We are IntechOpen,
the world's leading publisher of
Open Access books
Built by scientists, for scientists

4,800
Open access books available

122,000
International authors and editors

135M
Downloads

Our authors are among the

154
Countries delivered to

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com

Hippocampal Theta Activity During Stimulus Discrimination Task

Yuya Sakimoto and Dai Mitsushima

Additional information is available at the end of the chapter

Abstract

The configural association theory and conflict resolution model both propose that hippocampal function plays role in the solving a negative patterning task but not simple discrimination task. Some hippocampal lesion study showed that inactivity of rats' hippocampal CA1 area induced impairment of performance of a negative patterning task. Other previous studies, however, showed that the lesion did not affect the performance of the task. Thus, it did not reveal whether hippocampal function was important for solving the negative patterning task. Our recent research using an electrophysiological approach showed that the hippocampal theta power decreased with a compound stimulus of a negative patterning task, and that the hippocampal theta power was decreased by a compound stimulus of a feature negative task. These results indicate that a decrease in hippocampal theta activity is elicited by behavioral inhibition for conflict stimuli with overlapping elements. This finding strongly supports the conflict resolution model and suggests a hippocampal role in learning behavioral inhibition for conflict stimuli during nonspatial stimulus discrimination tasks.

Keywords: hippocampal theta power, negative patterning task, feature negative task, configural association theory, conflict resolution model

1. Hippocampal memory functions

After report of a patient H.M. [1], the various areas of research, including psychology, neuroscience, cognitive science, and behavioral science, have researched the hippocampal function for learning and memory. The patient H.M. suffered epileptic seizures as a child. He receives a resection of a portion of temporal lobe including hippocampus for treating the seizures when he was 27 years old. Although the treatment reduced the symptom of seizure without lack of

some his cognitive and memory functions, such as intelligence quotient (IQ), conversational ability, perceptual capability, working memory, semantic memory formed before surgery, and procedure memory, the patient H.M. had minor symptoms of retrograde amnesia and severs anterograde amnesia [1]. Thus, Scoville and Milner [1] suggested that the hippocampus is necessary for the encoding of episode memory but not retrieval and storage of the memory. After then, for understanding the hippocampal function in detail, animal researchers have examined what kind of learning task is necessary for being solved by hippocampal functions. In the electrophysiology study, O'Keefe and Nadel [2] showed that the rodents' hippocampal CA1 neuron was activated by the memory of placement. They named "place cell" as hippocampal CA1 neuron which associated information of placement and suggested the cognitive theory that hippocampus was important for solving spatial learning by using eight arms radical maze and Morris water maze. In the hippocampal lesion study, Bouffard and Jarrard [3] compared hippocampal lesion rat and control rat without hippocampal lesion on eight arms radical maze. For solving this task, rats need to learn the arms that were choose once time by using peripheral environmental cue outside of the maze. The performance of the rats with hippocampal lesion was less than that control rats. Also, it has examined on the Morris water maze. For solving the task, the rats need to understand own position and goal position from some environmental stimuli outside the maze and reach the goal position by cueing these stimuli. The rats with hippocampal lesion increase a latency that reached an invisible goal platform as compared with control rats on the maze [4]. In addition, several research studies showed the universal function that hippocampus plays role in a spatial learning over other species, such as fishes [5], birds [6, 7], and primate [8, 9], suggesting that the cognitive map theory is one of the popular hippocampal function theories having adaptive possibility for various species. On the other hand, some researchers have reported that hippocampal function was important for solving a certain type of nonspatial stimulus discrimination task.

2. Negative patterning task

Configural association theory suggests that the hippocampus plays role in learning the relationship between multiple sensory stimuli [10]. According to the theory, animals have two systems, elemental and configural association systems, for processing sensory information, and they adapt successfully to various situations in the external world by using them. The elemental association system forms representation of single stimulus, such as the single stimulus associated with reinforcement or punishment. However, in the external world, a compound stimulus combining multiple stimuli may sometimes have a significant meaning. The configural association system forms one of the configural representations by associating between multiple stimuli when some of them are presented simultaneously or serially. Sutherland and Rudy [10] proposed that hippocampal function was necessary for the formation of configural representations for compound stimuli. After then, the theory was revised by some researchers [11–13] and latest theory that the hippocampus is important for configural presentation for compound stimulus in exclusive-or (XOR) tasks such as negative patterning task and positive patterning task. In the negative

patterning task, rats are reinforced for operant responses when either one of two different sensory single stimuli, such as tone (T) or light (L), is presented (T+ or L+). In contrast, rats are not reinforced when both stimuli are presented (TL−). In this task, compound stimulus had overlapping element with single stimuli. For solving this task, rats need to, thus, form the configural representation for compound stimulus and discriminate between compound stimulus and single stimuli.

Gray and McNaughton [14] proposed the conflict resolution model for the hippocampal function and behavioral inhibition. The model suggests that the hippocampal function plays role in the resolution of conflict between incompatible goals or response tendencies. According to this model, the hippocampal function modulates the weight of negative information and, specifically, increases it, thereby inducing behavioral inhibition [14, 15]. Interestingly, this theory may also explain why the hippocampus is important for solving the compound stimulus in the negative patterning task. In the negative patterning task, either one of stimuli A and B is presented alone when they signal a "go" response, but the stimuli are presented simultaneously when they signal a "no-go" response. Thus, the compound stimulus had incompatible goals or response tendencies. Animals need to increase the weight of negative information and inhibit operant response for compound stimulus. Both the conflict resolution model and the configural association theory suggest a role of the hippocampus in solving the negative patterning task.

3. Hippocampal lesion and negative patterning task

Several previous studies reported that hippocampal lesions impair the negative patterning task performance [10, 16–18]. However, some studies have reported no effects of hippocampal lesions on the negative patterning task [19]. Davidson et al. [19] reported abnormal behavioral inhibition of the operant response after hippocampal lesions, suggesting a lack of learning ability for compound stimuli. Moreover, hippocampal lesions result in an abnormal operant response, such as response persistence [20]. Therefore, in order to build a more solid foundation for the configural association theory and conflict resolution model, the relationship between hippocampal activity and the negative patterning task needs to be investigated by means other than hippocampal lesions.

4. Hippocampal theta activity during negative patterning

It has been known that electroencephalography (EEG) was useful for neural activity of hippocampus without extensive hippocampal lesions in rodents. When we implanted a recording polar into the rats' hippocampal CA1 area, we can observe rhythmic EEG patterns. The EEG activity was grouped: theta waves (6–12 Hz), beta waves (12–30 Hz), gamma waves (30–100 Hz), and ripple waves (100–200 Hz). Specifically, it was known that hippocampal theta wave is related to psychological state and behavior. Several studies have reported that hippocampal

theta waves strongly are related to locomotor behavior such as running, jumping, ricking, and operant response [21–24]. In addition, it has reported that hippocampus theta activity is related to learning and memory [25–43]. Masuoka et al. [29] showed that rats' hippocampal theta activity increased during elevated radical eight mazes. Also, Olvera-Cortés et al. [30, 31] revealed that the hippocampal theta waves change during performance of spatial learning task. Thus, in addition, theta waves are thought to occur by the synchronization of neurons in the whole hippocampal formation [44], which would reflect hippocampal neural activity [45–48].

Recently, we have examined hippocampal theta activity in rats during the acquisition stages (early, middle, and late) of the negative patterning task (T+, L+, TL−) [38]. We observed a transient decrease in hippocampal theta power immediately after the presentation of a compound stimulus during the late stage of learning in the negative patterning task (**Figure 1**). In addition, the magnitude of the decrease in theta power strongly correlated with improved performance in the negative patterning task (**Figure 2**). Grastyán et al. [49] examined the relationship between hippocampal theta activity and the acquisition of an orientative conditioned response (CR) for a tone stimulus presentation in cats. Although the hippocampal theta activity increased with an association between stimulus and orientative CR, the hippocampal theta wave decreased after the formation of this association. Thus, the transient decrease in hippocampal theta activity during the late stage of learning in the negative patterning task observed in the current study may be related to mastery of the negative patterning task. However, our previous reports showed a greater decrease in hippocampal theta activity in the late learning stage of a negative patterning task compared to the simple discrimination task [32, 38]. Therefore, we suggest that the decrease in hippocampal theta power is induced by hippocampus-mediated information processing for compound stimuli in the negative patterning task. This is in agreement with the concepts of the configural association theory and conflict resolution model.

Further studies revealed characteristics of compound stimuli inducing a decrease in theta power by comparing simultaneous feature-negative (T+, TL−) and compound stimulus discrimination tasks (T_1+, T_2L−) [32]. In feature negative tasks, the compound stimulus had overlapping elements with single stimuli because these stimuli were composed of tone stimuli with the same frequency component. However, the compound stimulus in the compound stimulus discrimination task did not have overlapping elements with single stimuli because they were composed of tone stimuli with different frequency components (T_1: 2000 Hz, T_2: 4000 Hz). These studies reported a transient decrease in hippocampal theta activity following the presentation of a compound stimulus during the simultaneous feature-negative task compared to the simple discrimination task but not during the compound stimulus discrimination task. The compound stimulus of the simultaneous feature-negative task had an overlapping element shared with the single stimulus. This may justify the transient decrease in hippocampal theta activity during response inhibition for the compound stimulus of negative patterning and simultaneous feature-negative tasks. Therefore, we proposed that the decrease in hippocampal theta power is related to behavioral inhibition for conflict stimulus discrimination in which the single stimuli have overlapping elements.
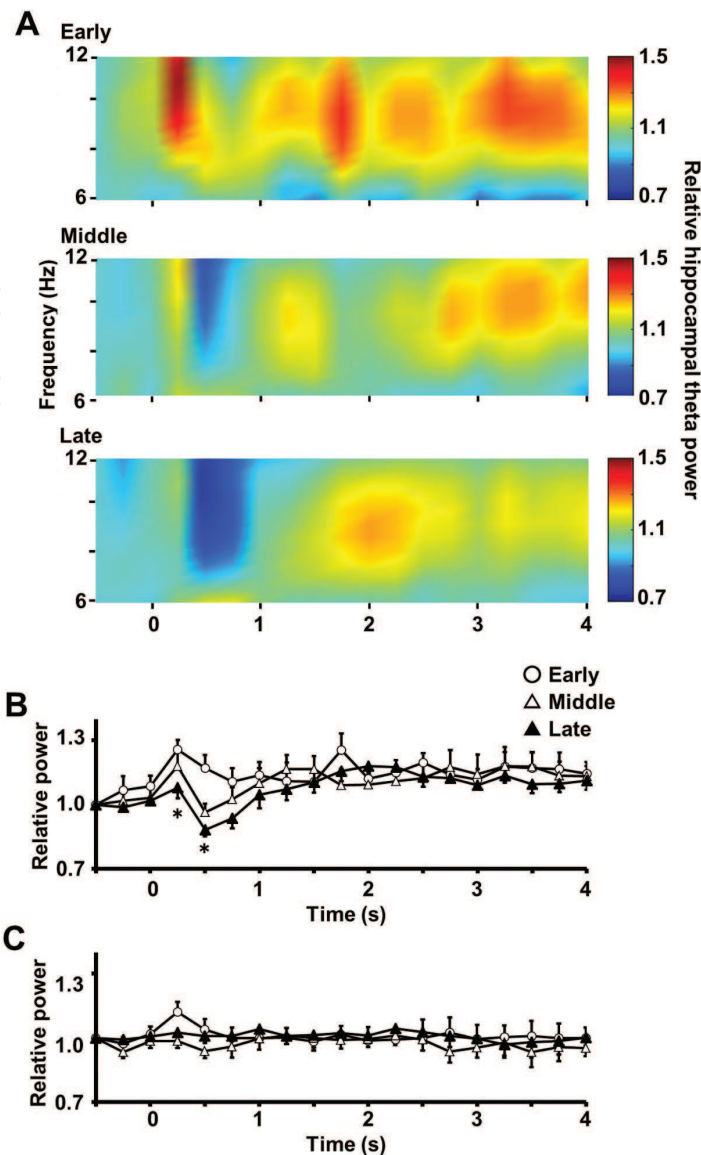
Figure 1. The change in theta power during a presentation of compound stimuli of the negative patterning task by using wavelet analysis (A). Upper side shows the change in hippocampal theta activity along a time course during compound stimulus on the early stage, Middle side shows theta activity on the middle stage, and Lower side shows theta activity on late stage of negative patterning task. The x-axis is time (ms), and the y-axis is frequency (Hz). In each panel, the period is from 500 ms before stimulus onset to 4000 ms after stimulus onset. The mean hippocampal theta power during 500 ms before stimulus onset was counted as the −500-ms period (no stimuli were present and no rats pressed the lever during this period), and the relative theta power calculated for each period (per 250 ms) was normalized to that during the −500-ms period (relative theta activity of each period = theta power of each period/theta power at the −500-ms period). Panel B contains a comparison of the mean (± S.E.M.) relative hippocampal theta activity at 6–12 Hz among each learning stage (early, middle, and late) throughout the time course of the experiment during compound stimuli of the negative patterning task. Two-way within-subjects ANOVA suggests that there is a significant interaction of learning stages (early, middle, and late) × epochs (−500 to 4000 ms, with each 250 ms; $F(36,180) = 2.37$, $p < 0.05$) and a significant effect of epochs ($F(18,90) = 4.80$, $p < 0.05$), but no significant effect of stages ($F(2,10) = 0.97$, n.s.) on relative hippocampal theta power during compound stimulus of the negative patterning task. *Post-hoc* tests showed that there was a significant simple main effect in the 250- and 500-ms epochs during compound stimulus. Multiple comparisons revealed that hippocampal theta power decreased in the 250-ms epochs during nonRFTs in the late stage compared with the early stage ($p < 0.05$) and in the 500-ms epochs during nonRFTs in the middle and late stages compared with the early stage (* $p < 0.05$). Panel C contains a comparison of the mean (± S.E.M.) relative hippocampal theta activity at 6–12 Hz among each learning stage (early, middle, and late) throughout the time course of the experiment during nonreinforced stimulus of the simple discrimination task. This figure was referred to Sakimoto et al. [38].
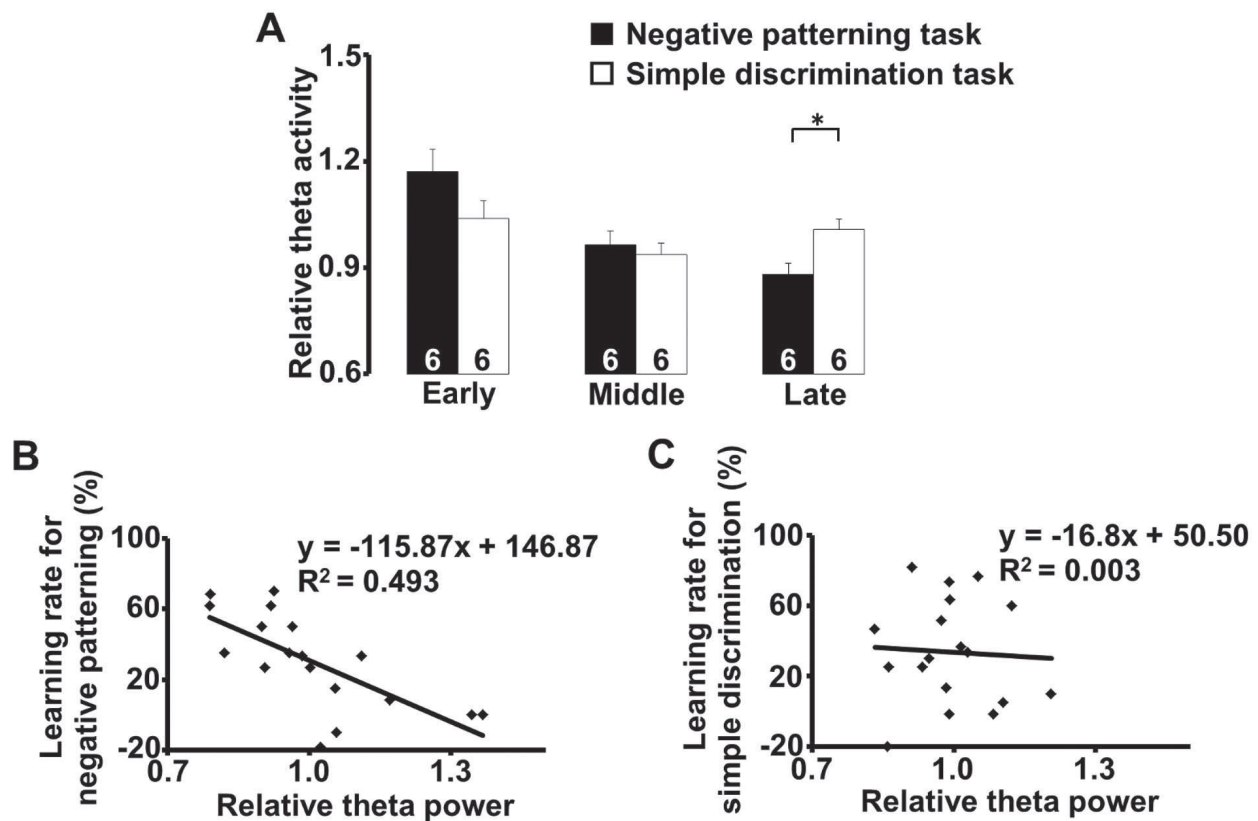
Figure 2. A comparison of the mean relative hippocampal theta activity between tasks. Panel A shows the relative hippocampal theta power during the 500-ms epochs between the negative patterning and simple discrimination task groups. A group (negative patterning task and simple discrimination task groups) × stage (early, middle, and late) ANOVA for hippocampal theta activity during a 500-ms epoch in the nonRFT showed a significant interaction ($F(2,20)$ = 6.12, $p < 0.05$). Multiple comparisons revealed that hippocampal theta power decreased during the late stage in the negative patterning task compared to the simple discrimination task group ($p < 0.05$; *: $p < 0.05$). Hippocampal theta power during the 500 ms nonRFT correlated with the discrimination rate in the negative patterning task ($r = −0.70$, $p < 0.05$; panel B) but not the simple discrimination task ($r = −0.06$, $p =$ n.s; panel C). This figure was referred to Sakimoto et al. [38].

5. Why does hippocampal theta amplitude decline?

Hippocampal theta power is affected by the activity of cholinergic and γ-aminobutyric acid (GABA) neurons of the medial septal/diagonal band area [44]. Monmaur and Breton [50] demonstrated that theta activity increases when the cholinergic agonist, carbachol, is injected into the intra septum in freely moving rats. In addition, Sun et al. [51] reported that hippocampal theta activity is abolished by the GABA antagonist bicuculline. Thus, we propose that the transient decrease in hippocampal theta activity during compound stimulus learning in the negative patterning task is induced by the activity of septal cholinergic or GABAergic neurons, or their interaction. In future studies, the relationship between the negative patterning task and septal cholinergic and/or GABAergic activity should be examined. Because septo-hippocampal GABAergic input to CA1 is essential for the generation of theta waves [52], the transient decrease

in presynaptic GABA release may cause a transient decrease in the hippocampal theta power immediately after stimulus presentation. We recently analyzed synaptic plasticity using the slice patch-clamp technique and measured a rapid decrease in presynaptic GABA release at hippocampal CA1 synapses immediately after the nonspatial contextual learning task, inhibitory avoidance (IA) [53]. Compared to untrained controls, the paired pulse ratio (PPR) of evoked inhibitory postsynaptic current (IPSC) increased immediately after IA training (at 0 min), suggesting an acute decrease in the probability of presynaptic GABA release. As the PPR returned to baseline 5 min after the training, the decrease in presynaptic GABA release seems to be transient. Moreover, we observed a sustained increase in the miniature excitatory postsynaptic current (mEPSC) and miniature inhibitory postsynaptic current (mIPSC) amplitudes 5–30 min after the IA task, suggesting long-term postsynaptic strengthening of α-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid (AMPA) and $GABA_A$ receptor-mediated synapses. In addition, the long-term increase in mIPSC frequency is probably due to an increase in the number of $GABA_A$ receptor-mediated inhibitory synapses after the training [53].

6. Conclusion

We discussed hippocampal function in a nonspatial stimulus discrimination task with a focus on the configural association theory and conflict resolution model. These functions were strongly supported by the observations that hippocampal theta power decreased during the presentation of a compound stimulus in a negative patterning task [32, 38]. A transient decrease in hippocampal theta activity was also observed during the presentation of a compound stimulus in the simultaneous feature-negative task but not in the compound stimulus discrimination task [32]. These results suggest that the decrease in hippocampal theta activity was elicited by behavioral inhibition of a conflict stimulus with overlapping elements. Therefore, we conclude that the hippocampus may play a role in this cognitive process. This conclusion strongly supports the conflict resolution model, in which the hippocampus plays a role in negative information processing for conflict stimuli in the nonspatial discrimination task. Moreover, data suggest a link between a decreased in theta power and decreased septal cholinergic activity and increased septal GABAergic activity. Finally, we conclude that the hippocampal neural activity derived from septal cholinergic and GABAergic activities plays a central role in behavioral inhibition for conflict stimuli with overlapping elements.

Author details

Yuya Sakimoto* and Dai Mitsushima

*Address all correspondence to: y-saki@yamaguchi-u.ac.jp

Department of Physiology, Graduate School of Medicine, Yamaguchi University, Minami-Kogushi, Ube, Japan

References

[1] Scoville WB, Milner B. Loss of recent memory after bilateral hippocampal lesions. Journal of Neurology Neurosurgery Psychiatry. 1957;**20**:11-21

[2] O'Keefe J, Nadel L. The Hippocampus as a Cognitive Map. Oxford, UK: Oxford University Press; 1978

[3] Bouffard JP, Jarrard LE. Acquisition of a complex place task in rats with selective ibotenate lesions of hippocampal formation: Combined lesions of subiculum and entorhinal cortex versus hippocampus. Behavioral Neuroscience. 1988;**102**:828-834

[4] Gallagher M, Holland PC. Preserved configural learning and spatial learning impairment in rats with hippocampal damage. Hippocampus. 1992;**2**:81-88

[5] Saito K, Watanabe S. Experimental analysis of spatial learning in goldfish. Psychological Record. 2005;**55**:647-662

[6] Watanabe S, Bischof H-J. Effects of hippocampal lesions on acquisition and retention of spatial learning in zebra finches. Behavioral Brain Research. 2004;**155**:147-152

[7] Pearce JM, George DN, Hallselgrove M, Erichsen JT, Good MA. The influence of hippocampal lesions on the discrimination of structure and on spatial memory in pigeons (*Columba livia*). Behavioral Neuroscience. 2005;**119**:1316-1330

[8] Baylis GC, Moore BO. Hippocampal lesions impair spatial response selection in the primate. Experimental Brain Research. 1994;**98**:110-118

[9] Parkinson JK, Murray EA, Mishkin M. A selective mnemonic role for the hippocampus in monkeys: Memory for the location of objects. Journal of Neuroscience. 1988;**8**:4159-4167

[10] Sutherland RJ, Rudy JW. Configural association theory: The role of the hippocampal-formation in learning, memory, and amnesia. Psychobiology. 1989;**17**:129-144

[11] Rudy JW, Sutherland RJ. Configural association theory and the hippocampal formation: An appraisal and reconfiguration. Hippocampus. 1995;**5**:375-389

[12] O'Reilly RC, Rudy JW. Computational principles of learning in the neocortex and hippocampus. Hippocampus. 2000;**10**:389-397

[13] O'Reilly RC, Rudy JW. Conjunctive representations in learning and memory: Principles of cortical and hippocampal function. Psychological Review. 2001;**108**:311-345

[14] Gray JA, McNaughton N. The Neuropsychology of Anxiety. 2nd ed. New York: Oxford University Press; 2000

[15] Davidson TL, Jarrard LE. The hippocampus and inhibitory learning: A gray area. Neuroscience & Biobehavioral Reviews. 2004;**28**:261-271

[16] Alvarado MC, Rudy JW. A comparison of kainic acid plus colchicine and ibotenic acid-induced hippocampal formation damage on four configural tasks in rats. Behavioral Neuroscience. 1995;**109**:1052-1062

[17] Rudy JW, Sutherland RJ. The hippocampal formation is necessary for rats to learn and remember configural discriminations. Behavioral Brain Research. 1989;**34**:97-109

[18] Sutherland R J, McDonald RJ. Hippocampus, amygdala, and memory deficits in rats. Behavioral Brain Research. 1990;**37**:57-79

[19] Davidson TL, McKernan MG, Jarrard LE. Hippocampal lesions do not impair negative patterning: A challenge to configural association theory. Behavioral Neuroscience. 1993;**107**:227-234

[20] Douglas RJ. The hippocampus and behavior. Psychological Bulletin. 1967;**67**:416-442

[21] Bland BH, Vanderwolf CH. Diencephalic and hippocampal mechanisms of motor activity in rat: Effects of posterior hypothalamic stimulation on behavior and hippocampal slow-wave activity. Brain Research. 1972;**43**:67-88

[22] Frederickson CJ, Whishaw IQ. Hippocampal EEG during learned and unlearned behavior in the rat. Physiology & Behavior. 1977;**18**:597-603

[23] Vanderwolf CH. Hippocampal electrical activity and voluntary movement in the rat. Electroencephalography and Clinical Neurophysiology. 1969;**26**:407-418

[24] Whishaw IQ, Vanderwolf CH. Hippocampal EEG and behavior: Changes in amplitude and frequency of RSA (theta rhythm) associated with spontaneous and learned movement patterns in rats and cats. Behavioral Biology. 1973;**8**:461-484

[25] Brankack J, Talnov A, Shin J, Matsumoto G. Task-related theta frequency changes in rats trained to perform an auditory discrimination. Abstracts—Society for Neuroscience. 1999;**25**:1386

[26] Gray JA. Sodium amobarbital, the hippocampal theta rhythm, and the partial reinforcement extinction effect. Psychological Review. 1970;**77**:465-480

[27] Gray JA, Ball GG. Frequency-specific relation between hippocampal theta rhythm, behavior, and amobarbital action. Science. 1970;**168**:1246-1248

[28] Kasicki S, Jeleń P, Olszewski M, Sławińska U. Electrical hippocampal activity during danger and safety signals in classical conditioning in the rat. Acta Neurobiologiae Experimentalis (Wars). 2009;**69**:119-128

[29] Masuoka T, Fujii Y, Kamei C. Participation of the hippocampal theta rhythm in memory formation for an eight-arm radial maze task in rats. Brain Research. 2006;**1103**:159-163

[30] Olvera-Cortés E, Cervantes M, González-Burgos I. Place-learning, but not cue-learning training, modifies the hippocampal theta rhythm in rats. Brain Research Bulletin. 2002;**58**:261-270

[31]   Olvera-Cortés E, Cervantes M, González-Burgos I. Increase of the hippocampal theta activity in the Morris water maze reflects learning rather than motor activity. Brain Research Bulletin. 2004;**62**:379-384

[32]   Sakimoto Y, Sakata S. The decline in rat hippocampal theta activity during response inhibition for the compound stimulus of negative patterning and simultaneous feature-negative tasks. Behavioral Brain Research. 2013;**257**:111-117

[33]   Sakimoto Y, Sakata S. Change in hippocampal theta activity with transfer from simple discrimination tasks to a simultaneous feature-negative task. Frontiers in Behavioral Neuroscience. 2014;**8**:159

[34]   Sakimoto Y, Sakata S. Hippocampal theta activity during behavioral inhibition for conflicting stimuli. Behavioral Brain Research. 2014;**275**:183-190

[35]   Sakimoto Y, Sakata S. Behavioral inhibition during a conflict state elicits a transient decline in hippocampal theta power. Behavioral Brain Research. 2015;**290**:70-76

[36]   Sakimoto Y, Sakata S. Change in hippocampal theta activity during behavioral inhibition for a stimulus having an overlapping element. Behavioral Brain Research. 2015;**282**: 111-116

[37]   Sakimoto Y, Hattori M, Takeda K, Okada K, Sakata S. Hippocampal theta wave activity during configural and non-configural tasks in rats. Experimental Brain Research. 2013;**225**:177-185

[38]   Sakimoto Y, Okada K, Takeda K, Sakata S. Transient decline in hippocampal theta activity during the acquisition process of the negative patterning task. PLoS One. 2013;**8**:e70756

[39]   Sakimoto Y, Okada K, Hattori M, Takeda K, Sakata S. Neural activity in the hippocampus during conflict resolution. Behavioral Brain Research. 2013;**237**:1-6

[40]   Sakimoto Y, Takeda K, Okada K, Hattori M, Sakata S. Transient decline in rats' hippocampal theta power relates to inhibitory stimulus-reward association. Behavioral Brain Research. 2013;**246**:132-138

[41]   Sato N, Sakata S. Hippocampal theta activity during delayed nonmatching-to-sample performance in rats. Psychobiology. 1999;**27**:331-340

[42]   Shin J, Lu BL, Talnov A, Matsumoto G, Brankack J. Reading auditory discrimination behaviour of freely moving rats from hippocampal EEG. Neurocomputing. 2001;**38-40**: 1557-1566

[43]   Teitelbaum H, McFarland WL, Mattsson JL. Classical conditioning of hippocampal theta patterns in the rat. Journal of Comparative and Physiological Psychology. 1977;**91**: 674-681

[44]   Yoder RM, Pang KC. Involvement of GABAergic and cholinergic medial septal neurons in hippocampal theta rhythm. Hippocampus. 2005;**15**:381-392

[45] Buzsáki G. Generation of hippocampal EEG patterns. In: Isaacson RL, Pribram KH, editors. The Hippocampus. Vol. 3. New York: Plenum Press; 1986. pp. 137-167

[46] Fox SE, Wolfson S, Ranck JB. Hippocampal theta-rhythm and the firing of neurons in walking and urethane anesthetized rats. Experimental Brain Research. 1986;**62**:495-508

[47] Mitchell SJ, Ranck JB. Generation of theta rhythm in medial entorhinal cortex of moving rats. Brain Research. 1980;**189**:49-66

[48] O'Keefe J. Hippocampal neurophysiology in the behaving animal. In: Andersen P, Morris R, Amaral D, Bliss T,O'Keefe J, editors. The Hippocampus Book. New York: Oxford University Press; 2008. pp. 475-548

[49] Grastyán E, Lissak K, Madarasz I, Donhoffer H. Hippocampal electrical activity during the development of conditioned reflexes. Electroencephalography and Clinical Neurophysiology. 1959;**11**:409-430

[50] Monmaur P, Breton P. Elicitation of hippocampal theta by intraseptal carbachol injection in freely moving rats. Brain Research. 1991;**544**:150-155

[51] Sun MK, Zhao WQ, Nelson TJ, Alkon DL. Theta rhythm of hippocampal CA1 neuron activity: Gating by GAB aergic synaptic depolarization. Journal of Neurophysiology. 2001;**85**:269-279

[52] Lee MG, Chrobak JJ, Sik A, Wiley RG, Buzsáki G. Hippocampal theta activity following selective lesion of the septal cholinergic system. Neuroscience. 1994;**62**:1033-1047

[53] Sakimoto Y, Mitsushima D. Rapid synaptic plasticity within 5 min: experienced episode increases diversity of excitatory and inhibitory synapses in the hippocampal CA1. Abstracts Journal of Physiological Science. 2016;**66**:s127