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Research article

Hippocampal gamma oscillations by sucrose instrumental memory retrieval in rats across sleep/wake cycle

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ABSTRACT

Memory reconsolidation is a process allowing previously consolidated memories to be updated. In order for memory reconsolidation to occur, a memory first needs to be reactivated. It has been shown recently that memory retrieval during awake/sleep phases may affect susceptibility to memory reactivation. Given the importance of hippocampal gamma frequencies in memory processes, the purpose of the present research was to study changes in gamma bands power during retrieval of instrumental appetitive memories. Local field potentials were recorded in the CA1 area of dorsal hippocampus of Sprague Dawley rats during retrieval of instrumental appetitive memory performed either during light or dark phases of the circadian cycle. Appetitive memory retrieval was performed by using a protocol of sucrose self-administration in operant chambers equipped with levers (Piva et al., 2018): rats were first trained to self-administer sucrose pellets and, after a 14-days forced abstinence stage, memory retrieval stage consisted in training context exposure. At the retrival stage performed during the light phase, a decreased low-gamma power was observed in CA1 when rats were not lever pressing compared to when they were lever pressing (actual instrumental memory retrieval). Moreover, results showed an inverse correlation between gamma power and rate of responding when retrieval was performed in the dark phase.

Our findings suggest that hippocampal gamma power is differently modulated when retrieval is performed during the light phase compared to the dark phase. Further investigations should explore the role of gamma oscillations as potential markers of instrumental appetitive memory reactivation in both light and dark conditions.

1. Introduction

Reactivation of previously consolidated memories may trigger a process of destabilization and lability of the memory trace [1,2]. Memory reactivation is thus followed by a process of restabilization (reconsolidation), which could take place during a temporal period of 1–6 h. Early studies showed that reconsolidation takes place only within specific 'boundary conditions' depending on memory features (e.g., age, strength) and on retrieval conditions (e.g., context, schedule and duration of retrieval) [3–6]. It was shown that mechanisms activated by some retrieval protocols might shift appetitive memory to a reconsolidation-resistant state, whereas different protocols may facilitate memory destabilization thus allowing reconsolidation occurrence [7,8]. Sleep is well-known to play a role in memory consolidation, but little is known on whether reconsolidation of memories after their reactivation also occurs during sleep, or whether sleep affects memory reactivation [9–11]. Recent studies suggested that awake/sleep state might be a condition affecting susceptibility to memory reactivation and reconsolidation [12–14]. For example, Klinzing et al. [15] showed that a 40 min night sleep facilitates reactivated declarative memories reconsolidation in humans. Moreover, in a recent study on rodents it was shown that REM sleep deprivation applied before methamphetamine reward memory retrieval impairs appetitive memory itself [16].

The aim of the current study was to assess differences in Local Field

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Potential (LFP) spectrum when appetitive memory retrieval was performed during dark or light phases in rats. In fact, LFPs allow to collect in-vivo information about what is happening inside the brain. Particularly, we focus on the study of changes in LFP patterns in dorsal CA1 during the retrieval of an instrumental appetitive (sucrose) memory. Studies of fear memory conditioning showed theta band synchronization between amygdala and hippocampus, and theta-gamma cross-frequency coupling in CA1 [17–22]. However, limited information is available on changes during appetitive memory reactivation, as well as on other LFP bands like gamma frequencies [23–26]. Our study was therefore a preliminary investigation exploring gamma band changes during appetitive memory retrieval during both dark and light phases.

We used a sucrose self-administration paradigm consisting of instrumental conditioning to lever pressing for sucrose pellets, followed by a period of forced abstinence, and finally, a sucrose memory retrieval session. All the stages were performed during the dark phase, except for memory retrieval, which took place either during dark or light phases.

In the present manuscript we will refer to reactivation as the memory process of reactivation of a memory that can lead to its reconsolidation; and to retrieval as the experimental manipulation applied to eventually induce memory reactivation.

2. Materials & methods

2.1. Animals

Sixteen male Sprague-Dawley rats (Charles River, Italy) were individually housed in temperature and humidity-controlled environment (19 − 23 °C, 60 ± 20 %) on a 12-h light/dark cycle, with light ON at 7:30 pm. Water was available *ad libitum*, except during experimental sessions. Food was available *ad libitum* until rats reached 300 g (8–10 weeks of age), then they were food restricted to maintain their body weight in the range of 300 ± 10 g, and food (10 − 20 g/day) was given at variable time intervals (30 min– 3 h after behavioural sessions) in order to avoid predictability for food availability. The percentage reduction of rats body weight with respect to their normal weighting range at the end of the experiments (after 28 days, reaching 12–14 weeks of age) was between 20 % and 25 %.

Animals were trained daily during the dark phase; retrieval was performed during either dark or light phases. All the experimental procedures were carried out complying with the ARRIVE guidelines and in accordance with the U.K. Animals (Scientific Procedures) Act, 1986 and associated guidelines, with EU Directive 2010/63/EU for animal experiments, and with EC Directive 86/609/EEC for animal experiments. All efforts were made to minimize animal suffering and to keep the lowest number of animals used. The project was approved by Italian Ministry of Health (authorization code: C46F4.3).

2.2. Apparatus

Rats were trained and tested in operant chambers (Coulbourn Instruments, Whitehall, PA, USA) 31 cm (width) × 25.5 cm (height) × 33 cm (depth). Operant chambers were encased in sound-insulated cubicles 64 cm (width) × 44 cm (height) × 50 cm (depth), equipped with ventilation fans (Ugo Basile, Varese, Italy) and provided with two levers. A detailed description of the apparatus can be found in Supplementary Material.

2.3. Surgery and local field potential recording device

Rats were handled for 5 days, 5 min/day before implanting electrodes in the dorsal hippocampal CA1 (coordinates with respect to Bregma: dorso-ventral −2.6 mm, rostro-caudal −3.3 mm and medio-lateral +1.5 mm [27]). After surgery, rats were allowed to recover for 6 days before starting the experiments. Recordings were carried out by means of Neurologger® 2A (Evolocus LCC, Tarrytown, NY, USA). For detailed descriptions of electrodes construction, surgery and recording device see Supplementary Material.

2.4. Behavioural procedure

All rats were initially shaped to associate right lever presses with sucrose pellets with schedule FR1: 45-mg sucrose food pellet, no time-out (TO), session duration up to 120 min or 100 reinforcements. After reaching 100 reinforcements rats started training in the conditioning context, which lasted for 6 days, 1 session/day. During training, right lever presses corresponded to sucrose delivery with the schedule FR1:45-mg sucrose pellet, 60-s TO + trigger, session duration up to 12 reinforcements or 120 min. During TO periods, right lever presses caused TO counter to reset. The house light was on throughout shaping and training sessions except for TO periods during which it switched off. Left lever presses were never associated with consequences.

Following training, rats were subjected to a 14-day period of forced abstinence during which they remained in home cages. On the fifteenth day, rats were divided into two groups, performing Retrieval session either during the dark or light phase. Rats performing Retrieval during the dark phase were moved in the experimental room at 9AM; rats performing Retrieval during the light phase were moved in the experimental room al 9 P M. The Neurologger was fixed on their implant and, after two hours of habituation, they were subjected to the Retrieval session in the same context as training one. Retrieval session had no TO, white house light always ON, session duration up to 20 active lever presses (ALP) or 60 min. Both levers were presented, but they were not associated with consequences.

2.5. Data analysis and statistics

All statistical analyses were performed using the GraphPad software package (Prism, version 6; GraphPad, San Diego, California, USA).

Behavioural data were analysed for Training and Retrieval stages, as described in Supplementary Material. Local field potential data analysis was performed using Matlab software (MathWorks, Natick, MA, USA) and its EEGLAB [28] and Chronux [29,30] toolboxes. A detailed description is presented in Supplementary Material. Briefly, low (30 − 60 Hz), high (60 − 100 Hz) and total gamma relative powers were extracted from lever pressing epochs (ALP epochs) and no lever pressing epochs (baseline epochs). Low- and high- gamma powers were tested for correlation with Retrieval rate of responding by means of Pearson's correlation coefficient; gamma powers for ALP and baseline epochs for Dark and Light groups were analysed by means of two-way repeated measures (RM) ANOVA for factors Lever Pressing (two levels: ALP and baseline) and Phase (two levels: dark, light). One subject from the group performing Retrieval during the dark phase was excluded because of technical issues with the recording logger that prevented us to properly save recording data; two subjects from the group performing Retrieval during the light phase were excluded because they did not reach the 20 ALP criterion to conclude the Retrieval session. Therefore, all data analysis were performed on 13 subjects in total. No subjects were excluded for electrodes misplacement. See Supplementary Material for a description and a representative figure of electrodes placement verification (Fig. S1).

3. Results

Behavioural performance at Training and Retrieval stages showed no difference between the groups (see Fig. S2 in Supplementary material).

Correlation analyses between low- and high-gamma relative powers and rate of responding during Retrieval session (measured as Inter Response Time -IRT-, seconds) showed a significant correlation

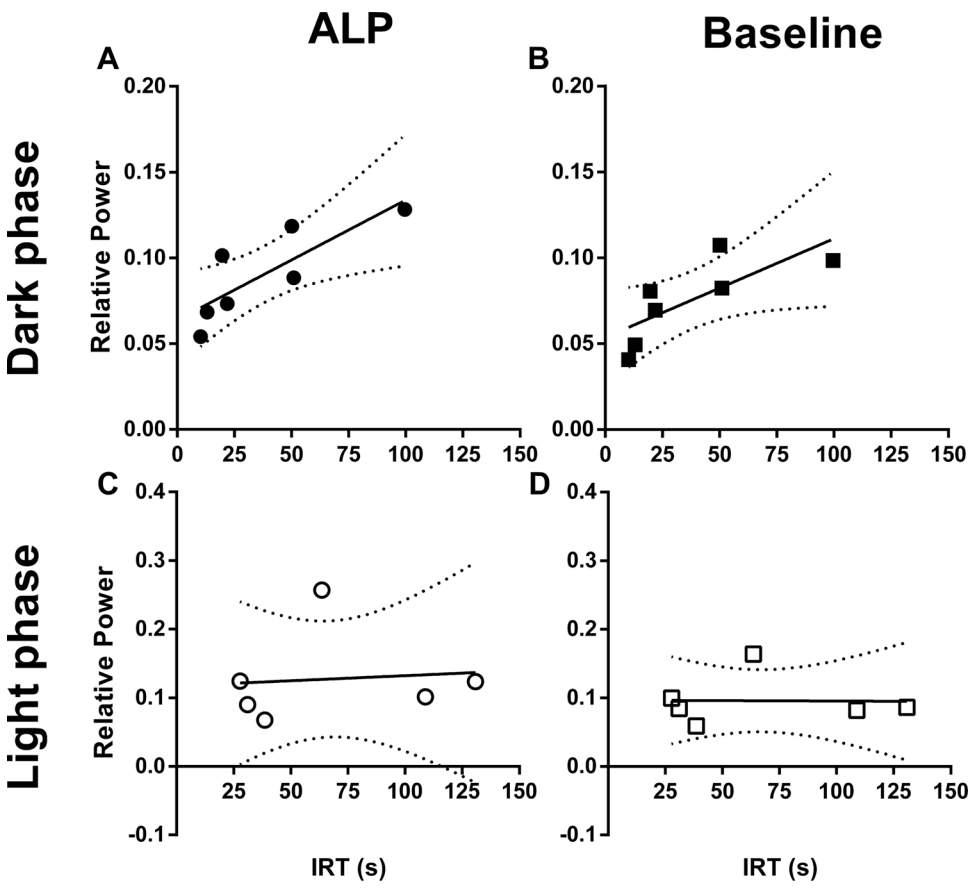

Fig. 1. Correlation between IRT and low-gamma relative power.
The graphs show correlation plots between Inter-Response Time (IRT; seconds) and low-gamma relative power for Active Lever Presses (ALP) epochs (A; closed circles) or baseline epochs (B; closed squares) during the dark phase Retrieval session, and low-gamma relative power for ALP (C; open circles) or baseline (D; open squares) during the light phase Retrieval session. Closed and open circles and squares represent data of single subjects (N = 7, dark; N = 6, light). Solid lines: linear regression line; dotted lines: 95 % confidence intervals. Pearson's correlation coefficient showed a significant correlation for both sub-plots in panels A and B.

between ALP/dark low-gamma and IRT (R = 0.6745; p = 0.0235) (Fig. 1, panel A), and between baseline/dark low-gamma and IRT (R = 0.5706; p = 0.0496) (Fig. 1, panel B). No significant correlation was found between ALP/dark high-gamma and IRT (R = 0.0005, p = 0.09613) and between baseline/dark high-gamma and IRT (R = 0.0615; p = 0.5917). No significant correlation was observed between ALP/light low-gamma and IRT (R = 0.0092; p = 0.8563) (Fig. 1, panel C), baseline/light low-gamma and IRT (R = 0.0002; p = 0.9772) (Fig. 1, panel D), ALP/light high-gamma and IRT (R < 0.0001; p = 0.9899) or baseline/light high-gamma and IRT (R = 0.2407; p = 0.3232).

Relative gamma power barplots are reported in Fig. 2. Two-way RM ANOVA on total gamma relative power for factors Lever Pressing (two levels: ALP and baseline) and Phase (two levels: dark, light) showed a main effect of factor Lever Pressing [F(1,11) = 13.30; p = .0038] but not of Phase [F(1,11) = 1.705; p = 0.218] or their interaction [F(1,11) = 1.721; p = 0.2163]. Sidak's *post-hoc* multiple comparisons test showed a significant difference between ALP/light and baseline/light (mean ± S.E.M.: 0.175 ± 0.036 vs. 0.131 ± 0.019; p < 0.05) but not between ALP/dark and baseline/dark (mean ± S.E.M.: 0.126 ± 0.013 vs. 0.105 ± 0.012; NS) (Fig. 2, panel A).

Two-way RM ANOVA on low- or high-gamma relative power confirmed what we observed on total-gamma relative power. Particularly, two-way RM ANOVA on low-gamma relative power showed a main effect of Lever Pressing [F(1,11) = 13.34; p = 0.0038] but not of Phase [F(1,11) = 1.708; p = 0.218] or their interaction [F(1,11) = 1.711;

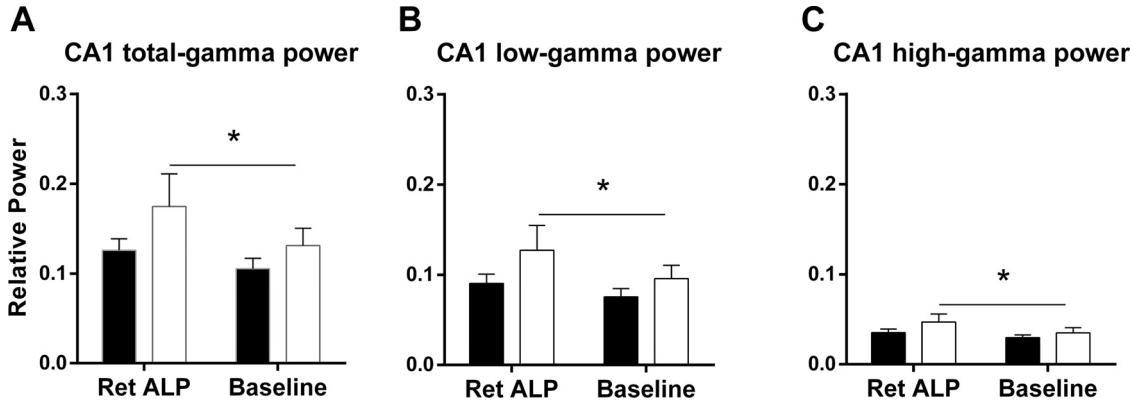

Fig. 2. Relative CA1 gamma power.
The graphs show relative gamma power for Retrieval Active Lever Presses (ALP) and baseline epochs during dark (solid columns, N = 6) and light (open columns, N = 7) phases in hippocampal CA1. (A) Total-gamma (30 – 100 Hz), (B) low-gamma (30 – 60 Hz) and, (C) high-gamma (60 – 100 Hz) relative power. Data are shown as mean + S.E.M. * = p < 0.05, two-way ANOVA followed by Sidak's *post-hoc* multiple comparisons test.

p = 0.2176]. Sidak's *post-hoc* multiple comparisons test showed a significant difference between ALP/light and baseline/light (mean ± S.E.M.: 0.127 ± 0.027 vs. 0.096 ± 0.015; $p < 0.05$) but not between ALP/dark and baseline/dark (mean ± S.E.M.: 0.090 ± 0.010 vs. 0.075 ± 0.009; NS) (Fig. 2, panel B).

Finally, two-way RM ANOVA on high-gamma relative power showed a main effect of factor Lever Pressing [$F(1,11) = 10.24$; $p = 0.0084$] but not of factor Phase [$F(1,11) = 1.352$; $p = .2695$] or their interaction [$F(1,11) = 1.375$; $p = 0.2657$]. Sidak's *post-hoc* multiple comparisons test showed a significant difference between ALP/light and baseline/light (mean ± S.E.M.: 0.047 ± 0.009 vs. 0.035 ± 0.006, $p < 0.05$) but not between ALP/dark and baseline/dark (mean ± S.E.M.: 0.035 ± 0.004 vs. 0.030 ± 0.003; NS) (Fig. 2, panel C).

Overall, significant effects in gamma power have been shown only for the within-group comparisons between ALP vs. baseline epochs, and not between Dark vs. Light conditions. However, these findings suggest that the Dark and Light conditions show different within-condition patterns of epoch-dependent changes, and that instrumental memory is associated to condition-dependent LFP changes.

4. Discussion

In summary, hippocampal CA1 low-gamma power values inversely correlate with Retrieval rate of responding when measured either when rats were actually lever pressing or not during the dark, but not the light phase. This finding suggests that low-gamma might be a specific correlational marker of instrumental sucrose memory reactivation, independently whether rats were lever-pressing or not during the active phase.

Moreover, our study showed that CA1 gamma bands power increased when rats were pressing the active lever during instrumental sucrose memory retrieval while in the light. This finding suggests that increasing gamma bands may be associated to actual instrumental responding retrieval - but not when rats were not pressing the levers - only during the inactive phase.

The dorsal hippocampus as well as its interaction with basolateral amygdala have been shown to be crucial for appetitive memory reconsolidation [25]. The same and other groups have previously showed a synchronization of amygdala and dorsal hippocampus [23,31]. It has been also described that memory retrieval specifically activates neuronal ensembles in dorsal hippocampus, see for instance [13] and [32].

However, little is known about local electrophysiological correlates during appetitive memory reactivation and reconsolidation. In fact, most of the scientific literature available on electrophysiological correlates of memory retrieval and reconsolidation comes from fear memory studies [20,33–35]. For example, Seidenbecher and colleagues showed that fear memory retrieval in mice is associated to theta frequency synchronization between lateral amygdala and dorsal CA1, upon presentation of the fear-conditioned stimulus [20]. Hippocampal gamma frequencies have been shown to be involved in memory processes. Low-gamma (25–55 Hz) and high-gamma (60–100 Hz) [36] play different roles: low-gamma couple CA1 activity to inputs from CA3; high-gamma in CA1 and CA3 are entrained by inputs from the medial entorhinal cortex (MEC). Thus, two independent gamma oscillations generators have been identified: one located in the MEC, the other one located in CA3, respectively producing high- and low- gamma frequencies in CA1 [37]. Particularly, low-gamma oscillations seem to facilitate the transfer of retrieved memories from CA3 to CA1 [38–40]; while high-gamma seem to be mainly involved in sensory information encoding [41,42] and were shown to be linked to running speed changes during spatial navigation tasks [43].

Our results show that low-gamma power correlates with Retrieval rate of responding during the dark phase, both when rats were lever pressing or not: the higher the rate of responding, the lower the low-gamma power. The same correlation was not observed for the high-gamma frequency band. Given hippocampal low-gamma involvement in memory reactivation processes, our results may suggest information transfer from CA3 to CA1 when Retrieval is performed during the dark phase under our conditions.

Moreover, when comparing gamma powers among groups performing Retrieval in either dark or light phases, our results showed that CA1 gamma bands (both low and high) power increased during instrumental sucrose memory retrieval in subjects performing Retrieval during the light phase when they were lever pressing compared to when they were not lever pressing. This finding suggests that gamma bands power may be specific for actual instrumental retrieval (i.e., lever pressing behaviour) during the light phase. In fact, the same difference was not observed when Retrieval was performed during the dark, active, phase.

As previously mentioned, CA1 low-gamma is driven by CA3, which is believed to be the hippocampal area where memories are stored and retrieved from [40,44]. Therefore, low-gamma increased power in CA1 may suggest that low-gamma power is associated to instrumental memory reactivation during the light/inactive phase. As for high-gamma power, based on the evidence that these oscillations are linked to changes in running speed during spatial navigation (Zheng et al. 2015), our results might suggest an association between high-gamma and lever-pressing related movement. However, the same difference was not observed for the group performing Retrieval while in the dark/active phase, ruling out that high-gamma band power increase was solely due to motor activation [40,44,45]. Considering that there was a trend to a lower rate of responding in the light group during Retrieval, we could speculate that gamma power increase is specifically associated to instrumental retrieval and meanwhile inversely correlated to the rate of instrumental responding.

The research reported in the present manuscript presents some limitations. A more detailed sleep analysis by monitoring slow wave sleep would have helped to assess which rats were actually sleeping during Retrieval in the light or dark phases, respectively. Moreover, detailed behavioural analysis during Retrieval gamma band epochs could have helped to inspect micro-behaviours (e.g., lever approaching, lever sniffing and/or licking, etc.) during Retrieval. Even if we did not observe significant differences between the groups in rate of responding during Retrieval, our data show a trend to more variable values in the light condition suggesting a state of 'sleepyness' in some subjects. For this reason, for future experiments we recommend accurate sleep and behavioural analysis during the light condition. Another potential confounding factor is related to feeding timing. In fact, food circadian rhythm could somehow influence the differences described in this study (see for instance [46]). Although we did not originally plan the study in order to control for feeding time, we have allowed feeding at variable time intervals to avoid predictability for food availability.

In conclusion, our study suggested two different involvements of gamma band oscillations during retrieval of sucrose instrumental memory in rats. Firstly, low-gamma band power inversely correlates to rate of responding for lever pressing during the whole dark/active phase Retrieval session, suggesting that decreasing low-gamma power in CA1 may increase output processing for instrumental memory reactivation, even though it cannot be excluded the opposite relationship i.e., increasing rate of responding negatively affects CA3-dependent low-gamma power in CA1 as a sort of negative-feedback. Secondly, ALP-associated gamma bands power increases during the light/inactive phase only, may be considered a potential LFP marker of the sucrose instrumental memory retrieval manipulation, even though memory reactivation occurrence cannot be demonstrated. Taken together, changes of gamma powers in CA1 are differently modulated by instrumental memory retrieval during the awake/sleep phase in rats depending on the actual lever pressing behaviour.

Data statement

Raw data will be available upon request to the corresponding author.

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CRediT authorship contribution statement

Laura Padovani: Conceptualization, Software, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Visualization, Project administration. **Chiara Tesoriero:** Conceptualization, Investigation, Writing - review & editing. **Alexei Vyssotski:** Methodology. **Marina Bentivoglio:** Conceptualization, Supervision, Funding acquisition. **Cristiano Chiamulera:** Conceptualization, Writing - original draft, Supervision, Funding acquisition.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:10.1016/j.neulet.2020.135255.

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