

EEG theta regulates eye saccade generation during human object-place memory encoding

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Summary

In this paper, we proposed a computational theory of human memory formation in the hippocampus and determined if electroencephalography (EEG) theta power is associated with eye saccades during object-place memory encoding. EEG theta power and saccade rate is significantly correlated with subsequent recall performance. This result suggests that information acquisition for object-place memory is processed by the theta rhythm network for memory system, attentional regulation and saccades.

1 Introduction

A neural dynamics "theta phase precession" observed in the rat hippocampus [1] [2] is considered to play an important role in online memory formation of the environment. In this phenomenon, the temporal sequence of place field activation is temporally compressed within the phase of every theta cycle and repeated in several theta cycles [2]. Since the time scale of this phase pattern matches the time-window of the spike-timing dependent plasticity (STDP) [3], theta phase precession results in synaptic plasticity. According to this evidence, Yamaguchi [4] proposed a computational theory: a behavioral input sequence is translated to theta phase precession in the entorhinal cortex, and stored into CA3 unidirectional connections according to STDP. Computer experiments demonstrated that theta phase precession is advantageous in memory formation with respect with various task demands [5].

The theory was further applied to human object-place memory, a model of human episodic memory [6] [7]. In the proposed computational network model [8], a visual input sequence consisting of object and scene information were assumed: the object input in the central visual field changes rapidly in relation to saccades, while the scene input in pe-

ripheral visual field changes continuously through several saccades (Fig. 1a).

By using computer experiments, it was found that theta phase precession of the visual input sequence results in a formation of a hierarchical cognitive map including scene unit layers and an object unit layer characterized by asymmetric connections. Thus, theta phase precession observed in the rat hippocampus could contribute to form human episodic memory.

The theoretical predictions of human memory formation have been evaluated in human experiments, as summarized in Figure 1b. First, the scalp EEG theta power during object-place memory encoding was found to significantly correlate with subsequent memory recall [9]. Second, theoretically simulated memory with human eye movement was also found to significantly correlate with human memory recall [10]. These results support the computational theory of human memory formation. In addition to this evidence, this theory would predict a positive correlation between EEG theta and eye saccades during successful memory encoding, although such a relation has not been evaluated.

In this paper, we elucidated the theoretical prediction of the relationship between EEG theta and eye saccades. If EEG theta is essential to encode

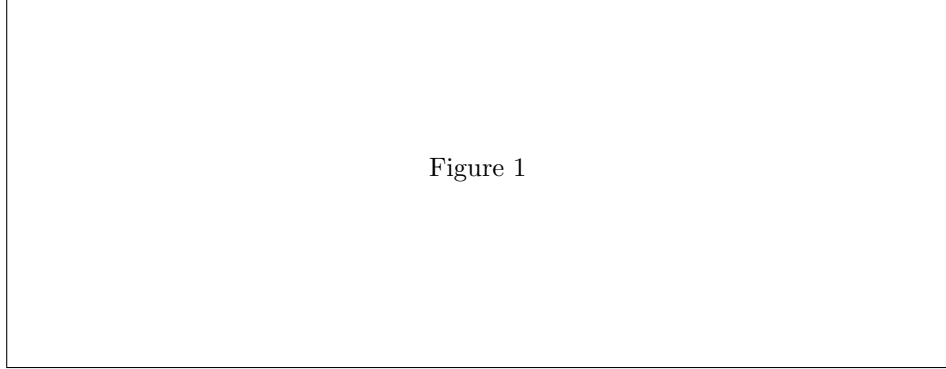


Figure 1

Figure 1: (a) A computational theory of object-place memory formation based on human theta phase precession [8]. (b) Supporting evidences of the computational theory.

object-place memory with visual input sequences, the EEG theta power-saccade rate coherence is expected to increase in relation to subsequently successful memory recall.

2 Methods

Scalp EEG and eye movement data reported in [9] were used. Eleven volunteers performed 350 trials of an object-place memory task that consists of an 8-sec encoding of a set of four object-place associations in 3-by-3 grids (subtended 15 by 15 degrees each), a 10-sec secondary task of random fixation, and a recall task of the objects configuration on the display using a mouse. During the task, 58-ch scalp EEG signals and 6-ch electro-oculography (EOG) signals were recorded with a Neuroscan amplifier (NeuroScan, US) and eye movement was recorded with a video-based eye-tracker (Eyelink I, SR Research, Canada). In the analysis, ocular artifacts in the EEG were corrected with the RAAA (revised aligned-artifact average) method using horizontal EOG, vertical EOG and radial EOG [11]. The coherence between wavelet EEG power of electrode i and saccade rate was further evaluated with a coherence value C_i defined by

$$C_i(f) = \left(\sum_{t=1}^N e_i(f, t) s(t) \right) / \left(\sum_{t=1}^N e_i(f, t) \sum_{t=1}^N s(t) \right), \quad (1)$$

where f is the frequency, N is the number of time points in a trial, and $e_i(f, t)$ is wavelet power at each time-point t , and $s_i(t)$ is the inter-grid saccade rate calculated by a 2-sec sliding window. A

Wilcoxon rank-sum test was used to compare the coherence values during encoding in each trial that were later either completely ("successful") or incompletely recalled ("failed"). As described in the previous report [9], saccade rate itself is not significantly correlated with subsequent memory recall ($t(10) = 1.59, p = 0.145 > 0.05$).

3 Results

Figure 2 represents an example of data processing: raw and corrected EEGs, raw and corrected wavelet EEG powers, eye movement, and saccade rate. EEG theta power intermittently increased with increased saccade rate. Note that the ocular artifacts in the lower frequency-range were well corrected as shown in the wavelet EEG power.

Figure 3 displays the topographical pattern of the increase in coherence values for each frequency power, in relation to subsequent memory recall. A significant increase of the EEG power-saccade rate coherence was found at the theta range (4.5-6.5 Hz) in the fronto-central region and in occipital region. These results are in a good agreement with the theoretical prediction. Note that the coherence indices of horizontal and vertical EOGs were not significantly correlated with subsequent memory recall, indicating that the coherence increase in theta range is not caused by residuals of EOG artifacts.

In order to remove residual ocular artifacts in EEG signals, we analyzed the coherence values only during eye fixation periods. The result is shown in Figure 4. A significant coherence in-

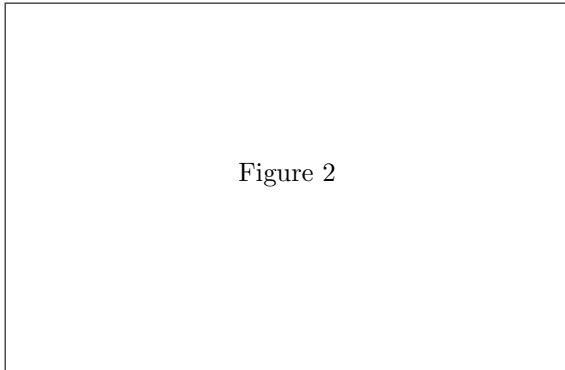


Figure 2: Results of EEG signals and eye movement recordings (subject 4860, Fz electrode, trial 19).

crease was again found at theta range (4.0-6.5 Hz) in the fronto-central region, confirming that the EEG theta power-saccade coherence increase is not caused by ocular artifacts. Moreover absence of significant effect in the occipital regions indicates that the subsequent memory effect in the occipital region is more related to periods of saccade occurrence. The subsequent memory effect in the fronto-central region is considered to be more independent of saccade timing.

4 Discussion

The EEG theta power-saccade rate coherence increase was found to significantly correlate with subsequent memory recall (Fig. 2, 3). The effect was found at a lower theta range (4.5-6.5 Hz) in fronto-central region. This differs from the subsequent memory related EEG power increase at higher theta range (6.5-7.5 Hz) in the posterior region (at 6.5 Hz), the central region (at 7.0 Hz), and the fronto-central region (at 7.5 Hz) (Fig. 3 in [9]). According to these results, there are two functional theta synchronization networks: a memory encoding system in higher theta (6.5-7.5 Hz) and a saccade regulation system in lower theta (4.5-6.5 Hz). Acquisition of object-place memory is processed by theta rhythm networks for memory, attentional regulation and saccades. These results support the computational theory of human object-place memory formation based on theta phase precession.

The current result suggests a functional role of the intermittent increase of EEG theta power

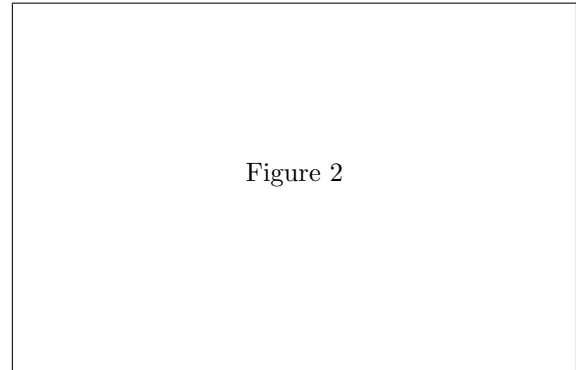


Figure 3: Topographical maps showing Wilcoxon rank-sum values difference of the EEG power-saccade rate coherence values between successful and failed trials. Filled red and blue circles represent electrodes showing a significant increase and decrease in coherence value ($p < 0.05$), respectively.

in the primate hippocampus [12] that is different from a continuous EEG theta observed in the rodent hippocampus [1] [2]. The intermittent EEG theta is expected to generate a set of visual input sequences that helps form an accurate memory within a limited encoding period (Fig. 5). The hippocampal local field potential (LFP) theta should increase in primates in relation to saccades, as recently pointed out by Ulanovsky and Moss [13].

Acknowledgments: All acknowledgments (if any) should be included at the very end of the manuscript before the references.

References

- [1] O'Keefe, J., Recce, M.L: Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus* **3** (1993) 317–330
- [2] Skaggs, W.E., McNaughton, B.L., Wilson, M.A., Barnes, C.A.: Theta phase precession in hippocampal neuronal populations and the compression of temporal sequences. *Hippocampus* **6** (1996) 149–172
- [3] Bi, G.Q., Poo, M.M.: Synaptic modifications in cultured hippocampal neurons: dependence

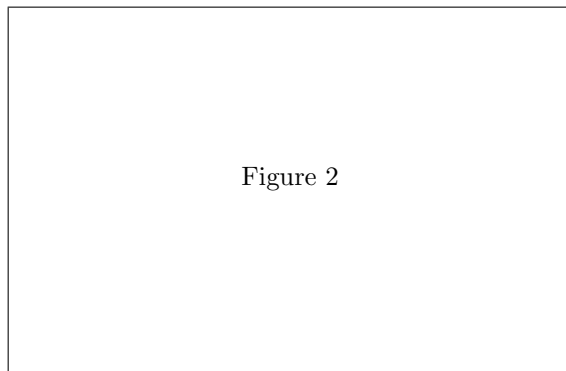


Figure 4: Topographical maps showing Wilcoxon rank-sum values difference of the EEG power-saccade rate coherence values between successful and failed trials, where saccade periods (from one oscillation cycle before saccade onset to one oscillation cycle after saccade offset) are excluded from the analysis.

on spike timing, synaptic strength, and postsynaptic cell type. *J. Neurosci.* **18** (1998) 10464–10472

- [4] Yamaguchi, Y.: A theory of hippocampal memory based on theta phase precession. *Biol. Cybern.* **89** (2003) 1–9
- [5] Yamaguchi, Y., Aota, Y., Sato, N., Wagatsuma, H., Wu, Z.: Synchronization of neural oscillations as a possible mechanism underlying episodic memory: A study of theta rhythm in the hippocampus. *J. Integ. Neurosci.* **3**(2) (2004) 143–157
- [6] Smith, M.L., Milner, B.: The role of the right hippocampus in the recall of spatial location. *Neuropsychologia* **19** (1981) 781–793
- [7] Stepankova, K., Fenton, A.A., Pastalkova, E., Kalina, M., Bohbot, V.D.: Object-location impairment in patient with thermal lesions to the right or left hippocampus. *Neuropsychologia* **42** (2004) 1017–1028
- [8] Sato, N., Yamaguchi, Y.: On-line formation of a hierarchical cognitive map for object-place association by theta phase coding. *Hippocampus* **15** (2005) 963–978
- [9] Sato, N., Yamaguchi, Y.: Theta synchronization networks emerge during human object-

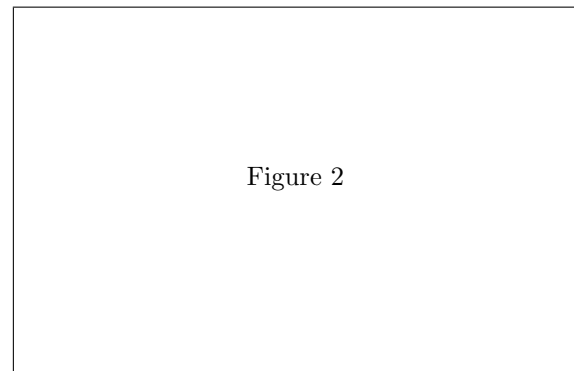


Figure 5: (a) A continuous visual input sequence. (b) A set of visual input sequences segmented by EEG theta.

place memory encoding. *NeuroReport* **18**(5) (2007) 419–424

- [10] Sato, N., Yamaguchi, Y.: An evidence of a hierarchical representation of object-place memory based on theta phase coding: A computational model- human experiment combined analysis, Program No. 366.25, Society for Neuroscience Abstracts, 2006
- [11] Croft, R.J., Barry, R.J.: Removal of ocular artifact from EEG: a review. *Neurophysical Clin.* **30** (2000) 5–19
- [12] Ekstrom, A.D., Caplan, J.B., Ho, E., Shattuck, K., Fried, I., Kahana, M.J.: Human hippocampal theta activity during virtual navigation. *Hippocampus*. **15**(7) (2005) 881–889
- [13] Ulanovsky N, Moss CF.: Hippocampal cellular and network activity in freely moving echolocating bats. *Nat Neurosci.* **10**(2) (2007) 224–233