

Mice remember experiences via conspecific-context: models of social episodic-like memory

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The ability to remember unique past events (episodic memory) may be an evolutionarily conserved function, with accumulating evidence of episodic-(like) memory processing in rodents. In humans, it likely contributes to successful complex social networking. Rodents, arguably the most used laboratory models, are also rather social animals. However, many behavioural paradigms are devoid of sociality, and commonly-used social spontaneous recognition tasks (SRTs) are open to non-episodic strategies based upon familiarity. We address this gap by developing new SRT variants. Here, in object-in-context SRTs, we asked if context could be specified by the presence/absence of either a conspecific (experiment 1) or an additional local object (experiment 2). We show that mice readily used the conspecific as contextual information to distinguish unique episodes in memory. In contrast, no coherent behavioural response emerged when an additional object was used as a potential context specifier. Further, in a new social conspecific-in-context SRT (experiment 3) where environment-based change was the context specifier, mice preferably explored a more recently-seen familiar conspecific associated with contextual mismatch, over a less recently-seen familiar conspecific presented in the same context. The results argue that, in incidental SRT conditions, mice readily incorporate conspecific cue information into episodic-like memory. Thus, the tasks offer different ways to assess and further understand the mechanisms at work in social episodic-like memory processing.

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1 Many animals are innately social species and live in groups^{1,2}. The demand
2 (upon individuals) of maintaining complex social dynamics within group living, is
3 thought to have contributed to evolutionary shaping of the brain^{1,2}. Recognition
4 memory is a necessary cognitive capacity to enable successful complex social living
5 and networking³⁻⁶. It can be modelled as a dual process where familiarity (knowing)
6 is distinct from recollection (remembering)^{7,8}. You may recognise that a conspecific
7 is familiar, but you may not remember any experiences of how you may know them.
8 This remembering, a core feature of episodic memory, one's memory for unique past
9 events⁹, allows for the basis of more complex sociality^{3,4}. For example, being vigilant
10 of a once trustworthy conspecific that you deem is no longer trustworthy, because
11 you remember the occasion that they stole your family's share of food (see^{3,10}).

12 When considering the evolutionary trajectory of episodic memory, some argue
13 that in its essence it is a human specific ability^{4,11}. Alternatively, some argue that a
14 form of episodic memory exists in many species, evidenced behaviourally¹²⁻¹⁴ and by
15 evolutionarily conserved neural mechanisms^{15,16}. Hence, a more nuanced approach
16 seeks to understand what elements of episodic memory are shared between
17 species¹⁷. In this way, episodic-like memory has been behaviourally characterised as
18 memory for a simultaneous integration of content (what) in its specific spatial
19 arrangement (where) and temporal context (when)¹². However, 'when' is not the only
20 way to specify episodes in memory. Animals may struggle to remember episodes via
21 an absolute moment in time and may instead rely upon 'how long ago'^{18,19} (recency-
22 based memory - susceptible to familiarity processing^{14,20,21}). Thus, integrated what-
23 where stimuli can also be remembered via contextual specifiers, including the
24 physical environment, acting as an 'occasion setter'¹⁴. This is a more holistic
25 interpretation which includes (but is not limited to) 'when' being used as the episode
26 specifier. In this work, we further explore temporal cues and the role of contextual
27 specifiers beyond the physical environment.

28 Rodents have been seen to display episodic-like memory in spontaneous
29 object recognition (SOR) paradigms using both temporal context and other
30 contextual markers to specify and remember episodes²⁴⁻²⁶. Interestingly, however,
31 where recency-based 'when' and context-based recognition strategies are available
32 in the same tasks²⁷, it seems to be context-based strategies that more commonly
33 shape behaviour overall²⁸⁻³⁰. This raises the question of what kinds of information
34 can readily be used as contextual specifiers, enough to motivationally drive
35 behavioural output during retrieval (over recency-based strategies or randomness),
36 especially in such 'spontaneous' tasks where there are minimal explicit external
37 reinforcers being used by experimenters³¹.

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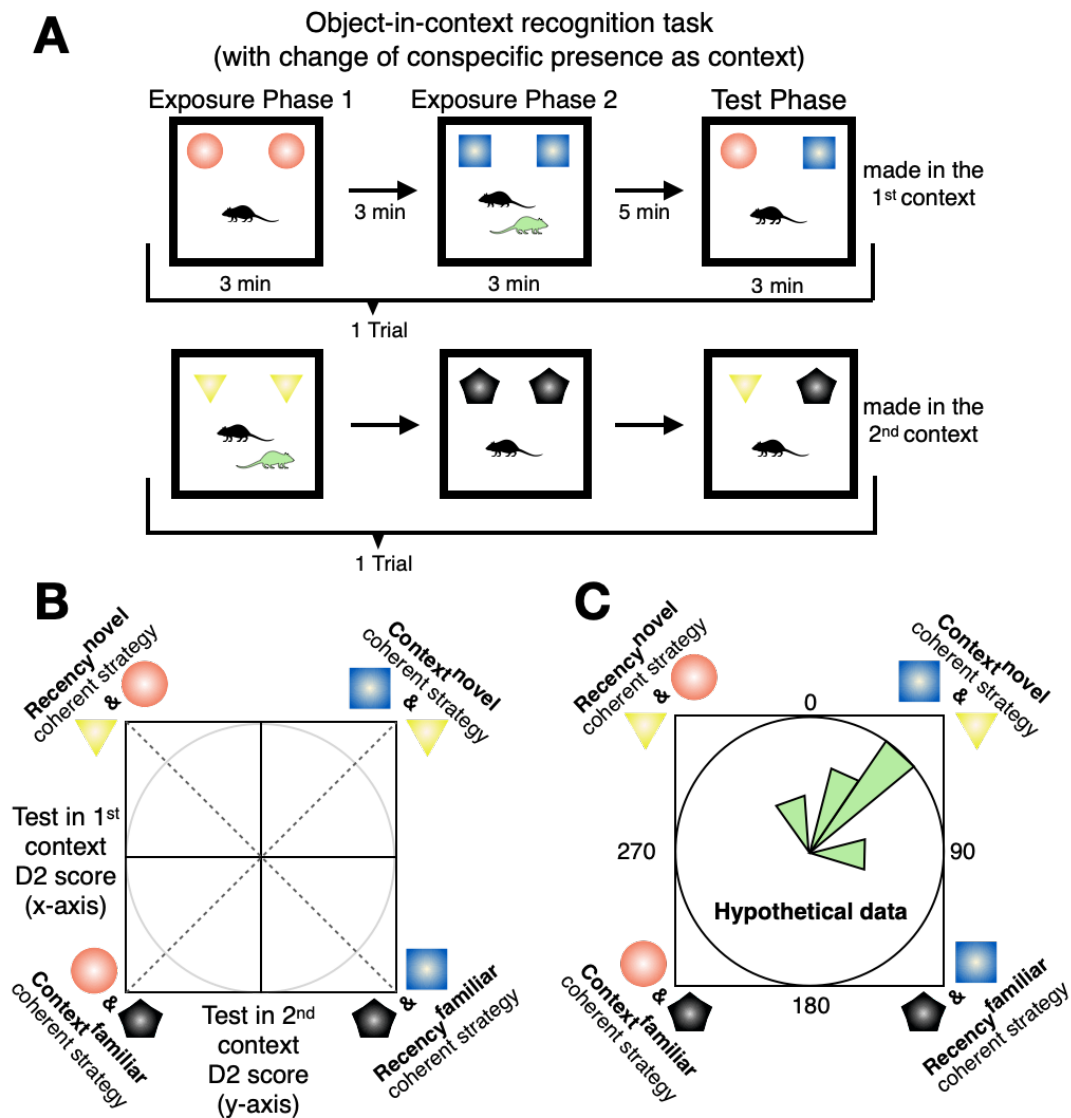


Figure 1. Schematics of the object-in-context recognition task with a conspecific partner as context example. **(A)** In the object-in-context task mice are presented with 2 exposure phases, both containing the same objects. ‘Context’ was specified as presence/absence of a freely roaming conspecific (experiment 1; green mouse in A; same-sex cage and litter mates). The test phase contained a copy of each object experienced from the exposure phases and was only made when the experimental subject was alone (black mouse in A; see main text for reasoning). The test phase could be made in the 1st context (upper), or it could be made in the 2nd context (lower). Thus, two exposure phases and a test phase constituted a single trial (4 trials in each experimental session per animal). **(B)** The D2 ratio scores from test in the 1st context trials can be plotted against test in the 2nd context trial D2 scores and expressed as circular data (via an arctangent function) to test for potentially coherent behavioural strategies across the two types of trials (see²⁷ and methods). Context^{novel} and recency^{novel} denote exploration based on object novelty preference, whereas context^{familiar} and recency^{familiar} denote familiarity-based exploratory preference. **(C)** Depicts hypothetical circular data plotted in an angular histogram. In this hypothetical example, the circular mean is ~45°, suggesting common context^{novel} strategy. One can conduct inferential circular statistics asking whether the data is uniformly distributed around the circle or not. In this hypothetical example, if the data is not uniformly distributed around the circle, and thus significantly clustered around the mean of ~45°, this is indicative of a coherent context^{novel} strategy. Such circular analyses are contingent upon evidence of behavioural recognition preference differing to chance level performance and can enhance explanatory power of the spontaneous recognition task data in terms of strategy.

40 In nearly all context-SOR rodent studies, changes in context are
41 operationalised as discrete manipulations of the global environment, typically
42 involving changes in visuo-tactile and or geometric cue information (of walls, floors,
43 and the extra-maze)^{24,28,30,32}. It is well-established that these kinds of changes can
44 evoke profound changes in ensembles of hippocampal neurons (see^{33,34}), and such
45 ensemble coding changes are thought to contribute to contextual episodic-like
46 memory processing^{16,35-38}. Yet, even in an experimental setting rodents can naturally
47 form complex social networks³⁹, can learn and retrieve hierarchal social status
48 information⁴⁰ and display pro-social behaviour dependent on nurture factors⁴¹. Thus,
49 such work suggests that rodents may flexibly incorporate social information into
50 episodic-like memory (c.f.⁴²).

51 Here, we use two new variants of the object-in-context SOR paradigm. In
52 the first object-in-context SOR experiment (Experiment 1), we asked if ‘context’
53 could be specified via the presence/absence of a freely roaming conspecific (**Fig. 1**).
54 In a second object-in-context SOR experiment (Experiment 2), we asked if ‘context’
55 could be specified via the presence/absence of an additional static local object. In
56 the first experiment, we show that mice readily use conspecific presence and
57 absence as contextual information to separate and distinguish particular events, and
58 this episodic-like strategy was over an object recency-based strategy that was also
59 possible in the SOR. In the second object-in-context SOR experiment, the presence
60 and absence of an additional local object (kept the same throughout the testing
61 session) did not elicit a coherent recognition strategy.

62 We also developed a new conspecific-in-context SR task (Experiment 3, **Fig.**
63 **2**), based broadly on the model of the standard object-in-context SR task, but
64 employing conspecifics instead of objects. Thus: a) as per the usual convention,
65 context was specified via environment-based change of the floor and wall visuo-
66 tactile cues; b) conspecifics were kept in stable locations (like objects) within wire
67 cups. Here, just as with the standard object-in-context SR task, we asked if mice
68 could detect, and thus preferentially explore, a novel conspecific-in-context
69 configuration (mismatch) over a previously presented conspecific-in-context
70 configuration. To directly pit contextual mismatch against recency-based exploration,
71 we introduced a third conspecific in the second exposure phase, so that in the test
72 phase the conspecific who was not part of the contextual mismatch was seen longer
73 ago (**Fig 2**). In this way, two novelty-oriented discriminatory strategies were
74 available: 1) explore the conspecific more in the novel conspecific-in-context
75 configuration (context mismatch strategy); 2) explore the conspecific more who was
76 seen longer ago (recency strategy). As we shall see, the results favoured a
77 conspecific-in-context episodic-like memory account.

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80 Results

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82 Experiment 1: conspecific presence/absence is sufficient to act as a 83 contextual specifier for mice to remember episodes

84

85 In this object-in-context task SOR variant (**Fig. 1A**), context was specified by
86 the presence and absence of a freely roaming conspecific partner for experiment 1.
87 This partner was a same-sex littermate and cagemate of the subject. We tested 10
88 subjects. Subject-partner dyads were kept the same throughout the testing session
89 (a session consisted of 4 trials) and so was the experimental environment. We have
90 recently shown that in object-in-context SOR tasks, animals can either use a
91 recency-based strategy (ignorant of contextual information) or a context-dependent
92 strategy, where the novelty stems from the contextual mismatch at test²⁷. The test
93 phase can be situated in the 1st context or in the 2nd context. We ran tests in both
94 contexts for each mouse, and it was imperative to analyse both types of trials
95 separately to assess overall coherent recognition behavioural strategy^{27,43} (**Fig. 1**).

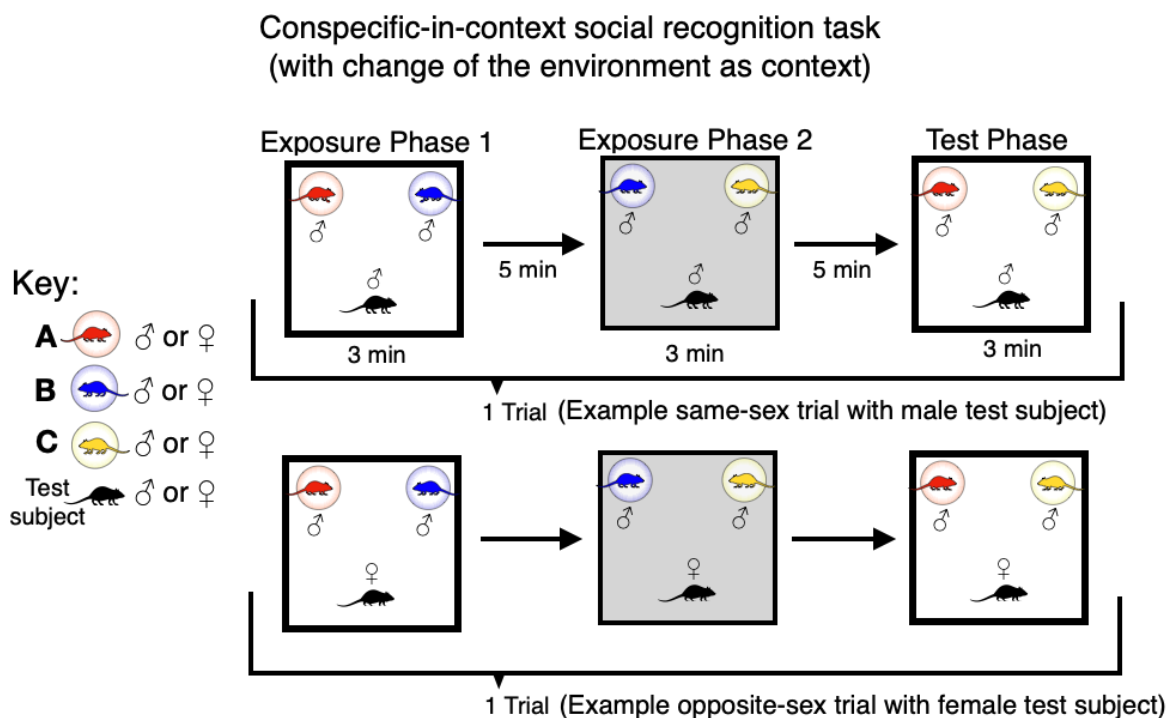


Figure 2. Schematics of the social conspecific-in-context recognition task variant with environment-based change as the context specifier. The conspecific-in-context task was constituted by 3 phases forming a single trial (2 exposure phases, left and middle, and a test phase, right). Here, context was specified via change of the physical environment. In the test phase, both conspecifics should be familiar (based on experience from the exposure phases), but one was seen less recently presented in the same context and place (A; red) and the other was more recently seen, yet now presented in a contextual mismatch (C; yellow). Conspecifics were same-sex cage and littermates in two separate sessions of a single trial per animal (an example male same-sex trial is shown; upper). However, in a final session we also tested opposite-sex littermates (an example opposite-sex trial with a female test subject is shown; lower).

96 It was important to impose a restriction upon the test phase; namely, that the
97 experimental subject should be alone. This was done for two reasons. 1) This
98 enables more straightforward comparisons to other object-in-context SOR variants,
99 where no conspecific is present. 2) The conspecific partner's behaviour could bias
100 the experimental subject. As the conspecific partner will have only been present in
101 one out of two of the exposure phases, one of the objects would be unfamiliar for
102 that partner (hence novel) if they were to be present in the test phase. This is
103 crucially different to what the experimental subject has experienced, interacting with
104 both objects during the exposure phases (i.e., both objects should be familiar at test
105 for the experimental subject). Indeed, even though conspecific presence has been
106 previously seen to enhance behavioural expression of learning and memory in
107 rodents^{44,45}, our SOR protocol differs to these where all animals had had the same
108 experience in SOR exposure and or test phases^{44,45}. Moreover, a subordinate's
109 behaviour could be constrained by a dominant conspecific's scent-marking or
110 aggression at test⁴⁶, and this in combination with the exposure phase difference
111 could mask the experimental subject's own strategic preference (or lack thereof).

112 Mice spent significantly more time exploring the novel object-in-context
113 (context^{novel}) configuration (M = 46.97s, SD = 16.77s) than the context^{familiar}
114 configuration (M = 35.14s, SD = 15.62s; $t_{(9)} = -2.43$, $p = 0.038$, $d = -0.77$, CI 95% -
115 0.04 to -1.46; **Fig. 3A**, left). In contrast, there was no difference between the
116 recency^{novel} (M = 41.02s, SD = 14.13s) and the recency^{familiar} configurations (M =
117 41.09s, SD 19.93s; $t_{(9)} = 0.01$, $p = 0.99$, $d = 0.004$, **Fig. 3A**, right). The discrimination
118 ratio 2 (D2) score data yielded a similar picture (context D2: M= 0.13, SD = 0.22; $t_{(9)}$
119 = 1.83, $p = 0.10$, $d = 0.58$; recency D2: M = -0.005, SD = 0.23; $t_{(9)} = -0.065$, $p = 0.95$,
120 $d = -0.02$). In fact, however, closer inspection showed that when tested in the 1st
121 context, the average context D2 score was positive and strongly different from zero
122 (**Fig. 3B**; M = 0.29, SD = 0.16; $t_{(7)} = 5.05$, $p = 0.001$, $d = 1.79$, CI 95% 0.62 to 2.91),
123 whereas this was not the case for testing in the 2nd context (**Fig. 3C**; M = 0.12, SD =
124 0.25; $t_{(9)} = 1.51$, $p = 0.17$). One possible explanation for this is relative recency of the
125 contextually specifying cue^{28,43}, which in this case the conspecific was more recently
126 seen in test in the 1st context trials compared to test in the 2nd context trials,
127 potentially making their absence at test more salient in such trials. Yet, this
128 emphasises the importance of context-based SOR research in reporting trial types
129 separately to better understand the possible differences in recognition behaviour
130 between them^{27,28,43}.

131 We next asked whether the circular data was uniformly distributed around the
132 circle or whether there was indication of directionality (**Fig. 1**). There was evidence
133 that the circular data was not uniformly distributed around the circle with some
134 biasing towards the context^{novel} quadrant (**Fig 3D**; $n = 20$, $\bar{\theta} = 79.9^\circ$, $v = 70.0^\circ$, $\bar{R} =$
135 0.25, Rao's spacing test: $U = 165.31$, $p < 0.05$).

136 These results overall suggested that mice used a context-based recognition
 137 strategy expressed via novelty preference. This was with performance being mainly
 138 driven from test in the 1st context trials, although there was some evidence of
 139 coherent context^{novel} object exploration across consecutive trials (that is, also across
 140 different trial types; **Fig. 3B-D**). Thus, mice are able to use conspecific presence and
 141 their absence as contextual information to separate and identify unique episodes in
 142 memory.
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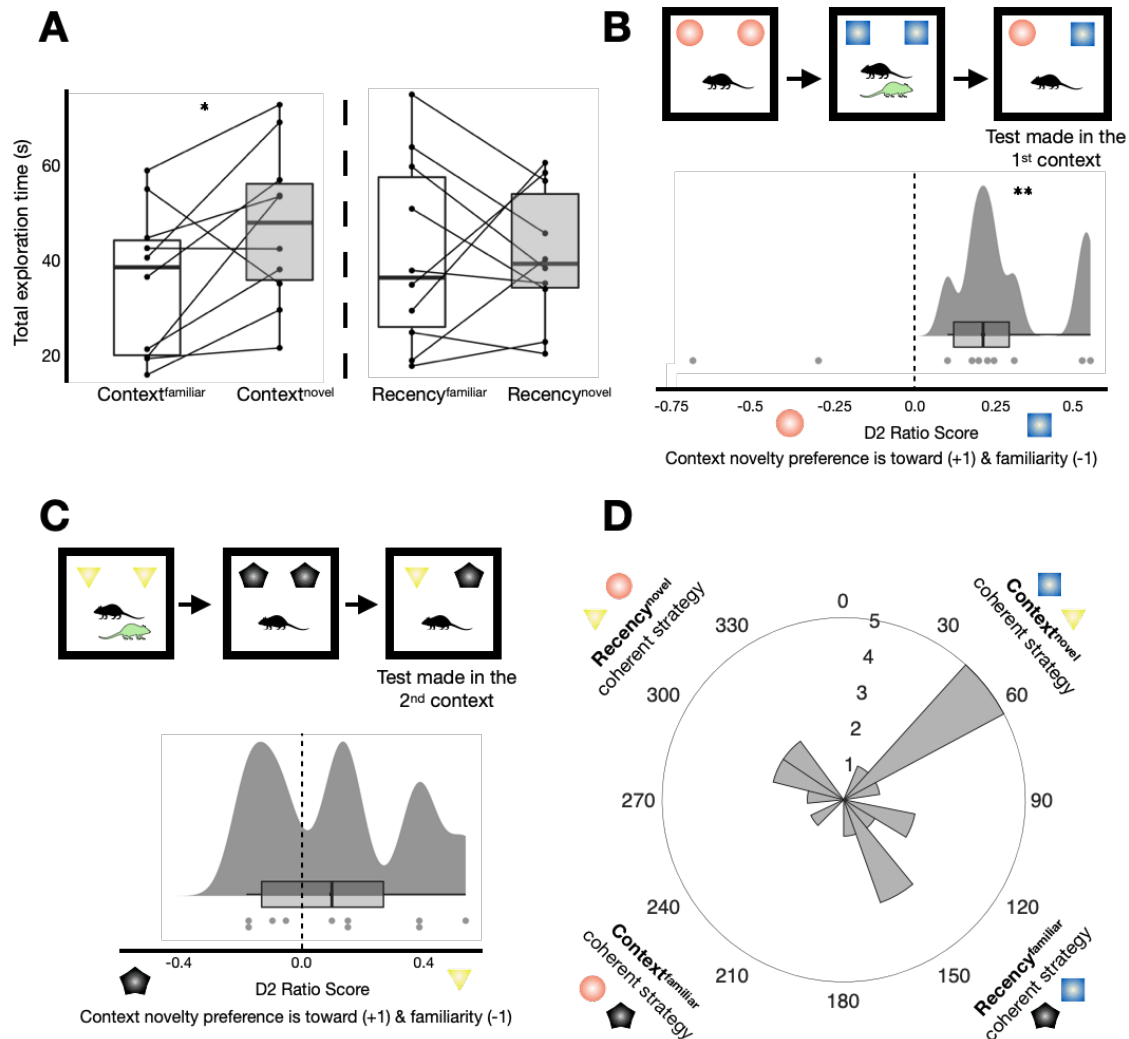


Figure 3. Experiment 1: conspecific presence and absence are sufficient to act as a contextual cue for mice to remember episodes. **(A)** Total exploration time (s) summed across all test phases. Mice explored the context^{novel} configuration (M = 46.97s, SD = 16.77s) significantly more on average than the context^{familiar} configuration (M = 35.14s, SD = 15.62s; $t_{(9)} = -2.43$, $p = 0.038$, $d = -0.77$, CI 95% 0.04 to -1.46). There was no difference between the recency configurations (recency^{novel}: M = 41.02, SD = 14.13s; recency^{familiar}: 41.09s, SD = 19.93s; $t_{(9)} = 0.01$, $p = 0.99$, $d = 0.004$). **(B)** Overall performance was particularly driven by tests situated in the 1st context. The average context discrimination 2 (D2) score was positive (M = 0.29, SD = 0.16) and differed significantly from zero ($t_{(7)} = 5.05$, $p = 0.001$, $d = 1.79$, CI 95% 0.62 to 2.91). **(C)** The average context D2 score for trials when the test made in the 2nd context was also positive (M = 0.12, SD = 0.25) but did not differ from zero ($t_{(9)} = 1.51$, $p = 0.17$, $d = 0.48$). **(D)** Angular histogram depicting the circular data; n = 20. D2 ratio scores were taken from consecutive trials to form circular data points and thus represents animal-trial data; see methods). Plotted in 16 bins of 22.5°, circular descriptive and inferential statistics are reported in the main text. *Denotes $p < 0.05$. **Denotes $p = 0.001$.

144 Experiment 2: no coherent strategy emerges when context is specified via an
145 additional local object

146

147 This object-in-context task variant used presence and absence of an
148 additional local object as contextual information. Similarly to the dyads of mice, the
149 object acting as a potential context specifier was kept the same throughout the
150 experimental session, as was the physical environment. And mice were only tested
151 in the absence of the object that potentially acted as a context-specifier, in order to
152 be comparable to the conspecific-context variant (experiment 1). Also, this
153 experiment was conducted at the end of the experimental timeline (**SFig. 1**), as this
154 aimed to minimise tedium and possible behavioural carryover affects from the
155 previous object-in-context SOR task⁴⁷.

156 There was no difference between the total time spent exploring the
157 context^{novel} configuration (**Fig. 4A**, left; $M = 42.83s$, $SD = 21.63s$) and the
158 context^{familiar} configuration ($M = 62.23s$, $SD = 29.09s$; $t_{(8)} = 1.47$, $p = 0.18$, $d = 0.49$).
159 In addition, there was no difference between the recency^{novel} (**Fig. 4A**, right; $M =$
160 $61.72s$, $SD = 39.96s$) and the recency^{familiar} configurations ($M = 52.70s$, $SD = 17.87s$;
161 $t_{(9)} = -0.64$, $p = 0.54$, $d = -0.20$). The D2 ratio data conveyed a similar picture (context
162 D2: $M = -0.03$, $SD = 0.30$; $t_{(9)} = -0.32$, $p = 0.76$, $d = -0.10$; recency D2: $M = -0.0003$,
163 $SD = 0.20$; $t_{(9)} = -0.005$, $p = 1.00$, $d = -0.001$). When analysing the different trial types
164 separately, the average context D2 scores for both when the test was situated in the
165 1st context (**Fig. 4B**; $M = -0.03$, $SD = 0.25$), and when situated in the 2nd context (**Fig.**
166 **4C**; $M = -0.03$, $SD = 0.44$) were clearly not different from zero ($t_{(9)} = -0.38$, $p = 0.72$,
167 $d = -0.12$; $t_{(9)} = -0.22$, $p = 0.83$, $d = -0.07$; respectively). Lastly, the circular data
168 (**Fig. 4D**; $n = 20$, $\bar{\theta} = 172.5^\circ$, $v = 74.2^\circ$, $\bar{R} = 0.16$) was uniformly distributed around
169 the circle (Rao's spacing test: $U = 138.84$, $p > 0.50$). Therefore, these results
170 suggested that there was no coherent strategy used in the 'additional local object as
171 context' variant.

172

173 Comparison of the context specifiers: conspecific partner (experiment 1) and
174 the additional local object (experiment 2)

175

176 Due to our protocol of testing the subject when they were only alone, another
177 possibility that could explain recognition behaviour (during test phases of these
178 object-in-context variants), is a simple object recognition strategy based upon
179 novelty-detection with ignorance of the contextual information. For example, this
180 could occur if there was little acquisition of objects when exposed in the presence of
181 the conspecific relative to when the subject was alone. Hence, mice would explore
182 the same object as predicted via a context^{novel} strategy but due to this object simply
183 being more unfamiliar (and thus novel) at test. We thus conducted control analyses

184 concerning the object exploration in exposure phases of experiment 1 and
 185 experiment 2 (SFig. 2).

186 A mixed repeated measures ANOVA comparing summed total exploration in
 187 exposure phases relative to test phases, revealed that for both experiment 1 and
 188 experiment 2 there was more exploration in exposure phases vs. test phases (SFig.
 189 2A-B; exploration of exposure phases was scaled to match that of test phases;
 190 Fisher's least significant difference, LSD, post-hoc tests: $p = 0.01$, $p < 0.001$,
 191 experiment 1 and 2; respectively). This suggested successful acquisition of objects

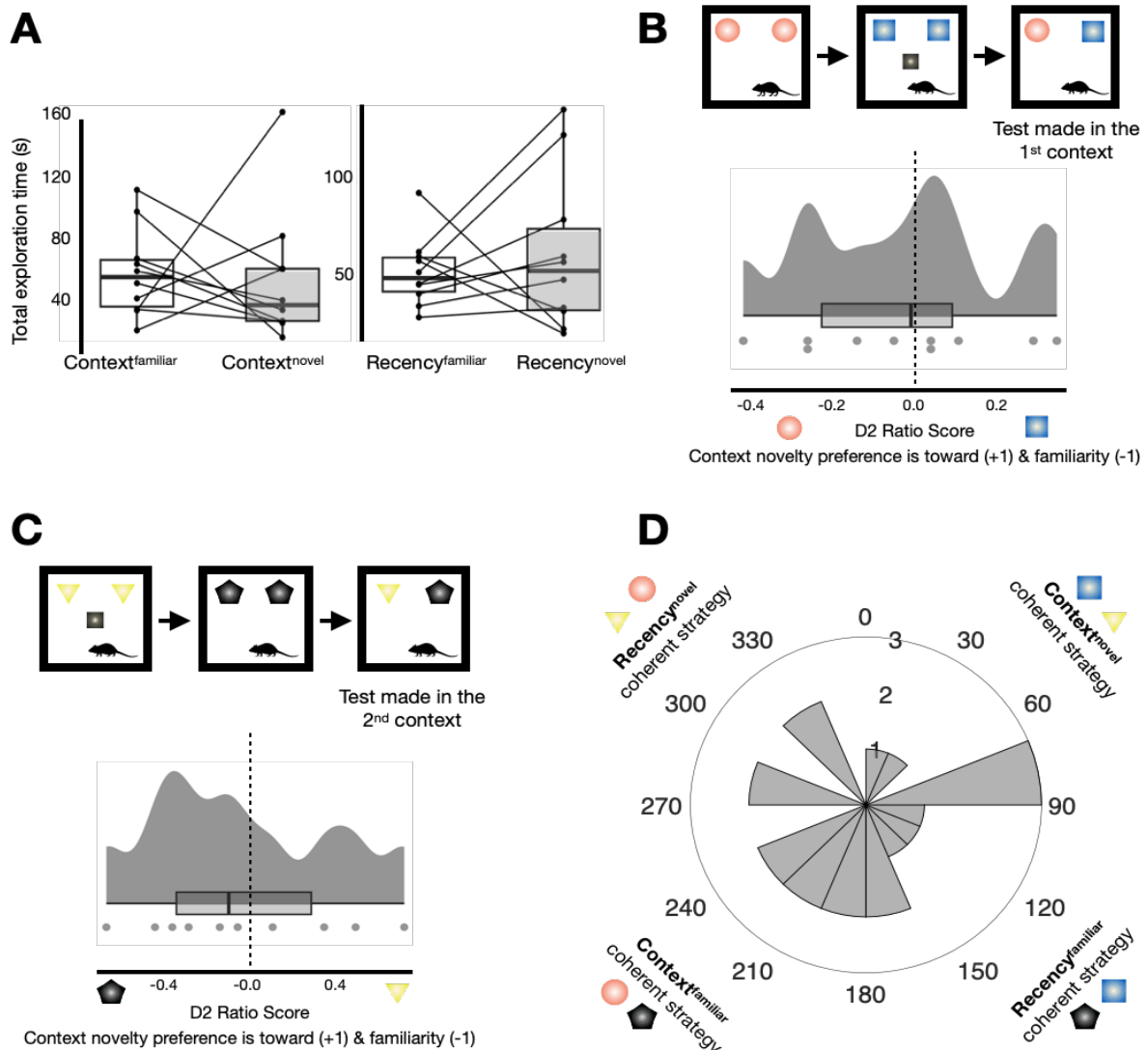


Figure 4. Experiment 2: no coherent strategy emerges when context is specified via an additional local object. (A) Total exploration time (s) summed across all test phases. There were no differences between exploration of any particular configurations (context^{novel}: M = 42.83s, SD = 21.63s; context^{familiar}: M = 62.23s, SD = 29.09s; $t_{(8)} = 1.47$, $p = 0.18$, $d = 0.49$; recency^{novel}: M = 61.72s, SD = 39.96s; recency^{familiar}: M = 52.70s, SD = 17.87s; $t_{(9)} = -0.64$, $p = 0.54$, $d = -0.20$). (B) The average test in the 1st context D2 score did not significantly from zero (M = -0.03, SD = 0.25; $t_{(9)} = -0.38$, $p = 0.72$, $d = -0.12$). (C) The average test in the 2nd context D2 score did not significantly from zero (M = -0.03, SD = 0.44; $t_{(9)} = -0.22$, $p = 0.83$, $d = -0.07$). (D) Angular histogram depicting the circular data (n = 20), plotted in 16 bins of 22.5°, circular descriptive and inferential statistics are reported in the main text. Of note, the objects used in this task variant were not the same as used in the conspecific as context task variant (i.e., the schematics are kept the same for clarity purposes).

192 did occur during exposure phases; in other words, objects at the test phases were
193 likely familiar to mice in both experiments 1 and 2. Interestingly, we also found
194 significantly more total exploration on average in experiment 2 ($M = 143.71$) relative
195 to experiment 1 ($M = 101.72$; $F_{(1,9)} = 14.04$, $p = 0.005$, $\eta_p^2 = 0.61$), indicating that
196 there was minimal decline in task motivation across experiments 1 and 2.

197 We next sought to compare exposure phases of the ‘context’ specifiers (i.e.,
198 conspecific partners in experiment 1 vs. an additional local object in experiment 2),
199 and ‘presence’ of the context specifier (that is, the context specifier’s presence vs. its
200 absence). A mixed repeated measures ANOVA yielded a significant interaction
201 between ‘context’ and ‘presence’ ($F_{(1,9)} = 9.11$, $p = 0.02$, $\eta_p^2 = 0.50$). Fisher’s LSD
202 post-hoc analyses indicated that within experiment 1, there was significantly more
203 object exploration in exposure phases when the conspecific was present (**SFig. 2C**;
204 $M = 34.59$) versus when mice were alone ($M = 26.08$; $p = 0.017$), which is in
205 accordance with previous reports^{44,45}. Contrastingly, within experiment 2, levels of
206 exploration in the presence of the additional local object ($M = 40.69$) were similar to
207 when it was absent ($M = 45.82$; $p = 0.32$).

208 In summary, the control analyses further support the notion that in experiment
209 1 mice were using a mnemonic strategy reliant on the contextual information (the
210 conspecific partner; **Fig 3**). However, in experiment 2, despite some indication of
211 successful object acquisition from exposure phases (similarly to that seen in
212 experiment 1; **SFig. 2A-B**) we found no evidence of a coherent recency-based or
213 context-based strategy when an additional local object could have been used as a
214 potential context specifier (**Fig. 4**).

215

216 Experiment 3: mice preferentially explore contextual mismatch information
217 associated with familiar conspecifics over a recency-based mnemonic strategy

218

219 Inspired by the object-in-context SOR paradigm, for experiment 3, we adapted
220 the standard social discrimination task^{22,23} to construct a conspecific-in-context
221 variant (see Introduction, **Fig. 2, SFig. 3**). The aim of the design was to make two
222 novelty-oriented discriminatory strategies available, and to pit them against each
223 other. Figure 2 pictorially illustrates the two potential strategies. In the test phase,
224 the mice could preferentially explore either: 1) the conspecific in the novel
225 conspecific-in-context configuration, seen more recently and presented in the same
226 place, but where there was now a contextual mismatch (conspecific C, yellow, in **Fig.**
227 **2**); or 2) the conspecific who was seen longer ago, presented in the same place and
228 context (conspecific A, red, in **Fig. 2**, recency strategy). In this way, we could
229 investigate the question of whether mice show a spontaneous exploratory preference
230 for a context-based or recency-based mnemonic strategy when both are available,
231 as in the context SOR tasks but now with respect to conspecifics.

232 Experiment 3 comprised three sessions of this conspecific-in-context design,
233 with a single trial per session. Two sessions were with conspecifics of the same sex,
234 and one of the opposite-sex (**SFig. 1**). Having a second same-sex session allowed
235 for examination of recognition behaviour once subjects had had further habituation of
236 the task conditions, whilst also allowing for within-subject counterbalancing of
237 context order and conspecific placement to enhance within-subject reliability.
238 Moreover, previous work in rodents has suggested that social interaction behaviour
239 and neuromodulatory mechanisms can be dependent on conspecific-sex, with
240 increased salience associated with members of the opposite sex⁴⁸⁻⁵⁰. Thus, the idea
241 of the final opposite-sex session was to examine whether recognition behaviour
242 would differ because of using opposite-sex conspecifics which should be more
243 socially salient stimuli. In this way, the to-be-recognised opposite-sex conspecifics
244 may hinder or boost preferential exploratory behaviour (of a particular recognition
245 strategy) relative to same-sex conspecific stimuli.

246 A mixed repeated measures ANOVA was conducted on the exploration
247 behaviour in the test phases across sessions (**Fig. 5A**). There was an overall
248 significant main effect of 'session' (same-sex sessions 1 and 2, and the opposite-sex
249 session 3; $F_{(1,24,11.13)} = 26.73$, $p < 0.001$, $\eta_p^2 = 0.75$). Bonferroni corrected post-hoc
250 tests showed that there were comparable levels of exploration across same-sex
251 session 1 ($M = 4.97s$) and same-sex session 2 ($M = 4.13s$, $p = 1.00$). Whereas there
252 was significantly more exploration in the opposite-sex session 3 ($M = 18.08s$) relative
253 to session 1 and 2 ($p = 0.003$, $p < 0.001$; respectively). There was also an overall
254 significant main effect of 'conspecific' (that is, conspecific A, red, vs. conspecific C,
255 yellow, see **Fig. 2** and **5**, $F_{(1,9)} = 5.67$, $p = 0.04$, $\eta_p^2 = 0.39$). Post-hoc tests showed
256 that across sessions there was more exploration of the contextually mismatched
257 conspecific C ($M = 10.34s$; **Fig. 5B**) relative to the least recently seen conspecific A
258 ($M = 7.78s$, $p = 0.04$) who was presented in the same context and place at test. This
259 is consistent with forming an episodic-like conspecific-in-context memory.

260 There was no overall interaction between session and conspecific ($F_{(2,18)} =$
261 1.32 , $p = 0.29$, $\eta_p^2 = 0.13$). Yet, similarly to the overall significant main effect of
262 session, post-hoc tests showed that regardless of conspecific (A or C) more
263 exploration was made session in 3 relative to session 1 and 2 (all $p \leq 0.006$;
264 comparable exploration levels across session 1 and 2, all $p \geq 0.60$). This very clear
265 result suggests the enhanced salience of members of the opposite-sex. Given these
266 marked differences in exploratory expenditure across same-sex sessions versus the
267 opposite-sex session, we next sought to check using the D2 ratio score (**Fig. 5C**;
268 which accounts for individual differences in exploration levels), whether preferential
269 exploration towards certain conspecifics differed across sessions. A repeated
270 measures ANOVA yielded no sign at all of differences in recognition performance
271 across sessions ($F_{(2, 18)}$, $p = 0.64$, $\eta_p^2 = 0.05$, Bonferroni post-hoc tests all $p = 1.00$).

272 This suggested that exploratory preference on average was similar across these
 273 sessions, validating our finding of overall exploratory preference towards conspecific
 274 C (**Fig. 5B**). Finally, post-hoc tests within sessions, revealed that there was

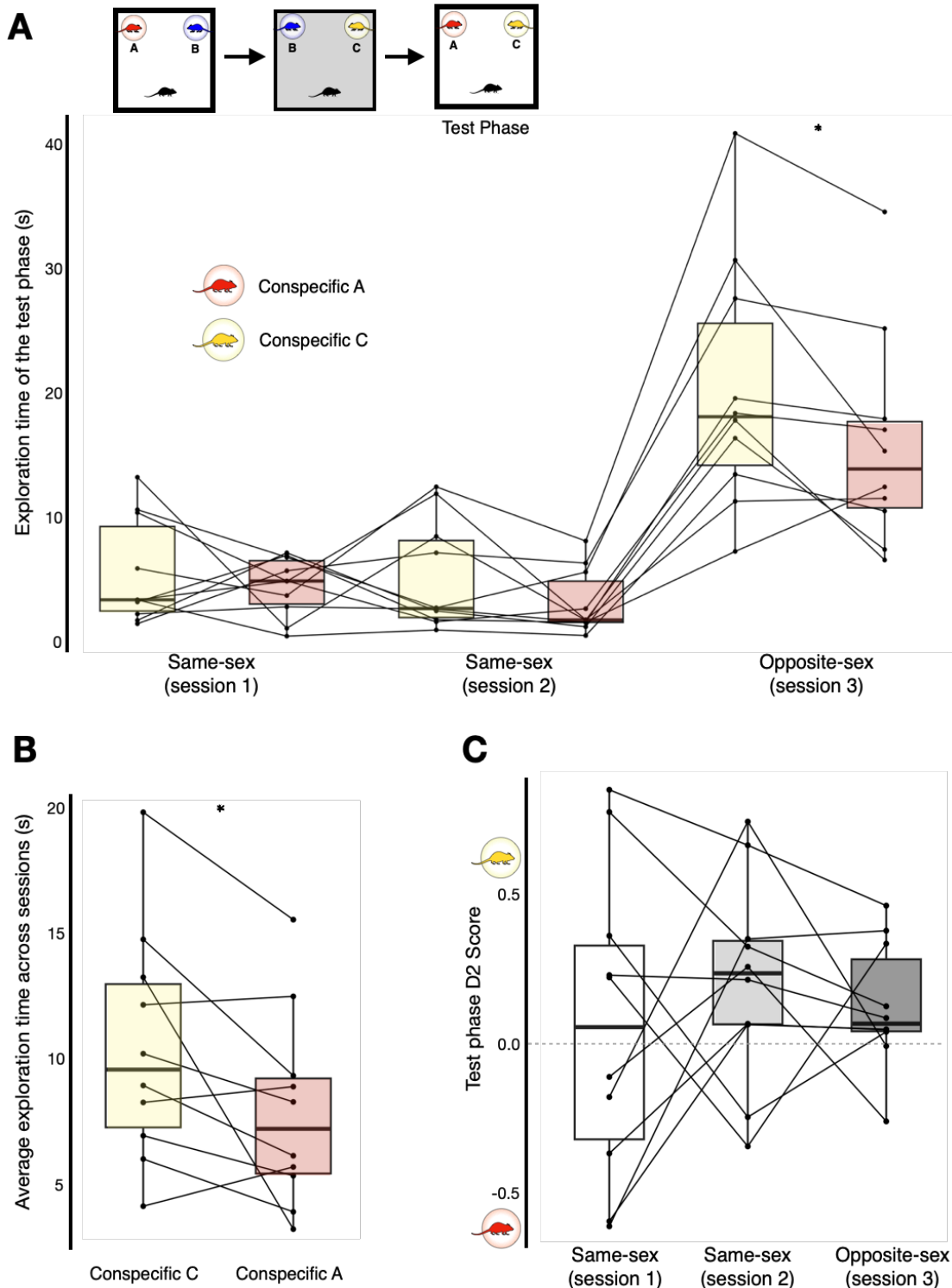


Figure 5. Experiment 3: mice preferentially explore contextual mismatch information associated with familiar conspecifics over a recency-based mnemonic strategy. **(A)** Upper left: reminder schematic of the conspecific-in-context task (see also Fig. 2). Lower: exploration times of conspecific A and C in the test phase by session. **(B)** Average exploration time of conspecific A ($M = 7.78s$) and C ($M = 10.34s$) across all sessions. **(C)** D2 ratio score of the test phase by session. (A-C) Descriptive and inferential statistics reported in the main text. *Denotes $p < 0.05$.

275 comparable levels of exploration towards conspecific A and C in session 1
276 (Conspecific C: $M = 5.52s$, Conspecific A: $M = 4.42s$, $p = 0.53$; D2 score: $M = 0.06$,
277 $SD = 0.52$, $t_{(9)} = 0.34$, $p = 0.75$, $d = 0.11$), and in session 2 (Conspecific C: $M =$
278 $5.19s$, Conspecific A: $M = 3.08s$, $p = 0.12$; D2 score: $M = 0.21$, $SD = 0.35$, $t_{(9)} = 1.89$,
279 $p = 0.09$, $d = 0.60$, CI 95% -0.09 to 1.26). However, in the opposite-sex session,
280 there was significantly more exploration of conspecific C ($M = 20.32$) versus
281 conspecific A ($M = 15.84$, $p = 0.044$; D2 score: $M = 0.12$, $SD = 0.21$, $t_{(9)} = 1.82$, $p =$
282 0.10 , $d = 0.58$, CI 95% -0.11 to 1.24). This suggested that the overall exploratory
283 preference toward the contextually-mismatched conspecific C (**Fig. 5B**) was
284 particularly driven by recognition behaviour in the opposite-sex session, possibly due
285 to the enhanced salience in the nature of the social stimuli⁴⁸⁻⁵⁰.

286

287 Discussion

288

289 Being able to flexibly remember episodes via social-context is of evolutionary
290 importance¹⁻⁴. Our experiments suggest that the same cohort of mice not only
291 preferentially explored conspecifics associated with environment-based contextual
292 mismatch information (experiment 3; **Fig. 5**), but used conspecific presence and
293 absence as a means to remember unique episodes in memory (experiment 1; **Fig.**
294 **3**). These findings echo the substantial evidence reported using SOR paradigms,
295 that when there is availability of both context-based novelty and recency-based
296 novelty, rodent exploratory behaviour is more directed to the unexpected contextual
297 change²⁸⁻³⁰.

298 Interestingly, no overall strategy emerged when context was specified by an
299 additional local object (experiment 2; **Fig. 4**), and this was seemingly not due to
300 reduced motivation nor lack of object acquisition during exposure phases (**SFig. 2**).
301 There are undeniable differences between conspecifics and a static local object, in
302 terms of the sensory cues that emanate from them and their biological relevance^{1,48-}
303 ⁵⁰. Yet, it would of course be premature to conclude from this experiment alone that
304 objects cannot be used by mice as contextual information in defining unique
305 episodes (especially when learnt via explicit reinforcing^{14,31}). What does seem
306 reasonable to conclude is that, the presence/absence of a conspecific has sufficient
307 ethological salience under incidental spontaneous conditions to be incorporated into
308 episodic-like memory, and this salience is clearly greater than that for a man-made
309 object, (especially when that object becomes increasingly habituated to over time, as
310 was the case in experiment 2).

311 A previous study suggested that when rats were exposed to an unfamiliar
312 context (a change in the physical environment), there was a reduction of
313 investigation and mild aggression towards a juvenile conspecific, who was
314 increasingly familiarised to from three previous sessions in a different, familiarised

315 context⁵¹. The experimenters argued that although rats still recognised the
316 conspecific, the behavioural change could be interpreted as increased habituation to
317 the conspecific⁵¹, that is, not only due to contextual novelty but perhaps a novel
318 association of the conspecific-in-context. We extend such work by showing in
319 experiment 3, that when mice are given a free choice to explore a more recently-
320 seen familiar conspecific associated with environment-based contextual mismatch
321 and a less recently seen familiar conspecific presented in the same place and
322 context, they preferentially explore the former.

323 Converging evidence demonstrates that successful social mnemonic
324 processing can strongly rely upon the hippocampal formation⁵²⁻⁵⁶. Hippocampal
325 principal cells can show place-dependent activity as rodents traverse their
326 environment, hence termed place cells³³⁻³⁵. But strikingly, hippocampal principal cells
327 may also flexibly integrate information about conspecifics in their responsivity⁵⁶⁻⁶¹, for
328 example place-like activity of these cells can also relate to positional information of
329 conspecifics (i.e., social place cells⁵⁸⁻⁶⁰). Notably, such social place cells were not
330 reported when rats' behaviour was dependent upon observationally tracking a
331 robot's movement⁶².

332 When substantial changes are made to the environment, place cells exhibit a
333 phenomenon known as 'remapping', whereby some cells fire in one environment, but
334 not another, or fire in different locations in each environment^{33-36,63-65}. Thus, at the
335 population-level, two sufficiently-different environments are represented distinctly, via
336 'global remapping'^{35,63}, in a manner that may specify two different contexts. Indeed,
337 the argument has been explicitly made, potentially finessing long-running issues with
338 defining 'context', that "electrophysiology opens the door to a measurement-based
339 approach with a clear definition: a new context is one that is sufficient to evoke
340 global remapping"⁶⁶.

341 It seems reasonable to infer that hippocampal place cell remapping occurs in
342 the majority of context-SOR studies, since these studies typically employ marked
343 changes in the physical environment to specify context. Moreover, increases in
344 rearing on hind legs typically accompanies place cell remapping in novel, physically
345 different, contexts⁶⁷⁻⁶⁹ implying a link between place cell remapping and context-
346 sensitive exploratory behaviour in rodents. How strong place cell remapping needs
347 to be, and in which hippocampal sub-regions, to act as a universal context-
348 differentiation readout signal remains unclear. Our behavioural observations here
349 suggest that conspecific presence/absence can define 'context' and thus distinguish
350 otherwise-similar episodes in the same physical environment. Taken together with
351 evidence of partial place cell remapping in sub-regions CA2 and ventral CA1 across
352 scenarios that differ only socially^{54,70,71} it seems reasonable to suggest that: 1) social
353 as well as physical-environmental cues can define behaviourally-relevant context
354 shifts in rodents as well as other species, especially humans; 2) remapping in

355 hippocampal place cells, even in rodents, may not need to be driven by changes in
356 physical-environmental cues, nor to be ‘complete/global’, in order to serve as a
357 context-shift signal.

358 In conclusion, we have implemented new spontaneous recognition task
359 variants to show that mice readily use social episodic-like memory to drive their
360 exploration. The tasks offer a novel way to tease apart the mechanisms of social
361 recognition memory in a crucially different way to the current, frequently used social
362 discrimination protocols. This is especially relevant in modelling atypical, disease
363 and neuropsychological disorders with rodent models, as in response to given
364 manipulations animals may display chance level performance or be using recency-
365 based or context-based (episodic-like) mnemonic strategies to guide their behaviour.

366 Methods

367 Subjects

368 Ten B6FVBF1 mice (5 male) were bred inhouse at the life science support unit
369 (Durham University, U.K.). They were ~10 weeks of age when habituation begun (Females
370 weight: M = 24.1g, SD = 1.0g; Males weight: M = 30.4g, SD = 1.8g) and were housed in two
371 cages in same-sex groups of 5. Each home cage measured 45 × 28 × 13 cm (l × w × h;
372 Model: MB1, NKP isotec., U.K.) and were equipped with 2 mouse tunnels and 2 igloos
373 (Datesand Limited., U.K.). The home room was maintained on a 12-h light-dark cycle (07:00-
374 19:00h), with daily monitoring of temperature and humidity (20 ± 1°C; 55 ± 10%;
375 respectively). All stages occurred during the light phase and mice had free availability of
376 food and water ad libitum throughout (i.e., were not food or water deprived). Animals were
377 not euthanised as part of the experiments. All experiments were conducted in accordance
378 with the U.K. Animals Scientific Procedures Act (1986), approved by Durham University
379 AWERB and in accordance with the Home Office (procedure licence number: P7B7D2E4B).
380 Reporting follows the recommendations in the ARRIVE guidelines.

381 Apparatus and objects

382
383 All reported experiments took place in an apparatus designed for spontaneous
384 recognition (Model CI.80514R-1, Campden Instruments., U.K.). The specifications of which
385 are previously reported²⁷. Only the open field area was used presently, white noise played
386 continuously from above the open area (62 ± 8.5 dB SPL) and an additional camera was
387 also used for behavioural recording (Model: MWC72ZD/A, iPhone 11 Pro). Environmental
388 contexts were comprised of sensorily distinct floors and were sometimes paired with a wall
389 cue (see SFig. 3A-C). The objects varied in material, shape, size, texture and visual
390 complexion, each object had a minimum of 3 duplicates and were paired quasi-randomly
391 (example pair shown in SFig. 3D). In experiment 2, the additional local object that could act
392 as context is shown in SFig. 3E. For experiment 3 the social conspecific-in-context
393 recognition experiments, conspecifics were placed within a wire cup, and all were weighed
394 down with the same object (see SFig. 3F). For all experiments, objects and conspecifics
395 were positioned towards the far corners of the open field opposite the door (i.e., mice
396 egocentrically had objects/conspecifics left and right to them, as they were placed into the
397 open field, always in the same direction, north towards the objects/conspecifics). At the end
398 of testing sessions for the experiments 1 and 2, objects, floors and the apparatus were
399 cleaned using disinfectant wipes (Clinell universal wipes, GAMA Healthcare Ltd., U.K.). For
400 experiment 3, the wire cups and floors were cleaned and dried between each phase and at
401 the end, this was to minimise the crossing of scent-marking cues of conspecifics between
402 phases.

403

404 Habituation

405

406 Mice were first handled in their home room for a minimum of 3 consecutive days,
407 before being transported (in cage groups) to the experimental room where all reported
408 testing took place (white noise played and the room was lit by diffuse white light from 2
409 lamps, 60 W & 100 W). The first-time mice were habituated to the open field was in context

410 X (see SFig. 3A) and they did so in cage groups (30 minutes). Following this, they were
411 habituated once in the same dyads as used for the experimental session, but objects were
412 now present (two of the same and they were not used in any experiments; 30 minutes). Prior
413 to experiment 3, context Y and Z (SFig. 3B-C) were habituated to on the same day in cage
414 groups (30 minutes each, ~1.5 hours between; the wire cups were present). Lastly, prior to
415 experiment 2, context X was re-habituated twice on separate days, once without objects and
416 once with the same habituation objects as used previously. Both habituations occurred in
417 cage groups and lasted for 20 minutes.

418 Procedure: object-in-context experiments (experiments 1 and 2)

419 A given trial was composed of 3 phases (Fig 1A; 2 exposure phases and a test
420 phase). The same pair of objects are placed in exposure 1, where mice explored them for ~3
421 minutes before being returned to a separate holding cage (for ~3 minutes, the same design
422 as the home cage and kept within the experimental room). A different pair of objects are
423 presented in exposure 2 and again mice explored them for ~3 minutes. Approximately 5
424 minutes elapsed before experiencing of the test phase, which contained a copy of an object
425 from exposure 1 and a copy of an object from exposure 2 and lasted for ~3 minutes
426 (example object pair shown in SFig. 3D). There was a ~3 minute interval before the next trial
427 begun. For experiment 1, a given dyad of mice were composed randomly of same-sex cage
428 (and litter) mates. The test subject was always placed into the context first and removed last,
429 being returned into the same holding cage as the partner. The partner who was not the test-
430 subject for that session was tested 6 days later (SFig. 1). For experiment 2, the additional
431 local object acting as a potential context specifier (see SFig. 3E) was placed in with the other
432 objects but kept the same throughout the session and was never present in the test phase
433 (like in experiment 1). The objects used in experiment 2 were not the same as used in
434 experiment 1. Test phases could be situated in the 1st context or test phases could be
435 situated in the 2nd context (Fig. 1A). Four trials comprised a single experimental session and
436 the trial order, object order and placement of the object-in-context novelty was
437 counterbalanced. Notably, the context specifier could not be counterbalanced as we
438 required the subject to always be alone in the test phase (see main text for reasoning).

439 Procedure: social conspecific-in-context recognition (experiment 3)

440 A given trial was composed of 3 phases (2 exposure phases and a test phase; see
441 Fig. 2). In the first exposure phase, the test subject experienced two conspecifics contained
442 within wire cups in a given environment-based context (~3 minutes), before being returned
443 alone into a holding cage. After ~5 minutes, the test subject was placed back into the
444 apparatus but now the context had been changed and they could explore a familiar
445 conspecific or a newly introduced unfamiliar conspecific in the task conditions altogether (~3
446 minutes). This was considered as a second exposure phase to allow for the scenario that
447 occurs in the test phase. Again after ~5 minutes elapsed, the test subject was returned into
448 the apparatus and the context was changed back to that experienced in the first exposure
449 phase. Subjects in the test phase could then explore a familiar conspecific, more recently-
450 seen in the same place, who now had a contextual mismatch or they could explore an also
451 familiar conspecific who was seen less recently, but presented in the same place and
452 context (lasting ~3 minutes). This experiment was conducted twice using same-sex cage

453 and littermates (the second session was within-subject counterbalanced) and lastly once
454 using opposite-sex littermates (SFig. 1; all randomly assigned as to which conspecifics were
455 to-be-recognised, and all mice experienced containing in the wire cups, within completion of
456 sessions across animals). The context and conspecific order were all counterbalanced and
457 hence so was the placement of the novel conspecific-in-context in test trials.

458 Behavioural analyses

459 Behaviour was measured off-line via the recorded footage of experimental trials.
460 Exploratory behaviour was regarded as when mice were within ~2cm of the object (or the
461 wire cup/conspecific) and actively exploring it (i.e., sniffing, touching, biting and visibly
462 whisking). Behaviour such as climbing and sitting upon objects, or the wire cup
463 configurations were not considered as exploration, and neither was using them to support
464 rearing. The duration of exploratory behaviour (s) with respect to objects, wire cups and
465 conspecifics (of all phases) was manually scored unblinded by the main experimenter (#1).
466 All reported statistics are based upon the main experimenter's scoring. Importantly, a
467 random subset (20% of each experiment test phase) was scored blinded by two other
468 trained experimenters (#2 and #3, who had less experience overall in comparison to
469 experimenter #1). Scoring between all experimenters were significantly and positively
470 correlated (#1 vs. #2: $r_{(54)} = 0.75$, $p < 0.001$, CI 95% 0.60 to 0.85; #1 vs. #3: $r_{(54)} = 0.83$, $p <$
471 0.001 , CI 95% 0.72 to 0.90; #2 vs. #3: $r_{(54)} = 0.89$, $p < 0.001$, CI 95% 0.81 to 0.93).

472 Additionally, intraclass correlation coefficient (ICC) analysis suggested good to excellent
473 reliability of scoring⁷² (The average measure ICC was 0.91, CI 95% 0.77 to 0.96, $F_{(55,110)} =$
474 19.07 , $p < 0.001$; 2-way random-effects model, absolute-agreement, $k = 3$, mean-rating).

475 Total exploration time (s) was the summed exploration across trials by animals of a
476 given configuration (e.g., the novel object-in-context) or else specified. In no case did side-
477 bias better explain recognition performance over a context or recency-based strategy (Fig.
478 3A; Fig. 4A; Fig. 5C; $t_{(9)} = -1.92$, $p = 0.09$; $t_{(8)} = -0.12$, $p = 0.90$; $t_{(9)} = 0.86$, $p = 0.42$;
479 respectively). The classically described discrimination ratio 2 (D2) scores for a context-
480 based or recency-based strategy is previously reported²⁷, from a context D2 ratio score
481 calculation novelty preference is toward +1 and familiarity preference toward -1, with 0
482 indicating no preference. For experiment 3 D2 scores, preference to explore the conspecific
483 associated with the contextual mismatch was indicated as values towards +1. For each
484 animal, the D2 score was calculated individually for each trial and then averaged across all
485 trials and finally across animals to give the reported overall mean D2 scores (unless
486 specified by trial/test type). All data was tested for normality (& sphericity where applicable)
487 and a non-parametric alternative (Greenhouse-Geisser correction) was used if $p < 0.05$,
488 using SPSS, v28 (2021, IBM Corp). Outlier cases were identified based on quartiles (where
489 $k = 2.07$)⁷³ and were excluded from statistical tests. All reported measures were two-tailed
490 tests.

491 We plotted animals' test in the 1st context D2 scores against test in the 2nd context D2
492 scores and formulated circular data (via an arctangent function, converted from radians to
493 degrees, $0 \pm 180^\circ$). Importantly, such circular analyses should be interpreted with
494 dependence upon evidence of exploratory preference differing to chance level performance,
495 but it can enhance explanatory power of the spontaneous recognition task data. Perfectly
496 coherent strategies across trial types (Fig. 1B) would be indicated by circular data points
497 aligning at 45° , 135° , -135° (225°) and -45° (315°). For example, $\sim 45^\circ$ for a coherent
498 context^{novel} strategy in a context-based SOR task (Fig. 1C). Data points aligning more

499 towards 0°, 90°, 180° and -90° (-270°) would suggest that exploratory preference is
500 exhibited in only 1 out of the 2 trial/test types. We designed the object-in-context
501 experiments (experiments 1 and 2) in such a way where test in the 1st context trials were
502 interleaved with test in the 2nd context trials, allowing 2 consecutive trials (i.e., the first and
503 last 2 trials from experiment 1 and 2)) to form animal-trial circular data points. We used the
504 MATLAB (2020b, The MathWorks, Inc) circular statistics toolbox⁷⁴ and package circular⁷⁵ in
505 R (2021.09.0, RStudio, PCB) to compute circular descriptive and inferential statistics. To use
506 a single circular test capable of accommodating distributions that were not expected to be
507 unimodal, we employed Rao's spacing test⁷⁴.

508 Data availability

509 The data that support the findings of this manuscript are available on the OSF
510 repository (<https://doi.org/10.17605/OSF.IO/QWZAM>) or on available request from T.W.R.,
511 the corresponding author.

512 Competing interests

513 The authors declare no competing interests.

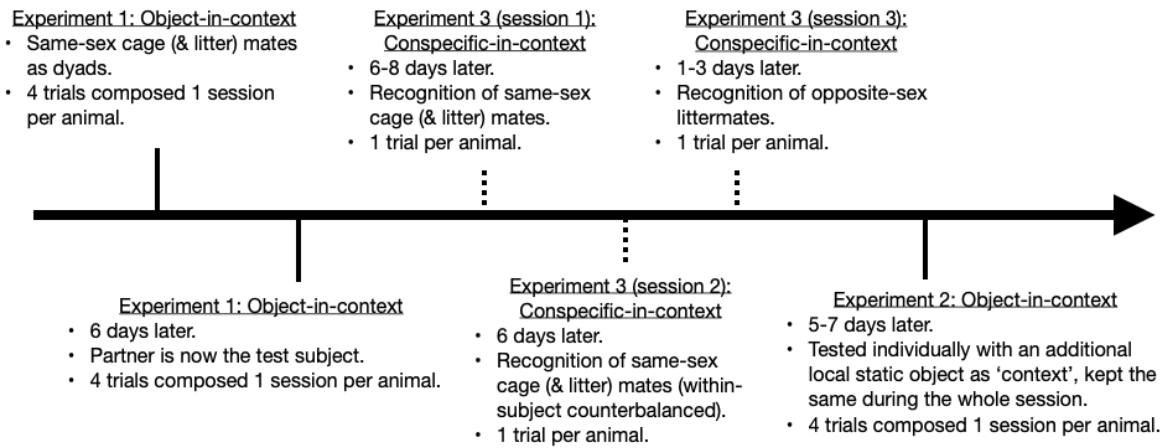
514 Contributions

515 All authors contributed to the conceptualisation of the experiments. T.W.R. designed
516 the experiments, collected the data and conducted the data analyses. S.L.P., C.L., and A.E.
517 supervised these stages. All authors interpreted the data. T.W.R. wrote the original
518 manuscript and edited it, and S.L.P., C.L., and A.E. reviewed the original manuscript and
519 edited it.

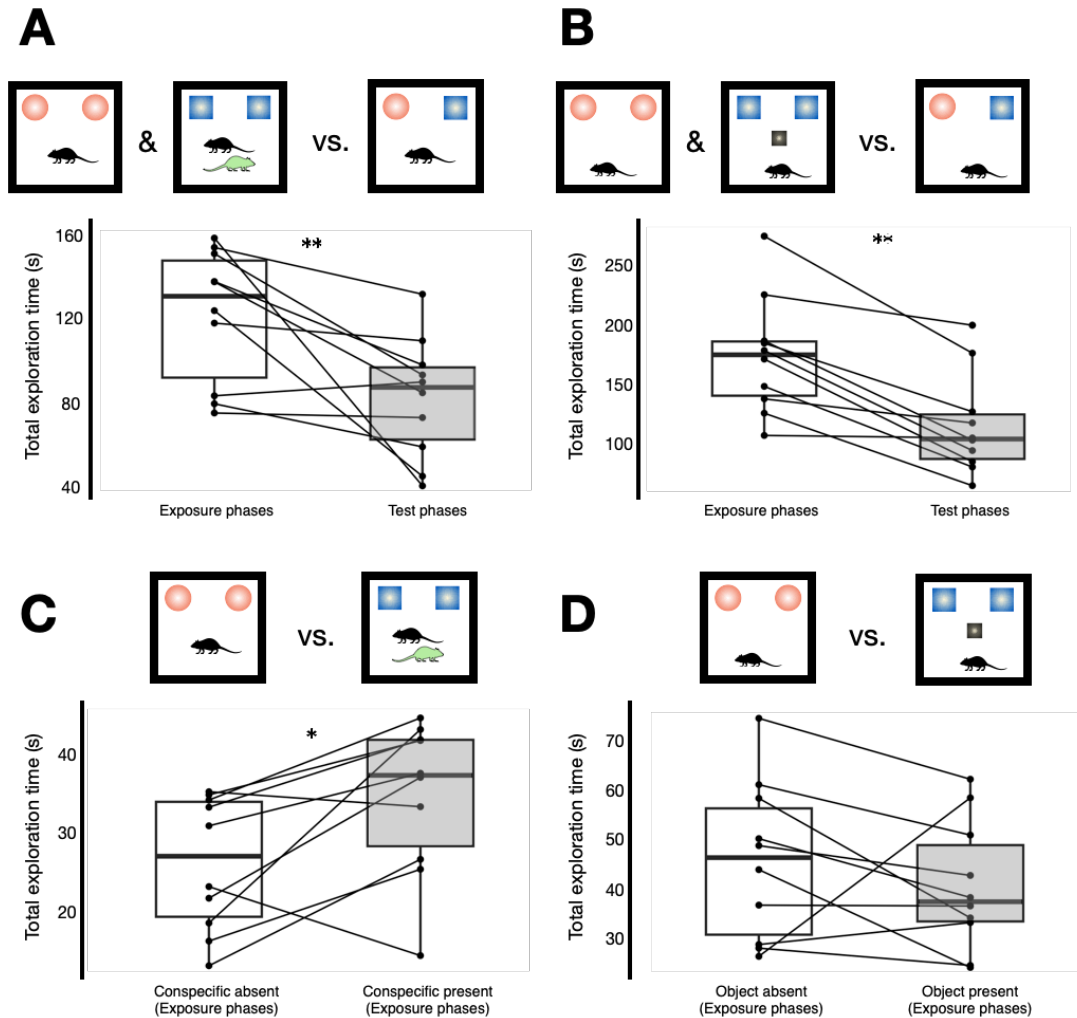
520 Acknowledgements

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523 science support unit (Durham, U.K.), and thank B.J.A. Slater. and G. Kan. for their
524 assistance with scoring.

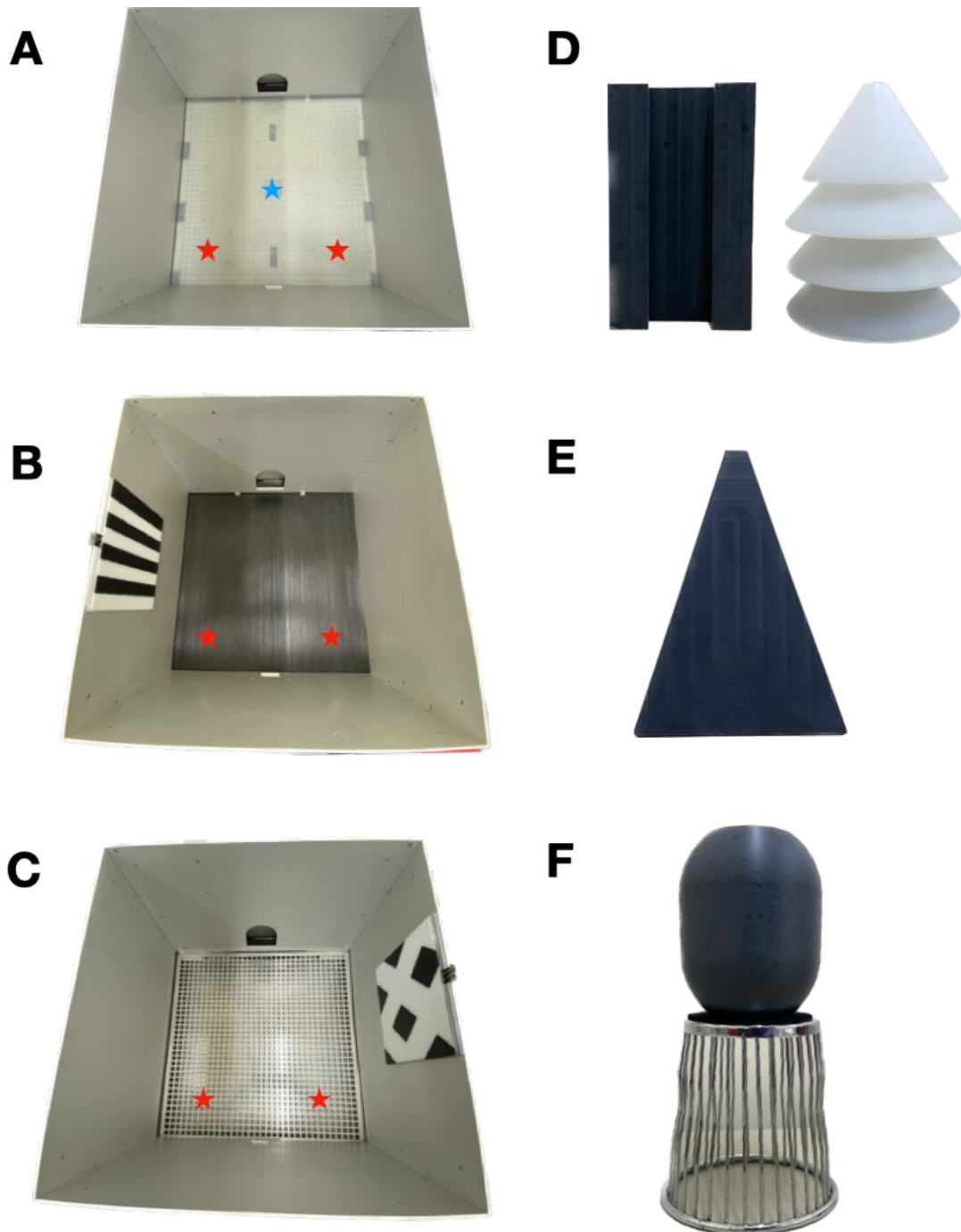
Experimental Timeline



Supplementary Figure 1. The timeline for all the presently described experiments.



Supplementary Figure 2. Analyses of object exploration during the exposure phases of the object-in-context variants. **(A)** Summed total object exploration during exposure phases scaled to compare against summed total exploration in the test phases. A mixed repeated measures ANOVA yielded a significant main effect of ‘context’ (conspecific, experiment 1, vs. object variant, experiment 2; $F_{(1,9)} = 14.04, p = 0.005, \eta_p^2 = 0.61$). Fisher’s least significant difference post-hoc (LSDph) analyses (for all following comparisons) revealed that there was significantly more exploration in Exp 2 ($M = 143.71$) vs. Exp 1 ($M = 101.72, p = 0.005$). There was also a significant main effect of ‘phase’ (exposure vs. test phase; $F_{(1,9)} = 46.70, p < 0.001, \eta_p^2 = 0.84$). Significantly more exploration in exposure phases ($M = 147.17$) vs. test phases ($M = 98.26, p < 0.001$). The ANOVA yielded no initial overall interaction between context and phase ($F_{(1,9)} = 1.25, p = 0.29, \eta_p^2 = 0.12$). However, post-hoc tests revealed that within context, there was significantly more exploration in the exposure phases of Exp 1 ($M = 121.33$) vs. the test phases ($M = 82.11; p = 0.01, shown in A$). **(B)** Post-hoc tests also revealed that there was significantly more exploration in the exposure phases of Exp 2 ($M = 173.01$) vs. the test phases ($M = 114.42; p < 0.001$). **(C)** A mixed repeated measures ANOVA was conducted for object exploration during only the exposure phases. Similarly to A, there was a significant main effect of context ($F_{(1,9)} = 12.33, p = 0.007, \eta_p^2 = 0.58$; more exploration in Exp 2, $M = 43.25$, vs. Exp 1, $M = 30.33, p = 0.007$). There was no main effect of ‘presence’ (conspecific/object presence vs. absence; $F_{(1,9)} = 0.25, p = 0.63, \eta_p^2 = 0.03$), nor ‘trial-type’ (test made in the 1st context vs. test made in the 2nd context trials; $F_{(1,9)} = 1.58, p = 0.24, \eta_p^2 = 0.15$). There was a significant 2-way interaction between context and presence ($F_{(1,9)} = 9.11, p = 0.02, \eta_p^2 = 0.50$). Post-hoc tests revealed that within presence, there was more exploration in Exp 2 in absence of the object ($M = 45.82$) vs. when mice were alone in Exp 1 ($M = 26.08, p = 0.001$). However, there was no difference between the presence exposure phases across Exp 1 and 2 (Exp 2: $M = 40.96$; Exp 1: $M = 34.59, p = 0.19$). As shown in C, within context (of Exp 1), there was significantly more exploration when there was conspecific presence ($M = 34.59$) vs. their absence ($M = 26.08, p = 0.017$). Finally, the ANOVA revealed no overall 3-way interaction between, context, presence and trial-type ($F_{(1,9)} = 0.11, p = 0.75, \eta_p^2 = 0.01$; within context & trial-type: test in the 1st context conspecific presence, $M = 32.66$ vs. alone, $M = 24.64, p = 0.09$. Test in the 2nd context conspecific presence, $M = 36.52$ vs. alone, $M = 27.52, p = 0.11$). **(D)** There was no difference between the exposure phases of Exp 2 (presence: $M = 40.69$ vs. absence: $M = 45.82; p = 0.32$). Within context and trial-type: test in the 1st context trials object acting as context present ($M = 44.75$), vs. absent ($M = 53.53, p = 0.43$). Test in the 2nd context trials object present ($M = 36.62$), vs. absent ($M = 38.11, p = 0.87$). Of note, schematics of only test in 1st context trials are shown for consistency, both trial types were considered for all the above reported analyses. *Denotes $p < 0.05$, **Denotes $p \leq 0.01$



Supplementary Figure 3. Environment-based contexts and objects. **(A)** Context X open field, used for the object-in-context spontaneous recognition variants (experiment 1 and 2). It was comprised of no wall cues and a translucent Perspex floor with no holes. For reference, the door was considered south and the objects were placed towards the far corners north indicated via the red stars. The blue star indicates placement of the additional local object (see E) that could act as context. **(B)** Context Y open field, one of the two contexts used for the social conspecific-in-context recognition experiment 3. It was comprised of a striped, textured rubber black floor, paired with a polarised striped cue card on the east wall. Red stars indicated approximate placement of the wire cups (see F) containing conspecifics. **(C)** Context Z open field, the other context used for the conspecific-in-context social recognition experiment 3. It was comprised of steel mesh flooring paired with a polarised diamond patterned cue card on the west wall. **(D)** Example object pair used for the object-in-context experiments. Black object: 5.5 × 5.5 × 9.0cm (l × w × h). White object: 8.0cm diameter, 9.0cm height. **(E)** The additional local object acting as context, kept the same throughout the session. Position indicated via the blue star in A. It measured 5.5 × 5.5 × 7.2cm. **(F)** The chrome steel wire cup (10.2cm diameter, 10.8cm height; Model: 31570, Spectrum Diversified Designs, Inc., Ohio, U.S.A.) used to contain conspecifics, and object used to weigh it down (8.0cm diameter, 9.0cm height). See red stars in B and C for approximate placement in the environment. Of note, the lighting during experimental testing was dimmer than that depicted in A-C.

References

1. Dunbar, R. I., & Shultz, S. Evolution in the social brain. *Science*, **317**(5843), 1344-1347 (2007).
2. O'Connell, L. A., & Hofmann, H. A. Evolution of a vertebrate social decision making network. *Science*, **336**(6085), 1154-1157 (2012).
3. Klein, S. B. *et al.* Evolution and episodic memory: An analysis and demonstration of a social function of episodic recollection. *Social Cognition*, **27**(2), 283-319 (2009).
4. Mahr, J. B., & Csibra, G. Why do we remember? The communicative function of episodic memory. *Behavioral and Brain Sciences*, **41**, e1 (2018).
5. Davidson, P. S., Drouin, H., Kwan, D., Moscovitch, M., & Rosenbaum, R. S. Memory as social glue: Close interpersonal relationships in amnesic patients. *Frontiers in Psychology*, **3**, 531 (2012).
6. Stiller, J., & Dunbar, R. I. Perspective-taking and memory capacity predict social network size. *Social Networks*, **29**(1), 93-104 (2007).
7. Tulving, E. Memory and consciousness. *Canadian Psychology/Psychologie canadienne*, **26**(1), 1 (1985).
8. Yonelinas, A. P. The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, **46**(3), 441-51 (2002).
9. Tulving, E. Episodic and semantic memory in *Organization of Memory*. (ed. Tulving, E. & Donaldson, W.) 381-402 (Academic Press, 1972).
10. Lempert, K. M. *et al.* Aging is associated with maladaptive episodic memory guided social decision-making. *Proceedings of the National Academy of Sciences*, **119**(42), e2208681119 (2022).
11. Tulving, E. Episodic memory: From mind to brain. *Annual Review of Psychology*, **53**(1), 1-25 (2002).
12. Clayton, N. S., Bussey, T. J., & Dickinson, A. Can animals recall the past and plan for the future?. *Nature Reviews Neuroscience*, **4**(8), 685-691 (2003).
13. Jozet-Alves, C., Bertin, M., & Clayton, N. S. Evidence of episodic-like memory in cuttlefish. *Current Biology*, **23**(23), 1033-1035 (2013).
14. Eacott, M. J., & Easton, A. Episodic memory in animals: remembering which occasion. *Neuropsychologia*, **48**(8), 2273-2280 (2010).
15. Allen, T. A., & Fortin, N. J. The evolution of episodic memory. *Proceedings of the National Academy of Sciences*, **110**(supplement 2), 10379-10386 (2013).
16. Ross, T. W., & Easton, A. The hippocampal horizon: Constructing and segmenting experience for episodic memory. *Neuroscience & Biobehavioral Reviews*, **132**, 181-196 (2022).
17. Templer, V. L., & Hampton, R. R. Episodic memory in nonhuman animals. *Current Biology*, **23**(17), 801-806 (2013).
18. Friedman, W. J. Memory for the time of past events. *Psychological Bulletin*, **113**(1), 44 (1993).
19. Roberts, W. A. *et al.* Episodic-like memory in rats: is it based on when or how long ago?. *Science*, **320**(5872), 113-115. (2008).
20. Brown, M. W., & Aggleton, J. P. Recognition memory: what are the roles of the perirhinal cortex and hippocampus?. *Nature Reviews Neuroscience*, **2**(1), 51-61 (2001).
21. Easton, A., Webster, L. A., & Eacott, M. J. The episodic nature of episodic-like memories. *Learning & Memory*, **19**(4), 146-150 (2012).
22. van der Kooij, M. A., & Sandi, C. Social memories in rodents: methods, mechanisms and modulation by stress. *Neuroscience & Biobehavioral Reviews*, **36**(7), 1763-1772 (2012).

23. Engelmann, M., Hädicke, J., & Noack, J. Testing declarative memory in laboratory rats and mice using the nonconditioned social discrimination procedure. *Nature Protocols*, **6**(8), 1152-1162 (2011).
24. Eacott, M. J., & Norman, G. Integrated memory for object, place, and context in rats: a possible model of episodic-like memory?. *Journal of Neuroscience*, **24**(8), 1948-1953 (2004).
25. Davis, K. E., Eacott, M. J., Easton, A., & Gigg, J. Episodic-like memory is sensitive to both Alzheimer's-like pathological accumulation and normal ageing processes in mice. *Behavioural Brain Research*, **254**, 73-82 (2013).
26. Dere, E., Huston, J. P., & Silva, M. A. D. S. Episodic-like memory in mice: simultaneous assessment of object, place and temporal order memory. *Brain Research Protocols*, **16**(1-3), 10-19 (2005).
27. Ross, T. W., & Easton, A. Rats use strategies to make object choices in spontaneous object recognition tasks. *Scientific Reports*, **12**(1), 16973 (2022).
28. Sep, M. S., Vellinga, M., Sarabdjitsingh, R. A., & Joëls, M. The rodent object-in context task: A systematic review and meta-analysis of important variables. *PLoS one*, **16**(7), e0249102 (2021).
29. Panoz-Brown, D. *et al.* Rats remember items in context using episodic memory. *Current Biology*, **26**(20), 2821-2826 (2016).
30. Oyanedel, C. N., Sawangjit, A., Born, J., & Inostroza, M. Sleep-dependent consolidation patterns reveal insights into episodic memory structure. *Neurobiology of Learning and Memory*, **160**, 67-72 (2019).
31. Chao, O. Y., de Souza Silva, M. A., Yang, Y. M., & Huston, J. P. The medial prefrontal cortex-hippocampus circuit that integrates information of object, place and time to construct episodic memory in rodents: Behavioral, anatomical and neurochemical properties. *Neuroscience & Biobehavioral Reviews*, **113**, 373-407 (2020).
32. Poulter, S. L., Kosaki, Y., Easton, A., & McGregor, A. Spontaneous object recognition memory is maintained following transformation of global geometric properties. *Journal of Experimental Psychology: Animal Behavior Processes*, **39**(1), 93 (2013).
33. Muller, R. U., & Kubie, J. L. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *Journal of Neuroscience*, **7**(7), 1951-1968 (1987).
34. Leutgeb, S. *et al.* Independent codes for spatial and episodic memory in hippocampal neuronal ensembles. *Science*, **309**(5734), 619-623 (2005).
35. Kubie, J. L., Levy, E. R., & Fenton, A. A. Is hippocampal remapping the physiological basis for context?. *Hippocampus*, **30**(8), 851-864 (2020).
36. Colgin, L. L., Moser, E. I., & Moser, M. B. Understanding memory through hippocampal remapping. *Trends in Neurosciences*, **31**(9), 469-477 (2008).
37. Wills, T. J., Lever, C., Cacucci, F., Burgess, N., & O'Keefe, J. Attractor dynamics in the hippocampal representation of the local environment. *Science*, **308**(5723), 873-876 (2005).
38. Jeffery, K. J., Anderson, M. I., Hayman, R., & Chakraborty, S. A proposed architecture for the neural representation of spatial context. *Neuroscience & Biobehavioral Reviews*, **28**(2), 201-218 (2004).
39. Williamson, C. M., Franks, B., & Curley, J. P. Mouse social network dynamics and community structure are associated with plasticity-related brain gene expression. *Frontiers in Behavioral Neuroscience*, **10**, 152 (2016).
40. Cordero, M. I., & Sandi, C. Stress amplifies memory for social hierarchy. *Frontiers in Neuroscience*, **13** (2007).

41. Ben-Ami Bartal, I., Rodgers, D. A., Bernardez Sarria, M. S., Decety, J., & Mason, P. Pro-social behavior in rats is modulated by social experience. *Elife*, **3**, e01385 (2014).
42. Dally, J. M., Emery, N. J., & Clayton, N. S. Food-caching western scrub-jays keep track of who was watching when. *Science*, **312**(5780), 1662-1665 (2006).
43. Tam, S. K., Bonardi, C., & Robinson, J. Relative recency influences object-in context memory. *Behavioural Brain Research*, **281**, 250-257 (2015).
44. Lipina, T. V., & Roder, J. C. Co-learning facilitates memory in mice: a new avenue in social neuroscience. *Neuropharmacology*, **64**, 283-293 (2013).
45. de França Malheiros, M. A. S. *et al.* Conspecific presence improves episodic-like memory in rats. *Frontiers in Behavioral Neuroscience*, **14**, 572150 (2021).
46. Wang, F., Kessels, H. W., & Hu, H. The mouse that roared: neural mechanisms of social hierarchy. *Trends in Neurosciences*, **37**(11), 674-682 (2014).
47. Cnops, V., Iyer, V. R., Parathy, N., Wong, P., & Dawe, G. S. Test, rinse, repeat: A review of carryover effects in rodent behavioral assays. *Neuroscience & Biobehavioral Reviews*, **135**, 104560 (2022).
48. Karigo, T. *et al.* Distinct hypothalamic control of same-and opposite-sex mounting behaviour in mice. *Nature*, **589**(7841), 258-263 (2021).
49. de la Zerda, S. H., Netser, S., Magalnik, H., & Wagner, S. Impaired sex preference, but not social and social novelty preferences, following systemic blockade of oxytocin receptors in adult male mice. *Psychoneuroendocrinology*, **116**, 104676 (2020).
50. Lukas, M., Toth, I., Veenema, A. H., & Neumann, I. D. Oxytocin mediates rodent social memory within the lateral septum and the medial amygdala depending on the relevance of the social stimulus: male juvenile versus female adult conspecifics. *Psychoneuroendocrinology*, **38**(6), 916-926 (2013).
51. Burman, O. H., & Mendl, M. The effects of environmental context on laboratory rat social recognition. *Animal Behaviour*, **58**(3), 629-634 (1999).
52. Hitti, F. L., & Siegelbaum, S. A. The hippocampal CA2 region is essential for social memory. *Nature*, **508**(7494), 88-92 (2014).
53. Tavares, R. M. *et al.* A map for social navigation in the human brain. *Neuron*, **87**(1), 231-243 (2015).
54. Oliva, A., Fernández-Ruiz, A., Leroy, F., & Siegelbaum, S. A. Hippocampal CA2 sharp-wave ripples reactivate and promote social memory. *Nature*, **587**(7833), 264-269 (2020).
55. Kogan, J. H., Frankland, P. W., & Silva, A. J. Long-term memory underlying hippocampus-dependent social recognition in mice. *Hippocampus*, **10**(1), 47-56 (2000).
56. Okuyama, T., Kitamura, T., Roy, D. S., Itohara, S., & Tonegawa, S. Ventral CA1 neurons store social memory. *Science*, **353**(6307), 1536-1541 (2016).
57. Rao, R. P., von Heimendahl, M., Bahr, V., & Brecht, M. Neuronal responses to conspecifics in the ventral CA1. *Cell Reports*, **27**(12), 3460-3472 (2019).
58. Danjo, T., Toyozumi, T., & Fujisawa, S. Spatial representations of self and other in the hippocampus. *Science*, **359**(6372), 213-218 (2018).
59. Omer, D. B., Maimon, S. R., Las, L., & Ulanovsky, N. Social place-cells in the bat hippocampus. *Science*, **359**(6372), 218-224 (2018).
60. Omer, D. B., Las, L., & Ulanovsky, N. Contextual and pure time coding for self and other in the hippocampus. *Nature Neuroscience*, **26**(2), 285-294 (2023).
61. Mou, X., & Ji, D. Social observation enhances cross-environment activation of hippocampal place cell patterns. *Elife*, **5**, e18022 (2016).
62. Bos, J. J. *et al.* Multiplexing of information about self and others in hippocampal ensembles. *Cell Reports*, **29**(12), 3859-3871 (2019).

63. Kim, S. H. *et al.* Global remapping in granule cells and mossy cells of the mouse dentate gyrus. *Cell Reports*, **42**(4), 112334 (2023).
64. Poulter, S., Hartley, T., & Lever, C. The neurobiology of mammalian navigation. *Current Biology*, **28**(17), 1023-1042 (2018).
65. Alme, C. B. *et al.* Place cells in the hippocampus: eleven maps for eleven rooms. *Proceedings of the National Academy of Sciences*, **111**(52), 18428-18435 (2014).
66. Lisman, J. *et al.* Viewpoints: how the hippocampus contributes to memory, navigation and cognition. *Nature Neuroscience*, **20**(11), 1434-1447 (2017).
67. Lever, C., Burton, S., & O'Keefe, J. Rearing on hind legs, environmental novelty, and the hippocampal formation. *Reviews in the Neurosciences*, **17**(1-2), 111-134 (2006).
68. Anderson, M. I. *et al.* Behavioral correlates of the distributed coding of spatial context. *Hippocampus*, **16**(9), 730-742 (2006).
69. Wells, C. E. *et al.* Novelty and anxiolytic drugs dissociate two components of hippocampal theta in behaving rats. *Journal of Neuroscience*, **33**(20), 8650-8667 (2013).
70. Alexander, G. M. *et al.* Social and novel contexts modify hippocampal CA2 representations of space. *Nature Communications*, **7**(1), 10300 (2016).
71. Wu, W. Y., Yiu, E., Ophir, A. G., & Smith, D. M. Effects of social context manipulation on dorsal and ventral hippocampal neuronal responses. *Hippocampus*, **33**(7), 830-843 (2023).
72. Koo, T. K., & Li, M. Y. A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *Journal of Chiropractic Medicine*, **15**(2), 155-163 (2016).
73. Hoaglin, D. C., Iglewicz, B., & Tukey, J. W. Performance of some resistant rules for outlier labeling. *Journal of the American Statistical Association*, **81**(396), 991-999 (1986).
74. Berens, P. CircStat: a MATLAB toolbox for circular statistics. *Journal of Statistical Software*, **31**, 1-21 (2009).
75. Lund, U., Agostinelli, C., & Agostinelli, M. C. Package 'circular'. *Repository CRAN*, **775** (2017).