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

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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.

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

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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].

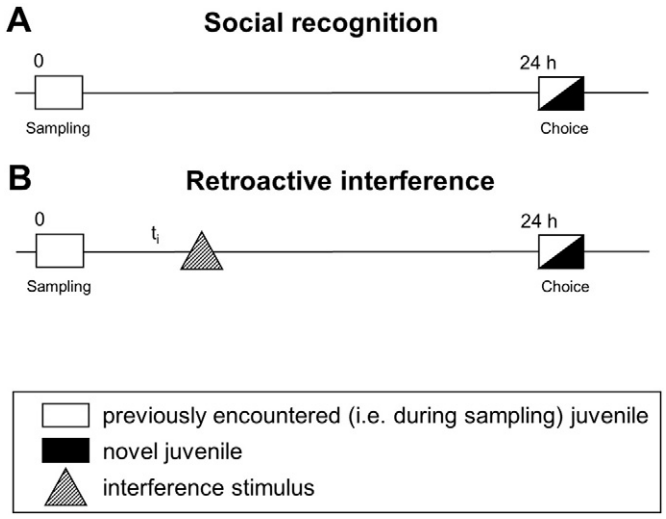

Fig. 1. Experimental procedure for retroactive interference with juvenile recognition memory. (A) Standard procedure for social discrimination memory and (B) modified procedure for testing the impact of potentially interfering stimuli (hatched triangle) on juvenile recognition memory. Sampling and 'interference 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 $p < 0.05$.

3. Results

Table 1 shows the investigation durations during sampling and towards the different stimuli presented during the retention interval. We did not monitor "investigation duration" for the presentation of the enantiomers of carvone as this was administered via an airstream that was always directed towards the head of the experimental subjects.

Presentation of a previously not encountered juvenile induced retroactive interference at $t_i = 3$ h and 6 h after sampling ($t_i = 3$ h: $t = 1.32$, $df = 18$, $p = 0.20$; $t_i = 6$ h: $t = 1.18$, $df = 17$, $p = 0.25$; Fig. 2A). If the juvenile was presented 22 h after sampling, the experimental subjects recognized the juvenile encountered during sampling indicated by the significantly increased investigation duration towards the novel juvenile during choice ($t = 2.79$, $df = 19$, $p = 0.0118$; Fig. 2A).

Also exposing the experimental subjects to a novel object at different t_i interfered with their juvenile recognition abilities (Fig. 2B; $t_i = 3$ h: $t = 0.05$, $df = 19$, $p = 0.964$; $t_i = 6$ h: $t = 0.23$, $df = 18$, $p = 0.822$; $t_i = 22$ h: $t = 5.37$, $df = 19$, $p < 0.001$).

Similarly, treatment for 1 min with either of the two carvone enantiomers 3 h and 6 h after sampling interfered with juvenile recognition. If carvone was administered 22 h after sampling juvenile recognition remained unaffected (Fig. 3A; (S)-(+)carvone: $t_i = 3$ h: $t = 0.47$, $df = 19$, $p = 0.644$; $t_i = 6$ h: $t = 0.11$, $df = 19$, $p = 0.912$; $t_i = 22$ h: $t = 5.35$, $df = 19$, $p < 0.001$; Fig. 3B; R-(−)-carvone: $t_i = 3$ h: $t = 1.62$, $df = 19$, $p = 0.121$; $t_i = 6$ h: $t = 1.96$, $df = 19$, $p = 0.065$; $t_i = 22$ h: $t = 3.73$, $df = 19$, $p = 0.001$). Identical observations were made when the caraway-like smelling (S)-(+)carvone was administered for 4 min ($t_i = 3$ h: $t = 0.94$, $df = 19$, $p = 0.357$; $t_i = 6$ h: $t = 0.22$, $df = 19$, $p = 0.616$; $t_i = 22$ h: $t = 3.14$, $df = 19$, $p = 0.005$, data not shown).

Fig. 4 shows the outcome of the tone administration. Presentation of this stimulus failed to produce an interference at $t_i = 3$ h and 22 h, but caused interference at $t_i = 6$ h ($t_i = 3$ h: $t = 3.60$, $df = 19$, $p = 0.002$; $t_i = 6$ h: $t = 0.57$, $df = 20$, $p = 0.574$; $t_i = 22$ h: $t = 2.62$, $df = 20$, $p = 0.016$).

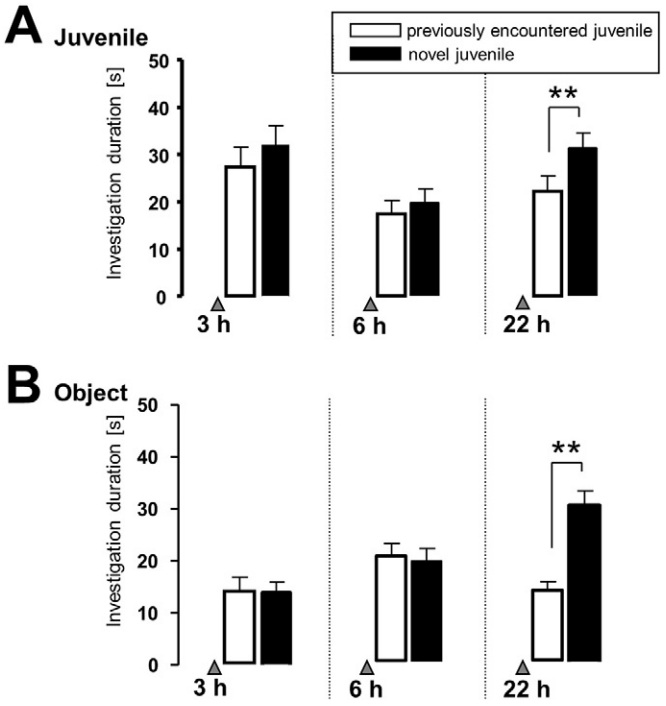

Fig. 2. Retroactive interference depends upon the time point of stimulus presentation after sampling. Analysis of the investigation times during choice (cf. Fig. 1b) revealed: A: Exposure of a previously not encountered juvenile and (B) an object 3 h and 6 h, but not 22 h, after sampling interfered with the recognition of the juvenile presented during sampling. Means + SEM; *$p < 0.05$; **$p < 0.02$ paired Student's t-test.

4. Discussion

The present study was designed to investigate in more detail the quality and the effects of timing of stimuli needed to induce retroactive interference in the social discrimination procedure. We first exposed the experimental subjects to a previously not encountered juvenile at different time points after sampling. This procedure caused retroactive interference if the 'interference juvenile' was presented at 3 h and 6 h, but not 22 h after sampling (Fig. 2A). These data correspond with the observations published previously [8], and, together, demonstrate that exposure to a different juvenile during the first 18 h after the learning session interferes with correct memory retrieval 24 h after the original sampling session [8]. It further supports the suggestion that the insensitivity of memory retrieval to the 'interfering juvenile' presented 22 h after sampling might be linked to underlying consolidation processes of the information coding for the originally encountered juvenile (incl. protein synthesis [6,7]). These seem — according to previous studies [6–8] — to be completed ~18 h after the learning session. Thus, the failure of all other stimuli used in the present study to induce interference if applied 22 h after sampling (Figs. 2–4) is likely to be linked to the fact that recognition memory is consolidated and insensitive to stimuli that at earlier time points than 18 h after sampling produce retroactive interference.

It is plausible that social stimuli activate different sensory modalities in the experimental subjects including taction [17], hearing, olfaction, and vision [18]. We further investigated which of these sensory modalities might be of particular importance for the induction of interference and presented selected stimuli at defined time points during memory consolidation (3, 6 or 22 h after sampling).

The impact of the two enantiomers of carvone on juvenile recognition was in accordance with the interference effects seen after presentation of the 'interference juvenile' (Fig. 3). This suggests that olfaction is a primary sensory modality via which interference can be induced in our model of social recognition memory. Indeed, different papers suggest that in the context of social recognition memory, olfaction plays a fundamental role in laboratory rodents [15,19] in which the processing of the non-volatile fraction of the olfactory signature may be directly linked to the intrinsically rewarding aspect of social interaction [20]. Juvenile exposure activates distinct cell populations not only within the

Table 1
Investigation durations (in seconds) during sampling and presentation of the interference stimuli (means ± SEM).

Interference stimulus	$t_i = 3$ h			$t_i = 6$ h			$t_i = 22$ h		
	Sampling	Interference	n	Sampling	Interference	n	Sampling	Interference	n
Juvenile	59.5 ± 8.3	54.0 ± 11.0	19	39.0 ± 5.8	23.9 ± 3.9	18	42.6 ± 6.4	43.9 ± 6.0	20
Object	23.6 ± 3.4	3.1 ± 0.5	20	33.5 ± 3.8	2.6 ± 0.7	19[c]	24.3 ± 2.6	4.4 ± 0.7	20
(S)-(+) carvone	37.6 ± 3.7	[a]	20	35.1 ± 3.5	[a]	20	36.8 ± 4.5	[a]	20
(R)-(−) carvone	26.3 ± 3.0	[a]	20	37.9 ± 4.5	[a]	20	49.6 ± 4.5	[a]	20
Tone	28.9 ± 3.7	[b]	20	26.6 ± 2.2	[b]	21	24.4 ± 2.0	[b]	21

[a] 1-min administration of the respective carvone enantiomer via an airstream towards the head of the experimental subject.
[b] 1-min presentation of a tone (12 KHz, 90 dB).
[c] One animal had to be excluded because of high aggressive behaviour towards the juveniles.

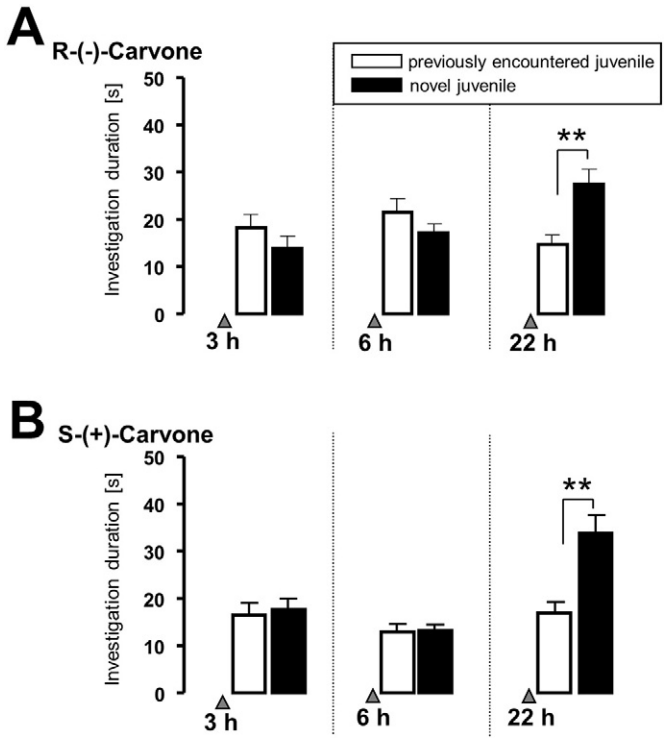

Fig. 3. Retroactive interference by carvone is independent upon the enantiomer, but depends upon the time point of presentation after sampling. Analysis of the investigation times during choice (cf. Fig. 1b) revealed: A: 1-min administration of (R)-(−)-carvone induced retroactive interference if presented 3 and 6 h, but not 22 h, after sampling. B: 1-min administration of (S)-(+)-carvone induced in a similar manner as shown in A. Means + SEM; **$p < 0.01$ paired Student's t-test.

accessory, but also in the main olfactory bulb (MOB) [6,8]. In contrast, the application of both enantiomers of carvone was shown to similarly stimulate cells in the MOB only [21]. This implies two alternative hypotheses that can explain the observed carvone effect: Either, long-term juvenile recognition memory may be predominantly based on the processing of the volatile components of the olfactory signature and, therefore, be particularly sensitive to interference by volatile stimuli such as carvone. Or, although both volatile and non-volatile components of the olfactory signature are of similar importance for juvenile recognition, the mere interference with one of the two components may render the whole signature "unreadable".

The object was chosen to primarily stimulate vision [22] and taction. Presentation of this stimulus also blocked recognition of the juvenile originally encountered during sampling at $t_i = 3$ h and 6 h (Fig. 2B).

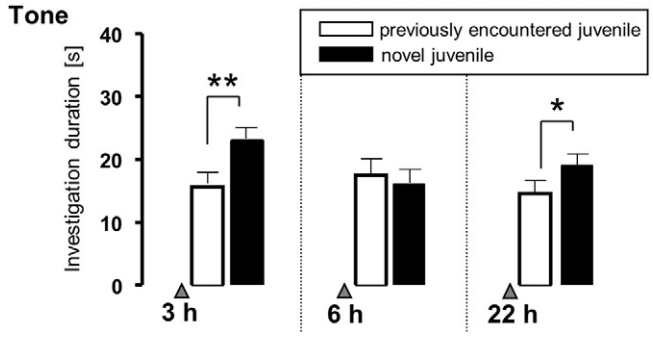

Fig. 4. Presentation of a loud tone interferes at 6 h after sampling only. Analysis of the investigation times during choice (cf. Fig. 1b) revealed that application of a loud tone (12 kHz, 90 dB) induced retroactive interference at 6 h after sampling only. Means + SEM; *$p < 0.05$; **$p < 0.02$ paired Student's t-test.

Thus, the object provided the quality to induce retroactive interference, suggesting that not only olfaction, but also vision and taction may take part in mouse juvenile recognition and the induction of interference. It is worth noting that — other than the interference stimulus 'juvenile conspecific' — the object did not actively move through the cage including approaching the experimental subject; it, therefore, can be deemed as being passive and less attractive for the experimental subjects. Indeed, the average investigation duration (inspection with <2 cm distance) of the object was in the range of 6–10% of that measured for the 'interference juvenile' (see Table 1). Nevertheless, it is of note that already this short duration was sufficient to interfere with correct social memory consolidation.

Of particular interest is the result obtained with the tone application. This stimulus produced retroactive interference at 6 h, but not 3 h (and 22 h) after sampling (Fig. 4). This stands in contrast to the effects of the other three stimuli at both time points and suggests that the interference phenomena observed here were indeed stimulus specific. Remarkably, systemic injection of the protein synthesis inhibitor anisomycin blocked juvenile recognition if injections were performed at 3 h, but not if done 6 h after sampling [6,8]. To date we can only speculate about the mechanisms underlying the impact of the tone presentation: One explanation might be that presentation of the loud tone caused stimulus-specific discomfort, stress and/or arousal in the animals [23,24]. Indeed, experimentally increased plasma corticosterone levels during memory consolidation were shown to inhibit long-term memory performance in tasks with low aversive stimulation, but not in tasks based on highly aversive stimuli [25]. As the social discrimination procedure is based on the intrinsic motivation of the experimental subjects to investigate conspecifics, stress might indeed interfere with memory consolidation in this task. Also, arousal was suggested to trigger central noradrenaline release which in turn may contribute to retrograde interference phenomena in humans [26]. Finally, interfering effects on the sleep–wake cycle on memory consolidation [27] by the presentation of the stimuli used here cannot be entirely excluded. This alone, however, cannot easily explain the distinct action of the loud tone at 6 h after sampling. Thus, further studies are needed to elaborate upon the impact of corticosterone and noradrenergic signalling in the brain on the interplay between arousal and/or stress and/or sleep for retroactive interference with social recognition memory.

The results of the present study suggest that the social recognition memory trace is sensitive to stimuli activating different sensory modalities in addition to olfaction as also object exposure and — at least at one time point tested here — also tone exposure interfered with the consolidation of social memory. This extends previous findings showing that the mere presentation of the volatile fraction of the olfactory signature during choice is insufficient to allow the experimental subjects to recognize a previously directly encountered to-be-recognized juvenile during sampling [15]. Originally this observation was primarily interpreted in terms of the interplay between volatile and non-volatile fraction of the olfactory signature [15]. The data obtained here suggest that not only the information linked to olfaction but also that associated with other sensory modalities (vision, hearing, taction) activated during sampling contributes to a rather complex "memory map" of the previously encountered conspecific. As a consequence, re-activating these individual sensory modalities at defined time points after learning produces memory interference. This may explain why also transferring to a novel cage 3 h after sampling for 4 min is sufficient to induce retroactive interference [10]. Interestingly, removing the mice from the home cage to apply a short-lasting isoflurane anaesthesia (e.g. to administer substances in pharmacological studies) fails to affect social memory in the social discrimination task [6–8,10] thereby suggesting that the potential interference producing information processing linked to this manipulation can — at least in some instances — be "erased" by the anaesthesia. Thus, further studies will investigate the impact of subsequent isoflurane anaesthesia on the induction of retroactive interference described here and whether the distinct features of the object

(visual versus tactile) can be further separated as studied by other authors [28].

Author contribution

JCP performed experiments and wrote parts of the manuscript. ME, CTW and OS planned the experiments and wrote the manuscript.

Conflict of interest

All authors declare no conflict of interest.

Submission declaration

The work described here has not been published previously, that it is not under consideration for publication elsewhere, that its publication is approved by all authors and tacitly or explicitly by the responsible authorities where the work was carried out, and that, if accepted, it will not be published elsewhere including electronically in the same form, in English or in any other language, without the written consent of the copyright-holder.

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