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Timing of presentation and nature of stimuli determine retroactive interference with social recognition memory in mice

Judith Camats Perna [a], Carsten T. Wotjak [b], Oliver Stork [c,d], Mario Engelmann [a,d,*]

[a] Otto-von-Guericke-Universität, Institut für Biochemie und Zellbiologie, Magdeburg, Germany
[b] Max-Planck-Institut für Psychiatrie, Kraepelinstr. 2, Munich, Germany
[c] Otto-von-Guericke-Universität, Institut für Biologie, Magdeburg, Germany
[d] Center for Behavioral Brain Sciences, Magdeburg, Germany

HIGHLIGHTS

- Stimuli inducing interference for social recognition memory in mice were investigated.
- Presentation of a juvenile, an object or odours produced interference if presented 3 h or 6 h, but not 22 h after sampling.
- A loud tone produced retroactive interference only 6 h after sampling.
- Different sensory modalities are involved in the induction of interference.

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ABSTRACT

The present study was designed to further investigate the nature of stimuli and the timing of their presentation, which can induce retroactive interference with social recognition memory in mice. In accordance with our previous observations, confrontation with an unfamiliar conspecific juvenile 3 h and 6 h, but not 22 h, after the initial learning session resulted in retroactive interference. The same effect was observed with the exposure to both enantiomers of the monomolecular odour carvone, and with a novel object. Exposure to a loud tone (12 KHz, 90 dB) caused retroactive interference at 6 h, but not 3 h and 22 h, after sampling. Our data show that retroactive interference of social recognition memory can be induced by exposing the experimental subjects to the defined stimuli presented <22 h after learning in their home cage. The distinct interference triggered by the tone presentation at 6 h after sampling may be linked to the intrinsic aversiveness of the loud tone and suggests that at this time point memory consolidation is particularly sensitive to stress.

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1. Introduction

Memory consolidation describes the phase during which perceived and processed external stimuli are transferred into long-term memory storage. This transition phase is prone to external interferences. In their pioneering monograph Müller and Pilzecker (1900) described the phenomenon of a dramatic loss in memory due to interference by subsequently acquired similar information. Although this process, known as retroactive interference [1], has been a subject of numerous psychological studies, only little is known about the underlying neural mechanisms and the detailed nature of the potentially interfering stimuli [2,3]. This is astonishing, since deeper insight into the underlying processes could have consequences for structuring learning events in daily life, such as school education. From a translational point of view, recognition memory seems to be a particularly interesting target for such studies as it is considered to represent a kind of declarative memory and is sensitive to retroactive interference phenomena [4].

In the past decade, animal experiments aimed at investigating the neurobiological basis of recognition memory increasingly focused on the use of the non-conditioned social recognition/social discrimination procedure. In this context it was shown that (i) mice require an intact hippocampus for retrieving social recognition memory [5], (ii) long-term memory consolidation is based on two stages of protein synthesis within 18 h after learning [5–7], and (iii) memory consolidation is susceptible to retroactive interference triggered by exposure to novel juveniles 3 and 6, but not 22 h after learning [8]. It is plausible that social stimuli activate not only olfactory, but also tactile, acoustic and visual sensory systems. However, the exact nature of the stimuli and their sensory modalities responsible for retroactive interference is far from being clear. The present study was designed to gain a deeper insight into the sensory modalities and the timing of stimulus presentation that are

* Corresponding author at: Otto-von-Guericke-Universität Magdeburg, AG Neuroendokrinologie & Verhalten, Institut für Biochemie und Zellbiologie, Leipziger Str. 44/Haus 1, D-39120 Magdeburg, Germany.
E-mail address: mario.engelmann@med.ovgu.de (M. Engelmann).

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needed to be activated to induce retroactive interference during consolidation of long-term social recognition memory in adult male mice. We exposed the experimental subjects to stimuli activating primarily olfactory, tactile/visual or auditory sensory systems, at three defined time points after learning. Memory interference was assessed 24 h after initial learning.

2. Material and methods

2.1. Animals

Adult male C57BL/6JOlaHsd mice (9–16 weeks old; Harlan-Winkelmann, Borchern, Germany) were used as experimental subjects. Animals of this strain were tested in previous studies in our laboratory (e.g. [7–9]) and, therefore, considered to be suitable for our experiments. They were housed in groups of five per cage (size: 20 × 37 × 15 cm) under standard laboratory conditions with a 12 h:12 h light–dark cycle (light on: 07:00) for at least one week before starting the experiments. Juvenile mice of both sexes of the C57BL/6JOlaHsd strain (25–38 days old) were used as a social stimulus. Extensive previous studies revealed that neither the age nor the sex of the juvenile significantly affects the recognition abilities of male adult experimental subjects [9,10].

All experimental manipulations were approved by the Committee on Animal Health and Care of the local governmental body and performed in strict compliance with the EEC recommendations for the care and use of laboratory animals (2010/63/EU).

2.2. Procedure

The social discrimination procedure has been described in detail elsewhere [10]. Briefly, experimental subjects were housed singly for at least 2 h before testing. The juvenile was presented in the home cage of the experimental subjects at two sessions, each lasting 4 min, spaced by 24 h. During the learning session (sampling) the experimental subject is exposed to a conspecific juvenile. During the memory retrieval session (choice) the previously encountered juvenile plus a novel, previously not encountered juvenile are exposed to the experimental subject (Fig. 1A). During both sessions the investigatory behaviour (sniffing, licking) towards the juvenile(s) is measured by a trained observer, unaware of the animals' treatment. During choice, a longer investigation duration towards the novel juvenile is taken as evidence of an intact social recognition memory [10,11].

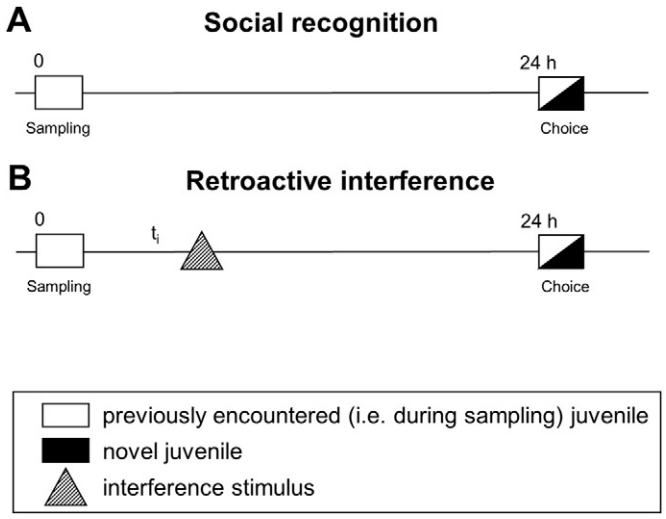

Fig. 1. Experimental procedure for retroactive interference with juvenile recognition memory. (A) Standard procedure for social discrimination memory and (B) modified procedure for testing the impact of potentially interfering stimuli (hatched triangle) on juvenile recognition memory. Sampling and 'interference stimulus'-exposure were separated by a defined interval t_i: 3 h, 6 h or 22 h. In all cases, long-term juvenile recognition memory was assessed 24 h after sampling during a 4-min choice phase.

To measure retroactive interference with juvenile recognition memory, stimuli of different sensory modalities were presented to the adult mouse in its home cage for 1, 4 or 10 min at defined time points after sampling (t_i, either 3 h, 6 h or 22 h; Fig. 1B). The duration of the exposure of a given stimulus was selected with the premise to equalize the interaction time with the different interfering stimuli. Those stimuli included: (1) a previously not encountered conspecific juvenile (composite stimulus, including olfactory, tactile, visual and auditory modalities; 4 min exposure), (2) an object (tactile and visual modalities [12]; cleaned with detergent (fit; fit GmbH, Zittau, Germany) containing water before each session; 10 min exposure), and (3) both enantiomers of carvone separately (the caraway like smelling (S)-(+)carvone and the spearmint like smelling R-(−)-carvone separately diluted 1:1 in diethylpthalate; all Merck Schuchardt OHG, Hohenbrunn, Germany), applied via an air stream that was produced by a computer cooling fan (olfactory modality see [6] for more details; 1 min and 4 min exposure). The size of the seven identical objects made out of solid black, custom made polyethylene used was 7.5 cm long × 4.5 cm wide × 7.5 cm high. It was chosen to meet roughly the criteria described elsewhere by Ref. [12] including that our objects contained several holes of different diameters and a big cavity to initiate nose poke investigation. Approaching the object with the head within a 2 cm distance was considered to indicate object investigation [12].

The fourth stimulus, a tone (12 KHz sine wave, 90 dB sound pressure; auditory modality), was presented for 1 min and generated by an audio stimulus generator (Jupiter 500, Function Generator; Black Star Ltd, Huntington, UK) via speakers. Particular care was taken to reduce as much as possible additional visual, auditory and olfactory stimuli during the social recognition testing. In this context it should be noted that power supplies, computer and monitor produced a constant ultrasonic noise in the ranges of: 20–35 KHz, 55–65 KHz, 90–100 KHz, 125–135 KHz and 140–145 KHz (analysed by a Mini-3 Bat detector, Ultra Sound Advice, London, U.K.). Alterations in the environmental ultrasonic noise have been suggested to affect the performance of laboratory rodents in behavioural testing [13]. However, ultrasonic noise produced by our experimental setup was similar in all sessions and, thus, is unlikely to have contributed to the results obtained in the present study.

The non-social stimuli were chosen according to previous studies. Complex objects were shown to be suitable for being used for object recognition in mice [12,14]. The application of both enantiomers of carvone was previously performed in our lab. In that context we could show that (S)-(+)carvone triggers c-Fos synthesis in the main olfactory system [6] and R-(−)-carvone provided interference if used to additionally scenting the juvenile stimulus mice in the social discrimination test [15]. These observations made both enantiomers suitable to be tested as potentially interfering stimuli. Tone frequency and sound pressure were selected to meet the criteria reported for being suitable to act as an unconditioned stimulus in conditioning experiments with C57BL/6JBomTac mice [16].

The group size of the animals varied between 18 and 21. For testing the interference of juvenile exposure, three separate groups of animals at $t_i = 3$ h, 6 h and 22 h were used. For the effect of the tone a separate group of animals was used for all intervals. A separate group of animals was exposed to the object and 4-min to (S)-(+)carvone (all t_i). Another group of mice was used for the 1-min exposure to both enantiomers of carvone and the object (all t_i).

2.3. Statistics

Data are shown as mean +/− SEM. Investigation durations during choice were analysed using paired Student's t-tests. Significance was accepted if $p < 0.05$.

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