], and a pioneering study of human patients suggested that oscillatory coupling in gamma band between the EC and hippocampus support working memory [13]. It has thus been a great interest whether oscillatory coupling sculpts connectivity in the EC–hippocampal projection during long-term learning.

The EC is anatomically divided into two distinct parts, lateral entorhinal cortex (LEC) and medial entorhinal cortex (MEC) (Figure 2a) [20]. LEC receives massive information from olfactory sensory regions and the perirhinal cortex, whereas MEC receives spatially modulated information mainly from the postrhinal cortex. As a result, cells in LEC are strongly modulated by odors [21] or

objects [22,23] and exhibit less spatial modulation [24]. In a recent study, we recorded neural activities in LEC and CA1 as rats learned an odor–place association task, and asked whether oscillatory coupling between LEC and CA1 evolved during the task learning [25\*\*]. It was previously reported that the acquisition of the odor–place association requires intact hippocampus [26], and rats learned this task in ~3 weeks. We found that LFP in both LEC and CA1 exhibited strong oscillations in the 20–40 Hz band (beta/gamma band) during sampling of the odor cues. Coherence analysis during the task learning showed that oscillatory coupling in the 20–40 Hz band did not exist in the early stage of the learning, but gradually increased during the task learning (Figure 2b). Interestingly, this coupling was lost when animals made errors in the task. Together, the results suggest that the oscillatory coupling in the 20–40 Hz band serves as a mechanism for enhancing communication between LEC and CA1 that underlies the odor–place association learning, and provide evidence for the role of beta/gamma oscillatory coupling in hippocampal learning.

The above study suggests the role of LEC–CA1 oscillatory coupling in the certain type of hippocampal learning. Is the circuit between the MEC and hippocampus

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