



Research report

Behavioral inhibition during a conflict state elicits a transient decline in hippocampal theta power

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HIGHLIGHTS

- It is thought that SD and fast FN learning use the same strategy.
- We show different hippocampal theta activity in fast FN-learning and SD-learning rats.
- Thus, fast FN learning and SD learning involve different strategies.

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ABSTRACT

Although it has been shown that hippocampal theta power transiently declines during response inhibition in a simultaneous feature negative (FN: A+, AB−) task, observations of additional changes after this initial decline have been inconsistent across subjects. We hypothesized that the cause of these inconsistencies might be that variations in the learning speed for the FN task differentially affect the changes in hippocampal theta activity observed during the task. In this study, we classified rats into three groups (fast, intermediate, and slow FN-learning groups) based on the number of sessions required to complete learning of the FN task. We then examined whether there was a difference in hippocampal theta power among the fast, intermediate, and slow FN-learning groups, and rats that learned a simple discrimination task (SD group). We observed that compared to the SD group, the slow FN-learning group, but not the fast FN-learning group, showed an increase in hippocampal theta power. In addition, a transient decline of hippocampal theta power occurred in the fast FN-learning group, but not in the slow FN-learning group. These results indicate that the hippocampal theta activity during response inhibition in the FN task differed between fast- and slow-learning rats. Thus, we propose that a difference in learning speed affected hippocampal theta activity during response inhibition under a conflict state.

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1. Introduction

The most prominent EEG frequency recorded from the hippocampal formation is composed of theta waves [1,2]. In the rat, hippocampal theta waves consist of rhythmic, often sinusoidal oscillations that vary in frequency from 6 to 12 Hz [3]. Theta waves are generated by the synchronization of electrical activity from cells throughout the entire hippocampal formation [3–6]. A number of studies have suggested that hippocampal theta activity is related

to learning [7–11] and movement [12–14]. Notably, previous study showed that increased hippocampal theta activity was observed in rats as they carried out voluntary motor movements, such as running, jumping, rearing, exploratory behavior, sniffing, and lever pressing [12]. Additional studies by Sinnamon have further shown a relationship between a decline in hippocampal theta power and behavioral inhibition [15,16] induced by the presentation of a negative cue that suppressed approach locomotion in rats. Sinnamon proposed that this decline was related to the preparation or planning of behavioral inhibition, as diminished theta power preceded locomotor suppression.

Recent studies from our group have indicated that a decline in hippocampal theta power occurs during response inhibition under a conflict state in a go/no-go stimulus discrimination task [17–21]. To induce a conflict state, a feature negative (FN) task was used in these previous studies [17,20]. Rats were trained to carry out a

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lever press response upon the presentation of stimulus A, and in contrast, to withhold a lever press response upon presentation of stimulus AB. To solve this task, rats were required to learn a go lever press response for stimulus A and a no-go lever press response for stimulus B of the compound stimulus (AB). As a result, a conflict state leading to response inhibition was induced in the case of the compound stimulus (AB), as it elicited a go and no-go response tendency.

Another recent study [22] has examined hippocampal theta activity during a stimulus eye blink conditioning-based discrimination task in rabbits, and found that there was variability in the number of trials required to completely learn the task. Moreover, hippocampal theta activity differed between fast- and slow-learning rabbits after they had completely learned the task. In a previous study, we similarly observed great variability in the number of sessions required to completely learn our FN task compared to a simple discrimination (SD) control task. However, it has not yet been determined whether a difference in learning speed affects hippocampal theta activity during response inhibition under a conflict state. To address this question in this study, we classified rats into three groups (fast, intermediate, and slow FN-learning groups) based on the number of sessions required to complete learning of the FN task and examined whether there was a difference in hippocampal theta power among these groups, as well as an SD-learning control group.

2. Materials and methods

2.1. Subject

Fourteen 3-month-old, naïve, male Wistar albino rats were included in this study (FN task group: $n = 8$; SD task group: $n = 6$). In addition, we used data collected from the FN task group ($n = 18$) and the SD task group ($n = 17$) in experiment 2 of two previous studies [15,19]. Thus, in this study, we used data from a total of 49 rats (FN task group: $n = 26$; SD task group: $n = 23$). All rats were housed in individual cages and kept on a 12:12-h light–dark cycle (lights on at 8:00 am). Throughout the experiment, all rats were maintained at 85% of their ad libitum weights and water was freely available. All procedures for animal treatment and surgery were conducted in accordance with the regulatory standards of Hiroshima University.

2.2. Experimental apparatus

The apparatus has been described in our previous studies [17,20]. Behavioral training and electroencephalogram (EEG) recording sessions were conducted in a standard operant chamber (ENV-007 CT; MED Associates, Inc., USA). The chamber was housed in a soundproof, electrically shielded room. For delivery of 45-mg food pellets, a cup was located in the center of the front wall at floor level and a light bulb (ENV-215; MED Associates, Inc.) was mounted over the cup to provide constant illumination. A lever was positioned on the left side of the front wall. A white super luminosity LED light (41 lx) was mounted on the ceiling to present the light stimulus. A tone (2000 Hz, 75 dB) was provided via a speaker placed on the interior shell. All events were controlled, and behavioral data was recorded on a personal computer (Epson MT7500).

2.3. Experimental procedure

Rats were habituated to the operant box for 30 min, and were then trained to press a lever. We used 45-mg food pellets (Bio-Serv, product #F0165) as reinforcement. Following the acquisition of this response, rats were given 2 days of continuous reinforcement training (100 reinforcements/day), followed by 3 days of training at variable intervals of 20 s (VI20; 40 reinforcements/day). Next,

rats were grouped into the FN and SD task groups. Following task training, electrodes for EEG recording were implanted into each rat, and after a 1-week recovery period, three retention tests for the task that was trained pre-surgery were conducted. EEG readings were recorded throughout the retention test.

2.4. Learning tasks

2.4.1. Feature-negative (FN) task

The FN protocol was described in our previous studies [17,20]. The rats were assigned to one of the two types of FN discrimination. For one group (T+, TL–), rats were trained to learn a reward was associated with lever responses for tone stimuli (T+), but not for compound stimuli that simultaneously presented a tone and light (TL–). For the other group (L+, TL–), rats were trained to learn a reward was associated with lever responses for light stimuli (L+), but not for compound stimuli (TL–). All stimuli remained on until either 10 s had elapsed or until the rat pressed the lever. Each trial was separated by variable inter-trial intervals (20–40 s). The stimuli sequences were randomly determined, but no more than four trials of the same type occurred in succession. We calculated the response rates for reinforcement trials (RFT; number of lever presses for RFTs in a session/number of total RFTs in a session) and non-RFT (number of lever presses for non-RFTs in a session/number of total non-RFTs in a session). The task criteria were met when the RFT response rate reached at least 90%, and the non-RFT response rate was no more than 50%. Learning was considered complete when the criteria were met for 3 consecutive days or for a total of 5 days.

2.4.2. Simple discrimination (SD) task

The SD protocol was described in our previous studies [17,20]. In the simple discrimination task, rats were trained to discriminate between two individually presented stimuli (tone or light). Rats were randomly assigned to one of the two groups. For one group, the rat's lever-press responses were rewarded when the tone stimulus (T: 2000 Hz, 75 dB) was presented, but not when the light stimulus (L: five white LED) was presented (T+, L–). For the other group, the stimuli were reversed (L+, T–). Each session consisted of 120 trials made up of 60 RFTs and 60 non-RFTs. All stimuli remained on until either 10 s had elapsed or until the rat pressed the lever. Each trial was separated by variable inter-trial intervals (20–40 s). The stimuli sequences were randomly determined, but no more than four trials of the same type occurred in succession. We calculated the response rates for RFT (number of lever presses for RFTs in a session/number of total RFTs in a session) and non-RFT (number of lever presses for non-RFTs in a session/number of total non-RFTs in a session). The task criteria were met when the RFT response rate reached at least 90%, and the non-RFT response rate was no more than 50%. Learning was considered complete when the criteria were met for 3 consecutive days or for a total of 5 days.

2.5. Electrode implantation

Several studies have shown that the hippocampal theta activity is associated with learning [7–11] and movement based on CA1 recordings [12–14]. We therefore recorded hippocampal CA1 theta activity during our behavioral task. After rats were deeply anesthetized with thiamylal sodium (50 mg/kg, i.p.), they were placed in a stereotaxic apparatus (Narishige, Japan). EEG was recorded using the bipolar method, with the recording electrodes implanted stereotaxically in the hippocampal region, 2.4 mm below the skull surface, 3.5 mm posterior to bregma, and ± 2.0 mm lateral to the midline. The reference electrodes were attached to the skull 6.0 mm anterior to bregma and +2.0 mm lateral to the midline. Polyurethane-insulated stainless steel wire electrodes (200- μ m diameter; Unique Medical Co., Ltd., Japan) were used

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