

## **Distance- rather than location-based temporal judgments are more accurate during episodic recall in a real-world task**

Maneesh V. Kuruvilla<sup>a,b</sup>, Akira R. O'Connor<sup>a</sup> & James A. Ainge<sup>a\*</sup>

*<sup>a</sup>School of Psychology & Neuroscience, University of St Andrews, St Mary's Quad, St Andrews, Fife, United Kingdom; <sup>b</sup>Wicking Dementia Research and Education Centre, University of Tasmania, Hobart, Australia*

\*Correspondence:

Dr James A. Ainge

[jaa7@st-andrews.ac.uk](mailto:jaa7@st-andrews.ac.uk)

+44 (0) 1334 462057

Word count: 7120 words

1 **Distance- rather than location-based temporal judgments are more**  
2 **accurate during episodic recall in a real-world task**

3 Definitions of episodic memory typically emphasize the importance of spatiotemporal  
4 frameworks in the contextual reconstruction of episodic retrieval. However, our ability to  
5 retrieve specific temporal contexts of experienced episodes is poor. This has bearing on the  
6 prominence of temporal context in the definition and evaluation of episodic memory,  
7 particularly among non-human animals. Studies demonstrating that rats rely on elapsed time  
8 (distance) rather than specific timestamps (location) to disambiguate events have been used to  
9 suggest that human episodic memory is qualitatively different to other species. We examined  
10 whether humans were more accurate using a distance- or location-based method for judging  
11 when an event happened. Participants (n = 57) were exposed to a series of events and then asked  
12 either when (e.g. 1:03 p.m.) or how long ago (HLA; e.g. 33 minutes) a specific event took place.  
13 HLA judgements were significantly more accurate, particularly for the most recently  
14 experienced episode. Additionally, a significantly higher proportion of participants making  
15 HLA judgements accurately recalled non-temporal episodic features across all episodes. Finally,  
16 for participants given the choice of methods for making temporal judgements, a significantly  
17 higher proportion chose to use HLA judgements. These findings suggest that human and non-  
18 human temporal judgements are not qualitatively different.

19 Keywords: human episodic memory; episodic-like memory; passive encoding; temporal  
20 estimation; mental time travel

21

22

23

## 24 **Introduction**

25 Episodic memory is a fundamental memory process that allows the apparently  
26 automatic encoding of attended experience (Morris & Frey, 1997). It is often defined as  
27 memory for events and the temporal-spatial properties that allow us to distinguish  
28 memory for one event from other similar events (Tulving, 1983). In principle, any piece  
29 of information that is specific to an event can be used to disambiguate that memory  
30 from other memories including spatial location, contextual features of the event (e.g.  
31 weather, mood, specific stimuli) and time (Persson, Ainge, & O'Connor, 2016). Time is  
32 a particularly interesting and attractive candidate for disambiguating specific events in  
33 memory as each event will have a unique timestamp. In contrast, it is relatively rare for  
34 other features of an event to be completely unique. Consequently, many theories and  
35 definitions of episodic memory stress the importance of a temporal component  
36 (Clayton, Bussey, & Dickinson, 2003; de Kort, Dickinson, & Clayton, 2005; Roberts,  
37 2002; Tulving, 1983).

38 Temporal memory can, however, take a number of forms. Friedman (2001) puts  
39 forward two main strategies used to recall when a previously experienced episode  
40 occurred, referred to as 'distances' and 'locations' (Friedman, 2001). A distance-based  
41 approach involves remembering how long ago an event took place relative to the  
42 present. In contrast, a location-based strategy employs the use of information stored in  
43 memory, such as knowledge of personal, natural or social time patterns, to reconstruct  
44 the specific instance of when an event occurred. Location-based strategies would be  
45 consistent with the influential Temporal Context Model of episodic memory (Howard  
46 and Kahana, 2002). According to this model, information is stored either as context or  
47 content representations. As new content is encoded corresponding new context is  
48 associated with it. The contextual representation is an aggregation of previous

49 experiences and serves as source of location information to help disambiguate memories  
50 from other memories.

51 Both distance- and location-based strategies have plausible neurobiological  
52 mechanisms. Mechanisms that support distance-based strategies would need to show  
53 gradual change in representations that can be correlated with time passed. The  
54 hippocampus and surrounding parahippocampal cortices have been shown to have  
55 gradually changing representations that could represent changes in time elapsed at short  
56 (seconds-minutes; Eichenbaum, 2014; Kraus, Robinson, White, Eichenbaum, &  
57 Hasselmo, 2013; MacDonald, Lepage, Eden, & Eichenbaum, 2011; Pastalkova, Itskov,  
58 Amarasingham, & Buzsaki, 2008; Tsao et al., 2018) and medium (hours-days; Mankin,  
59 Diehl, Sparks, Leutgeb, & Leutgeb, 2015; Mankin et al., 2012; Mau et al., 2018)  
60 timescales. Recordings of hippocampal long-term potentiation (LTP) suggest a slow  
61 decrement over weeks-months providing a potential mechanism for distance-based  
62 strategies at even longer timescales (Abraham, Logan, Greenwood, & Dragunow,  
63 2002). The hippocampus also displays robust responses to stimuli that could be used to  
64 support location-based strategies including, most obviously, spatial location (Colgin,  
65 Moser, & Moser, 2008; O'Keefe & Dostrovsky, 1971), but also contextual features of  
66 the environment (Anderson & Jeffery, 2003; Leutgeb et al., 2005; Muller & Kubie,  
67 1987), motivation (Kennedy & Shapiro, 2009), social environment (Danjo, Toyozumi,  
68 & Fujisawa, 2018; Omer, Maimon, Las, & Ulanovsky, 2018) and on-going behavioural  
69 tasks (Ainge, Tamosiunaite, Woergoetter, & Dudchenko, 2007; Ainge, van der Meer,  
70 Langston, & Wood, 2007; Ferbinteanu & Shapiro, 2003; Lee, Griffin, Zilli,  
71 Eichenbaum, & Hasselmo, 2006; Smith & Mizumori, 2006; Wood, Dudchenko,  
72 Robitsek, & Eichenbaum, 2000).

73           A key difference between location- and distance-based strategies is that location-  
74 based memory involves the recall of specific source information from the encoding  
75 event to place the event in a temporal context (Diana, Van den Boom, Yonelinas, &  
76 Ranganath, 2011; Yonelinas, 1999). Distance-based strategies, however, rely on a  
77 familiarity-based retrieval mechanism that allows the age of a memory to be inferred  
78 from the relative strength of the memory trace. This lack of specific source information  
79 in distance-based temporal memories has been used to suggest that distance-based  
80 strategies are not episodic (Clayton et al., 2003; Roberts, 2002; Roberts & Feeney,  
81 2009; Suddendorf & Busby, 2003). This distinction between episodic and potentially  
82 non-episodic strategies for remembering when something happened has become  
83 relevant when examining non-human animals' memory for time. It has been suggested  
84 that reliance on distance-based strategies in some animals is evidence that human and  
85 non-human animal (hereafter animal) episodic memory are qualitatively different  
86 (Roberts et al., 2008).

87           Over the past two decades, episodic memory research in animals has  
88 considerably expanded, not least with the aim of finding an animal model of the first  
89 major symptom of Alzheimer's disease that can be used to test potential therapeutic  
90 targets. These studies have focused on demonstrating that animals can remember trial-  
91 unique combinations of specific stimuli within spatial locations at specific times. This  
92 integrated memory of what, where and when has been termed episodic-like memory in  
93 non-human animals and has been demonstrated in many species of birds (Clayton &  
94 Dickinson, 1998, 1999; Clayton, Yu, & Dickinson, 2001; de Kort et al., 2005; Feeney,  
95 Roberts, & Sherry, 2009, 2011; Zinkivskay, Nazir, & Smulders, 2009), primates  
96 (Martin-Ordas, Haun, Colmenares, & Call, 2010), cuttlefish (Jozet-Alves, Bertin, &  
97 Clayton, 2013), and rodents (Babb & Crystal, 2005, 2006a, 2006b; Davis, Easton,

98 Eacott, & Gigg, 2013; Eacott & Norman, 2004; Kart-Teke, De Souza Silva, Huston, &  
99 Dere, 2006). However, the degree to which episodic-like memory for what, where and  
100 when is equivalent to episodic memory in humans is still greatly debated (Suddendorf,  
101 2013; Suddendorf, Addis, & Corballis, 2009; Suddendorf & Busby, 2003; Tulving,  
102 1983). One of the defining characteristics of human episodic memory is the ability to  
103 mentally travel in time and relive an experience, auto-noetic consciousness, but in the  
104 absence of a test for mental time travel in animals it has not been possible to definitively  
105 say whether or not animals have human-like episodic memory. One route of enquiry  
106 would be to ask whether animals remember time using the apparently more episodic  
107 location-based strategies or whether they rely on distance-based time estimation.

108         Roberts et al. (2008) asked whether rats were capable of using a location-based  
109 strategy to remember time or whether, instead, they rely on a distance-based strategy.  
110 Rats were split into three groups and trained on an episodic-like memory task using a  
111 radial arm maze. The rats had to learn when cheese would be replenished or pilfered on  
112 a specific arm during the test trial using either a location-based strategy that they called  
113 ‘when’ (time of day that they received their sample trial) or a distance-based strategy  
114 that they called ‘how long ago’ (the elapsed time between test and sample trial). Rats  
115 using a how long ago (*HLA*) strategy were more accurate at learning a temporal rule to  
116 guide behavior than those using a *when* strategy. When specific location-based cues  
117 were minimized by testing in the middle of the light-dark cycle, rats could no longer  
118 accurately use *when* strategies. These findings were used to suggest that animals use a  
119 different temporal strategy to humans when performing a what-where-when memory  
120 task, raising questions about the similarity between episodic-like memory in animals  
121 and episodic memory in humans.

122           However, the Roberts study sought to specifically minimize location-based cues  
123 and, as such, it is not clear that humans would use location-based strategies in the same  
124 situation. In order to conclude that rats and humans have fundamentally different  
125 mechanisms for remembering when things happened, we must first ask how humans  
126 would perform when asked to solve a temporal memory problem using either distance-  
127 or location-based strategies. While it would not be logistically possible to train human  
128 subjects on the same type of paradigm that Roberts et al. (2008) used for their rat  
129 studies, we have sought to test the same cognitive mechanisms supporting temporal  
130 memory. In the current study, we examined what type of temporal information humans  
131 use to remember episodes and whether temporal accuracy is affected by asking  
132 participants to use different temporal strategies. Participants were signed up to take part  
133 in a study of ‘Technology and Social Interaction’ to ensure that they were unaware that  
134 this was a memory experiment and prevent them actively trying to remember the details  
135 of the episodes. During a one-hour testing session each participant experienced 3 events  
136 that happened in different spatial locations at specific times (after 3, 23 and 33 minutes).  
137 At the end of testing participants were asked to provide details of the events they had  
138 experienced including when it happened and critically were assigned to one of three  
139 groups depending on the temporal strategy they were required to employ (location,  
140 distance, and location or distance). The design of the experiment captured many of the  
141 key aspects of the animal studies whilst also aiming to provide an ecologically valid  
142 way of testing how we integrate the temporal features of an event into an episodic  
143 memory. Participants were required to make temporal judgements of real-world trial  
144 unique experiences that were passively encoded offering a realistic assessment of  
145 episodic memory compared with most lab studies. We also investigated which temporal

146 strategy participants chose to use when given an option between location- and distance-  
147 based approaches.

148         Considering work by Friedman (1993) and Roberts et al. (2008), we predicted  
149 that participants using a location-based temporal strategy would be more accurate at  
150 recalling when episodes occurred as well as specific non-temporal aspects of those  
151 episodes. We also expected that participants would actively choose to use a location-  
152 based temporal approach when given a choice.

## 153 **Materials and methods**

### 154 *Participants*

155 Fifty-seven University of St Andrews students (36 female) took part in a study approved  
156 by the University Teaching and Research Ethics Committee. All participants were paid  
157 £8 for their participation.

### 158 *Apparatus and materials*

159 The experiment took place in a 17x9 foot room with no potential time cues. Windows  
160 were blocked, and the room was well isolated from ambient sound. Participants sat  
161 around a long table. One end of the table faced a purple wall and the other end had a  
162 white backdrop. Metal cabinets were located in a corner of the room opposite the door.  
163 Participants were provided with magazines, a board game and a pack of playing cards.  
164 At the end of the experiment, participants were asked to fill out a questionnaire  
165 pertaining to the three *episodes* that took place during the study (see *Procedure*).



166 ***Design***

167 The experiment was advertised as a study examining the role of technology on human  
168 social interaction. This was done to prevent participants from trying to keep track of  
169 time as well as to provide a logical reason for requiring participants to surrender  
170 electronic devices that could display time. In the first two experimental conditions,  
171 participants had to recall the time of episodes either using a location- (*when*) or  
172 distance-based (*HLA*) strategy. A third condition was included to allow participants to  
173 freely choose either temporal strategy. A total of 12 experimental sessions were  
174 conducted, each running for 45 minutes with a group of 5 participants. Participants were  
175 assigned to a specific experimental condition depending on the session number they  
176 signed up for (Sessions 1, 4, 7 and 10 – *when* condition; Sessions 2, 5, 8 and 11 – *HLA*  
177 condition; Sessions 3, 6, 9 and 12 – *free choice* condition). Four sessions were run every  
178 day (10:00, 12:00, 14:00 and 16:00) over three days. Although 20 participants were  
179 recruited in total for each condition, one participant in each condition did not attend.  
180 Therefore, sessions 3, 4, and 5 only had four participants.

181 Participants had to make temporal judgements on three distinct episodes that  
182 took place. The episodes occurred 3 minutes, 23 minutes and 33 minutes from the start  
183 of the session. The time points at which the episodes took place were chosen to have  
184 one episode at the midpoint of the session and two episodes on either side of the  
185 halfway mark but not at symmetrical points from the start and end of the session  
186 respectively to avoid participants using that as a strategy for estimating time.

187 ***Procedure***

188 All participants were required to email their completed consent forms ahead of time to  
189 ensure that they were compliant with surrendering their electronic devices as well as to  
190 avoid any feelings of succumbing to peer pressure, should they want to withdraw at the

191 start of the experiment, given the group nature of the study. Participants were also made  
192 aware that their consent had not been sought regarding the video or audio recording of  
193 the session and, therefore, no such footage would be captured. This was clarified so that  
194 participants would be incentivised to interact with each other naturally. The two  
195 temporal landmarks available to all participants beforehand were the start time and  
196 duration of the experiment as featured in the study advertisement and information sheet.  
197 Precautions were taken to limit participants using these cues as reference points. The  
198 study duration was advertised as being 90 minutes long while the actual session lasted  
199 45 minutes. When participants arrived for the study, they were met at an adjoining  
200 building and then walked over to the testing room. Upon arriving in the room,  
201 participants were asked to surrender all electronic devices. There was an approximate  
202 15-minute delay between when the participants arrived for the study and the start of the  
203 experimental session. Before the start of the experiment participants were asked to read  
204 a New York Times article about technology and social interaction entitled ‘Step away  
205 from the phone!’ (Tell, 2013). This reinforced the false nature of the experiment and  
206 created a gap in time between when participants surrendered their devices and the start  
207 of the test session.

208           Participants were instructed to interact with each other freely by talking or  
209 making use of materials provided in the room. The researcher then left the room and  
210 discreetly started a timer. Three minutes into the experiment, the researcher re-entered  
211 the room claiming to collect a diary on top of one of the cabinets. At the 23-minute  
212 stage, the researcher returned to the room with bottles of water and plastic cups for the  
213 participants and placed them at the near end of the table close to the purple wall. At 33  
214 minutes, the researcher brought in a pack of playing cards for the participants to use and  
215 placed it at the opposite end of the table next to the white wall. During each of these

216 three episodes the researcher made sure to knock clearly and loudly before entering the  
217 room and to speak to and make eye contact with all participants so that they were all  
218 aware of the event taking place. At the end of the 45 minutes, the researcher entered the  
219 room for the final time and informed the participants that the study had finished.  
220 Participants were then handed questionnaires. Participants were asked to complete the  
221 three questions below for each of the three episodes during which the experimenter  
222 entered the room. Questions 1 and 2 were common for participants across all time  
223 strategy groups. Question 3 was modified depending on the experimental condition.  
224 Participants in the *when* group received question 3a, those in the *HLA* group answered  
225 3b and ones in the free choice group responded to 3c. Below are the task instructions  
226 with episodic memory questions for the first out of three episodes, which were referred  
227 to as *situations* to the participants:

228

229 *Please answer the following questions in as much detail as possible regarding the 3*  
230 *situations, in order of sequence (from first to last), when the experimenter entered the*  
231 *room between the start and end of the experiment.*

232

233 Situation 1

234 (1) What happened, i.e., what did the experimenter do/want?

235 (2) Where did it happen, i.e., which part of the room specifically?

236 (3a) When did it happen, i.e, at what specific time? Please be as specific as possible  
237 (e.g. 3.13pm)

238 (3b) How long ago did it happen? Please be as specific as possible (e.g. 53 minutes  
239 ago)

240 (3c) When or how long ago did it happen? Please be as specific as possible and  
241 choose to respond in only one format (e.g. either 3.13pm or 53 minutes ago).

## 242 *Statistical analyses*

243 Of the 57 participants who completed the final questionnaire, responses from ten  
244 participants were excluded because participants either did not consistently use a  
245 when/HLA strategy for all three episodes (n=2) or did not complete one or more of the  
246 temporal judgements (n=8). Therefore, the final dataset included responses from 47  
247 participants. Data from the *free choice* condition were assigned to the *when* or *HLA*  
248 conditions depending on participants' chosen time strategy for initial analysis. For the  
249 majority of the variables (7/12), homogeneity of variance assumption was not violated  
250 (see Supplementary Material). To assess the accuracy of time judgements of episodic  
251 memories, we calculated mean temporal estimation errors, for each episode. This was  
252 calculated as the difference between the reported and actual time of an episode. This can  
253 be calculated in two ways using either signed or unsigned values. The unsigned,  
254 absolute value of mean temporal estimation errors provides an absolute measure of  
255 temporal accuracy, while the signed value allows the examination of systematic bias for  
256 either under- or over-estimation of time elapsed. Both are presented here.

257 For sessions that involved participants using a *HLA* strategy, a composite end  
258 time was generated and used as a baseline time from which to calculate when all the  
259 participants in a particular session predicted how long ago each episode took place. The  
260 baseline time, calculated separately for each session, was the midpoint between when  
261 the questionnaires were administered and when the last questionnaire was completed. A  
262 baseline time was required as a consequence of administering paper rather than digital  
263 questionnaires. Paper questionnaires were used to ensure quick and efficient distribution

264 of survey materials and recording of responses in a group setting devoid of electronic  
265 devices.

266 To examine whether participants were aware of the three times the experimenter  
267 entered the room, participants were scored on whether or not they could correctly recall  
268 the non-temporal features of each of the three episodes: *what*, *where* and combined  
269 *what and where*. For example, if a participant correctly recalled that the experimenter  
270 entered the room to collect a diary at episode one, then the participant would receive a  
271 score of 1 under the *what* category for episode one. Conversely, an incorrect answer  
272 would result in a score of 0. A summary table with descriptive statistics of temporal  
273 error and accuracy of non-temporal episodic aspects across both time strategies can be  
274 found in the Supplementary Material. Shapiro-Wilk tests of normality were conducted  
275 to establish the normality of the current dataset (see Supplementary Material). Although  
276 some data were not normally distributed, parametric tests (mixed ANOVAs) were  
277 performed for temporal estimation errors. This is because *F*-tests produced by  
278 ANOVAs have been shown to be robust to Type 1 error, with data transformations or  
279 non-parametric analyses not providing any additional benefit for non-normally  
280 distributed data (Blanca, Alarcon, Arnau, Bono, & Bendayan, 2017). This is true even  
281 for groups with unequal sample sizes, as is the case with the present study. In instances  
282 where the sphericity assumption was violated for the repeated measures factor, a  
283 Greenhouse-Geisser correction was applied.

284 A 3 X 2 mixed ANOVA, with the three episodic events as the repeated measures  
285 factor and temporal strategy (*when vs HLA*) as the independent factor, was performed  
286 for temporal estimation errors. The same analysis was repeated using only temporal  
287 estimation errors from memories where the non-temporal components were correctly  
288 recalled. *Post-hoc* comparisons using Bonferroni corrections were conducted on

289 significant main and interaction effects. Bonferroni corrections were carried out in the  
290 usual way by dividing the p-value by the number of comparisons. Mann-Whitney *U*  
291 tests were conducted on the accurate recall for each of the three non-temporal *what*,  
292 *where* and *what and where* episodic features across the three episodes. Chi-square tests  
293 of association were conducted between the two temporal groups to assess whether there  
294 was a significant difference in the proportion of participants who correctly recalled non-  
295 temporal episodic aspects across all three episodes. A binomial test from chance was  
296 used to assess whether there was a preferred temporal strategy in the *free choice*  
297 condition. All analyses were performed using IBM SPSS Statistics 26.0<sup>®</sup>.

## 298 **Results**

### 299 ***Temporal estimation errors***

300 We first examined temporal estimation errors to see how accurate participants were at  
301 recalling the time at which an episode had taken place depending on the strategy  
302 employed. If human episodic memory relies primarily on location-based strategies, then  
303 we would expect memories based on this *when* strategy to be more accurate. Figure 1a.  
304 shows that this was not the case with no systematic difference between the groups as  
305 evidenced by no significant main effect of strategy ( $F_{(1, 45)} = 3.79, p = .058, \eta_p^2 = .078$ ).  
306 Accuracy of temporal judgements for the three episodes did not change significantly  
307 across the testing session demonstrated by a non-significant main effect of episode  
308 ( $F_{(1.66, 74.50)} = 1.11, p = .325, \eta_p^2 = .024$ ). Interestingly though, there was a significant  
309 episode x strategy ( $F_{(1.66, 74.50)} = 10.60, p < .001, \eta_p^2 = .191$ ) interaction. *Post hoc* tests  
310 revealed that this interaction effect was primarily driven by a difference in performance  
311 between the two strategies at episode three. Independent sample *t*-tests revealed that  
312 using a *when* relative to a *HLA* strategy at episode three resulted in significantly greater

313 temporal error judgements ( $t_{(45)} = 3.79, p < .001$ ). Differences in temporal errors  
314 between the two strategies were non-significant at episodes one ( $t_{(45)} = -0.59, p = .556$ )  
315 and two ( $t_{(45)} = 0.48, p = .632$ ). This clearly demonstrates that the predicted increased  
316 accuracy by those using a *when* strategy was not found. Indeed, the only significant  
317 difference between the groups was an interaction driven by increased accuracy of the  
318 HLA group at timepoint three.

319         Additionally, one-way ANOVAs revealed a significant difference in temporal  
320 error judgements across episodes for participants using both *when* ( $F_{(2, 30)} = 6.84, p =$   
321  $.004, \eta_p^2 = .313$ ) and *HLA* ( $F_{(1.60, 47.92)} = 4.49, p = .023, \eta_p^2 = .130$ ) strategies.  
322 Bonferroni-corrected pairwise comparisons showed that significantly greater temporal  
323 errors were made for those employing a *when* strategy at episode three relative to  
324 episodes one ( $M = -6.82, SE = 2.43, p = .040$ ) and two ( $M = -6.63, SE = 2.09, p = .019$ ).  
325 There was a similar but opposing pattern of results for those adopting a HLA strategy,  
326 with participants making significantly greater temporal errors at episode one relative to  
327 episode three ( $M = 4.68, SE = 1.77, p = .039$ ). Overall, participants adopting a *when*  
328 strategy made significantly greater temporal estimation errors by specifically  
329 overestimating the time at which episode three took place.

330         We next went on to examine signed temporal estimation errors to see whether  
331 there was systematic under or over-estimation of when events took place. Figure 1b  
332 shows that temporal judgements were more accurate using a *HLA* than a *when* strategy,  
333 again contrary to our initial prediction. This higher accuracy was seen for every episode  
334 and was confirmed by a significant main effect of strategy ( $F_{(1, 45)} = 6.98, p = .011, \eta_p^2$   
335  $= .134$ ). Accuracy of temporal judgements for the three episodes did not change  
336 significantly across the testing session demonstrated by a non-significant main effect of  
337 episode ( $F_{(1.47, 66)} = 2.86, p = .080, \eta_p^2 = .060$ ). Consistent with the unsigned analysis

338 there was, however, a significant episode x strategy ( $F_{(1.47, 66)} = 3.69, p = .043, \eta_p^2 =$   
339  $.076$ ) interaction on temporal estimation errors. *Post hoc* tests again confirmed that this  
340 interaction effect was primarily driven by a decrease in the performance of participants  
341 employing a *when* strategy at episode three. Independent sample *t*-tests revealed that  
342 using a *when* relative to a *HLA* strategy at episode three resulted in significantly greater  
343 temporal error judgements ( $t_{(45)} = -3.60, p < .001$ ). Differences in temporal errors  
344 between the two strategies were non-significant at episodes one ( $t_{(45)} = 0.92, p = .365$ )  
345 and two ( $t_{(45)} = 1.43, p = .160$ ). Additionally, one-way ANOVAs revealed a significant  
346 difference in temporal error judgements across episodes for participants using a *when*  
347 ( $F_{(2, 30)} = 4.51, p = .019, \eta_p^2 = .231$ ) but not a *HLA* ( $F_{(1.30, 38.96)} = 0.83, p = .398, \eta_p^2 =$   
348  $.027$ ) strategy. Bonferroni-corrected pairwise comparisons showed that significantly  
349 greater temporal errors were made for those employing a *when* strategy at episode three  
350 relative to episode one ( $t_{(15)} = -2.74, p = .015$ ). There was no significant difference in  
351 temporal errors made between episodes one and two ( $t_{(15)} = -1.35, p = .198$ ) or episodes  
352 two and three ( $t_{(15)} = -1.72, p = .106$ ). Overall, participants adopting a *when* strategy  
353 made significantly greater temporal estimation errors by overestimating the time at  
354 which an episode took place (Figure 1b), although it is clear from the interaction that  
355 this effect is primarily driven by a difference in accuracy between groups at timepoint  
356 three. These analyses were conducted on data collapsed across free and forced choice  
357 but the difference in temporal accuracy was maintained when we examined forced  
358 choice only ( $t_{(31)} = -2.48, p = .019$ ).

### 359 ***Temporal strategy choice***

360 While it is clear that participants' accuracy in making temporal judgements was better  
361 when forced to use a *HLA* strategy, it could be the case that this strategy is not routinely



362 employed by humans remembering episodes from their lives. To test this, we examined  
363 which strategy participants voluntarily chose to adopt in the *free choice* condition. A  
364 binomial test indicated that the proportion of participants who chose a *HLA* strategy  
365 (.860) was significantly above chance [.500;  $p = .013$ ; Figure 2a]. Within this group the  
366 temporal estimation errors between the *when* and *HLA* participants showed the same  
367 pattern as in the forced choice condition [Figure 2b-e]. Additionally, and in line with the  
368 data shown in Figure 1, participants tended to overestimate *when* but not *how long ago*  
369 an episode took place. Again, this effect is driven by an interaction whereby the *when*  
370 group overestimated the time at which event three took place.

371         One issue related to the strategy choice of those in the free choice condition is  
372 that it created unequal group sizes in the main analysis of temporal estimation error. To  
373 determine the likelihood of the reported effects persisting in groups of equal size, we  
374 ran bootstrapped Monte Carlo simulations using random selections without replacement  
375 of 16 out of the 31 participants in the *HLA* group, comparing them to the 16 participants  
376 in the *when* group. For each simulation we ran the same ANOVA as we had previously  
377 used on the unsigned data, but this time with equal group sizes and without Greenhouse-  
378 Geisser adjustments to the degrees of freedom. This was repeated 100,000 times. The  
379 proportion of matches between these simulations with equal group sizes and the original  
380 analyses were: Between subjects effect matches: 76.6%, Within subjects effect matches:  
381 99.7%, Interaction matches: 99.7%.

### 382 *Accuracy of non-temporal episodic features*

383 One potential explanation for the difference in temporal accuracy is that *HLA*  
384 judgements are used to support simpler non-episodic memories whereas memories  
385 supported by *when* judgements come with the rich contextual detail associated with  
386 episodic memory. If this is the case, we would expect memories driven by *when*

387 judgements to be associated with greater accuracy for the non-temporal features of  
388 episodic memory. To test this, we examined whether memories supported by *HLA* and  
389 *when* strategies were similarly accurate for the non-temporal contents of the memory.  
390 Figure 3 depicts the proportion of participants in both groups who correctly recalled  
391 non-temporal episodic features across the three episodes. Mann-Whitney *U* tests were  
392 conducted on the accurate recall for each of the three non-temporal *what*, *where* and  
393 *what and where* episodic features. For the *what* episodic features, there was a significant  
394 difference in recall accuracy between the two groups at episode one ( $U = 323.50, z =$   
395  $2.04, p = .042$ ) but not at episodes two ( $U = 247.50, z = -0.03, p = .979$ ) and three ( $U =$   
396  $255.00, z = 0.29, p = .769$ ). At episode one, *what* recall accuracy was significantly  
397 higher for participants in the *HLA* group (mean rank = 26.44) compared to those in the  
398 *when* group (mean rank = 19.28). For the *where* episodic features, there was no  
399 significant difference in recall accuracy between the two groups at episodes one ( $U =$   
400  $253.00, z = 0.14, p = .893$ ), two ( $U = 269.00, z = 0.58, p = .559$ ) and three ( $U = 246.00,$   
401  $z = -0.06, p = .953$ ). Similarly, for the *what and where* episodic features there was no  
402 significant difference in recall accuracy between the two groups at episodes one ( $U =$   
403  $299.50, z = 1.35, p = .177$ ), two ( $U = 269.00, z = 0.58, p = .559$ ) and three ( $U = 261.50,$   
404  $z = 0.39, p = .696$ ). Overall, participants in the *when* group showed poorer recall,  
405 relative to their *HLA* counterparts, specifically for *what* happened towards the start  
406 rather than the middle or end of the experiment. This indicates that aspects of episodes  
407 that happened further back in time were recalled with reduced accuracy while using a  
408 *when* strategy. There was no difference between groups on recall accuracy for *where*  
409 and *what and where* aspects across all three episodes. Taken together, these results are  
410 not consistent with the suggestion that memories supported by *HLA* judgements, are  
411 simpler and lacking in contextual details.

412 Another potential issue is that the previous findings of increased temporal  
413 accuracy in *HLA* may be driven by memories that do not contain fully accurate recall of  
414 integrated episodes. To test this, we assessed whether there was a difference in temporal  
415 accuracy when using different temporal recall strategies specifically on trials where  
416 non-temporal episodic aspects were correctly recalled. Consistent with our previous  
417 analysis, there was main effect of strategy ( $F_{(1, 39)} = 5.00, p = .031, \eta_p^2 = .114$ ) with  
418 participants using a *HLA* strategy making more accurate temporal judgements relative  
419 to their *when* counterparts. Therefore, even in specific cases where participants  
420 accurately recalled all features of an integrated episode, adopting a *HLA* strategy  
421 resulted in significantly more accurate temporal judgements [Figure 4]. There was no  
422 main effect of episodic feature ( $F_{(1.69, 65.87)} = 1.64, p = .204, \eta_p^2 = .040$ ) or episodic  
423 feature x strategy ( $F_{(1.69, 65.87)} = 1.14, p = .319, \eta_p^2 = .028$ ) interaction effect. These  
424 results were obtained using unsigned temporal error data. The same pattern of results  
425 was observed when signed temporal error data were analysed [strategy: ( $F_{(1, 39)} = 9.53, p$   
426  $= .004, \eta_p^2 = .196$ ); episodic feature: ( $F_{(2, 78)} = 0.24, p = .787, \eta_p^2 = .006$ ); episodic  
427 feature x strategy: ( $F_{(2, 78)} = 0.20, p = .818, \eta_p^2 = .005$ )].

428 One of the key characteristics of episodic memory is integration of features to  
429 form a coherent representation of a specific event. Another useful line of enquiry,  
430 therefore, is to ask whether the two strategies produce fully integrated *what*, *where*, and  
431 *when* memories. To test this, we compared the proportion of participants who correctly  
432 recalled all the episodic aspects for all three episodes and whether this differed  
433 depending on the type of temporal strategy adopted. Chi-square tests revealed there was  
434 a significant association between strategy and the proportion of participants who  
435 correctly recalled all three pairs of *what and where* episodic features ( $\chi^2(1) = 3.92, p =$   
436  $.048$ ), with .484 of participants in the *HLA* group correctly recalling all *what and where*

437 episodic features from the experiment compared with .188 of participants in the *when*  
438 group. In contrast there was no significant association between strategy and the  
439 proportion of participants who correctly recalled either all *what* ( $\chi^2(1) = 2.52, p = .112$ )  
440 or all *where* ( $\chi^2(1) = 1.27, p = .260$ ) episodic features. These results point specifically to  
441 a *HLA* strategy in facilitating the integration and accurate recall of multiple episodic  
442 features.

443

#### 444 **Discussion**

445 Temporal judgements of when an event occurred have been suggested to be a  
446 critical feature of episodic memory (Clayton et al., 2003; de Kort et al., 2005; Roberts,  
447 2002; Roberts et al., 2008; Tulving, 1983). These temporal judgements can either be  
448 supported by distance-based strategies, where the time of an event is inferred from the  
449 relative memory strength, or by location-based strategies where source information  
450 from the encoding event is retrieved to provide a temporal context (Friedman, 2001).  
451 Here we tested the suggestion that episodic memory is supported by location-based  
452 temporal judgments in humans (Roberts et al., 2008). We report three key findings.  
453 Firstly, there was an interaction between temporal strategy and time of episode such that  
454 participants using distance-based strategies were significantly more accurate than those  
455 making location-based temporal judgments for recently experienced events. There was  
456 no difference in accuracy between those using different temporal strategies for events  
457 experienced less recently. Secondly, given a choice, most participants used a distance-  
458 based strategy to report when an event took place. Thirdly, a greater proportion of  
459 participants using a distance-based temporal strategy correctly recalled all *what and*  
460 *where* non-temporal episodic features. These data clearly show that in conditions

461 outlined in the present study, distance-based judgements are more accurate for more  
462 recently experienced events and also the preferred method of remembering when an  
463 event took place.

464         The main finding of the study is the significant interaction of strategy and event  
465 such that participants asked to remember when something happened using a location-  
466 based *when* strategy were less accurate for events that were recently experienced  
467 compared to participants using a distance-based *HLA* strategy. There was no difference  
468 between the groups for events experienced less recently. One potential reason for the  
469 difference between the groups is that the *when* strategy involves the additional cognitive  
470 load of calculating the precise clock time relative to the last known time, the start of the  
471 experiment. This additional load could introduce error due to increased demands not  
472 present for the *HLA* group. It is possible that if we asked participants to use a different  
473 location-based strategy based on internal representations of time that this cognitive load  
474 would be reduced, and that temporal estimation may improve. Further studies would be  
475 needed to examine whether location-based strategies not based on clock time would  
476 produce similar results to the current study.

477         Another interesting issue is that the *HLA* group may use a different reference  
478 point from which to estimate elapsed time, the current time. This raises the possibility  
479 that both groups may be using the same distance-based temporal strategy for estimating  
480 elapsed time but anchored to different reference points. As distance-based strategies  
481 will accumulate error with time this would explain the difference in accuracy at time  
482 point three as this is close to the reference point for the *HLA* group and far away from  
483 the reference point for the *when* group. If this were the case, however, we would expect  
484 to see an equivalent difference in temporal accuracy at timepoint one where the *when*  
485 group would be expected to more accurate than the *HLA* group as they are making

486 judgments close to their reference point. The fact that there is no difference between the  
487 groups at timepoint one argues against this suggestion, however, and suggests that the  
488 two groups are not using the same distance-based time estimation strategy.

489         Another issue that could affect the recall of multiple events in time is salience of  
490 these events. More salient events could be remembered more clearly and improve the  
491 ability to remember details accurately. Given that the order of the events was kept  
492 constant across groups and conditions this would leave open the possibility that  
493 differences in salience of the events could affect memory above and beyond temporal  
494 recall strategy. However, the key comparisons in the study were across groups and as  
495 such any issues caused by differential salience of events would equally affect both  
496 groups.

497         A final methodological consideration is potential bias introduced by providing  
498 inaccurate information regarding the duration of the experiment. Information provided  
499 to the participants indicated that the experiment would last 90 minutes when in fact the  
500 experiment lasted 45 minutes. When making temporal judgements participants might  
501 then be biased by their belief that the experiment had indeed lasted 90 minutes. As  
502 previously noted participants making *when* judgements might use the start of the  
503 experiment as a reference point. This start time could be combined with the advertised  
504 experiment duration to give another reference point for when the experiment was  
505 supposed to finish. This could manifest as participants in the *when* condition biasing  
506 their temporal judgements for the later events towards this reference point which could  
507 provide a potential explanation for the decreased performance by the *when* group  
508 reported here. However, if participants are biased by the misleading advertised  
509 experiment duration, we would also expect those making *HLA* judgements to also be  
510 affected. This would manifest in those making *HLA* judgements as increased error at the

511 first time point as they would be biased towards adding more time to their reference  
512 point which is the end of the study. The fact that we do not see this argues against the  
513 data being explained by bias. It is possible that *when* judgements are affected by bias  
514 whereas *HLA* are not but this would be consistent with the main conclusion that *HLA* is  
515 a more accurate (less prone to bias) method of making temporal judgements in humans.

516         While participants in the current study were instructed which temporal strategy  
517 to use, there was nothing stopping them from using another strategy to help support  
518 memory retrieval. Those instructed to use *when* judgements duly did so despite this  
519 resulting in a larger error. These participants could have used a *HLA* strategy and then  
520 attempted to convert this into a *when* judgement to improve accuracy. The failure of  
521 convergence at the very least suggests that these processes are based on separate  
522 mechanisms that do not spontaneously cue each other to produce the most accurate  
523 memory. Alternatively, the convergence failure could be a metacognitive failure to  
524 evaluate the accuracy of these judgements to identify the strategy that most likely  
525 produces the correct response. This possibility could be tested by taking confidence  
526 judgements following both *when* and *HLA* judgements to evaluate our knowledge of the  
527 accuracy of our temporal judgements. A final possibility is that participants forced to  
528 make *when* judgements typically did use a *HLA* strategy and the resulting temporal  
529 estimation errors resulted from poor conversion of *HLA* judgements into *when*  
530 judgements. However, the pattern of results seen with the free choice group indicates  
531 that even participants who actively chose a *when* strategy were poorer at making  
532 temporal judgements than those adopting a *HLA* approach.

533         The present findings show that distance-based temporal judgments can be used  
534 to support the retrieval of integrated representations of an event. This is consistent with  
535 previous studies that have shown that integrated representations of what-where-when

536 (Easton, Webster, & Eacott, 2012) and temporal source memory (Persson et al., 2016)  
537 can be retrieved using familiarity or distance-based temporal strategies. However, these  
538 findings violate the standard assumptions of source memory under the dual process  
539 theory, which suggests that source memory can only be retrieved using a recollection  
540 strategy (Yonelinas, Kroll, Dobbins, & Soltani, 1999). This either suggests that  
541 distance-based temporal strategies for remembering when an event took place do not  
542 map exactly onto the familiarity-based retrieval process defined in dual process theory  
543 or that in circumstances where recollection is accompanied by high familiarity that  
544 familiarity could be used as a temporal source. These memories would clearly be  
545 episodic as they describe integrated representations of trial unique experiences.  
546 However, these memories would include a distance-based judgement of when  
547 something happened. While we are certainly not arguing that the presence of accurate  
548 distance-based temporal judgements within a memory defines it as episodic it is clear  
549 that reliance on distance-based temporal judgments to support a memory does not  
550 necessarily detract from its episodic nature.

551         While the current study used a significantly different design to the animal  
552 studies that addressed the same issue, these findings are at odds with studies suggesting  
553 that a reliance on distance-based temporal judgements by animals performing episodic-  
554 like memory tasks is evidence that they process time in a qualitatively different way to  
555 humans (Roberts et al., 2008). Indeed, the current study suggests that under conditions  
556 with similar memory demands both humans and rats are more accurate when using  
557 distance-based temporal judgements and will choose to use distance-based temporal  
558 judgements over location-based ones to support recall of integrated features of an event.  
559 Additional studies could strengthen this argument further using an experimental design  
560 that more accurately mimics the animal studies, e.g. memory testing based on



561 observation of memory-guided behaviour rather than the reporting of time to a verbal  
562 cue. This would involve long periods of trial and error training, as in the animal studies,  
563 but would serve to reinforce the current findings that human memory for temporal  
564 judgments is similar to that of animals when tested in a similar way. Despite this  
565 proviso, the current data are inconsistent with the suggestion that animals do not possess  
566 episodic memory because they rely on distance or familiarity-based temporal  
567 judgements (Clayton et al., 2003; Roberts et al., 2008). Further support for the  
568 suggestion that humans do not have a qualitatively different mechanism of remembering  
569 time comes from studies in rats demonstrating that they can remember the time of day  
570 that an event took place (location-based; Zhou & Crystal, 2009) and replay sequences of  
571 events in a manner that is independent of familiarity cues (Panoz-Brown et al., 2018).

572 Further support for the suggestion that distance-based temporal judgements can  
573 be used to support episodic memory comes from research examining the neural  
574 mechanisms underlying time perception in memory. Time cells in the hippocampus and  
575 entorhinal cortex of rats have been shown to encode elapsed time at the level of  
576 seconds, hours and days (Kraus et al., 2013; MacDonald et al., 2011; Mankin et al.,  
577 2012). However, these representations of time become less accurate as time from the  
578 event increases in a manner consistent with them providing distance-based information.  
579 These cells have also been shown to integrate information about specific trials and  
580 spatial location with time giving a neural mechanism at the level of the single cell for  
581 episodic integration. The fact that these cells are found within the hippocampus, a  
582 structure critical for episodic memory, suggests that distance-based temporal  
583 information can be an integrated feature of memory for an event.

584 The current study examines relatively short-term memory and while this is  
585 consistent with many lab-based studies of episodic memory it is possible that preference

586 for distance-based temporal judgements, and increased accuracy when using them,  
587 would diminish at longer time intervals. Indeed studies have shown that distance-based  
588 temporal judgements are more prevalent for recently remembered events (Friedman,  
589 1987; Huttenlocher, Hedges, & Bradburn, 1990) and that accuracy of location-based  
590 temporal judgments improves over time (Janssen, Chessa, & Murre, 2006). However,  
591 this does not detract from the current findings and their relevance to our comparative  
592 understanding of temporal judgments in humans and animals. It would be interesting to  
593 examine whether reliance on distance-based temporal judgements changes in humans  
594 and animals over longer timescales.

#### 595 **Acknowledgements**

596 The authors thank Nina Haanes Hessen, Harvey Owen and John Trevor for their help  
597 with data collection.

#### 598 **Declaration of interest**

599 The authors declare that they have no conflict of interest.

#### 600 **Data availability**

601 The data that support the findings of this study are available from the corresponding  
602 author, JAA, upon reasonable request.

603

604 **References**

- 605 Abraham, W. C., Logan, B., Greenwood, J. M., & Dragunow, M. (2002). Induction and  
606 experience-dependent consolidation of stable long-term potentiation lasting  
607 months in the hippocampus. *Journal of Neuroscience*, *22*(21), 9626-9634.
- 608 Ainge, J. A., Tamosiunaite, M., Woergoetter, F., & Dudchenko, P. A. (2007).  
609 Hippocampal CA1 Place Cells Encode Intended Destination on a Maze with  
610 Multiple Choice Points. *Journal of Neuroscience*, *27*(36), 9769-9779.  
611 doi:10.1523/jneurosci.2011-07.2007
- 612 Ainge, J. A., van der Meer, M. A. A., Langston, R. F., & Wood, E. R. (2007). Exploring  
613 the role of context-dependent hippocampal activity in spatial alternation  
614 behavior. *Hippocampus*, *17*(10), 988-1002. doi:10.1002/hipo.20301
- 615 Anderson, M. I., & Jeffery, K. J. (2003). Heterogeneous modulation of place cell firing  
616 by changes in context. *Journal of Neuroscience*, *23*(26), 8827-8835.  
617 doi:23/26/8827 [pii]
- 618 Babb, S. J., & Crystal, J. D. (2005). Discrimination of what, when, and where:  
619 Implications for episodic-like memory in rats. *Learning and Motivation*, *36*(2),  
620 177-189. doi:10.1016/j.lmot.2005.02.009
- 621 Babb, S. J., & Crystal, J. D. (2006a). Discrimination of what, when, and where is not  
622 based on time of day. *Learn Behav*, *34*(2), 124-130.
- 623 Babb, S. J., & Crystal, J. D. (2006b). Episodic-like Memory in the Rat. *Current*  
624 *Biology*, *16*(13), 1317-1321. doi:10.1016/j.cub.2006.05.025
- 625 Bjork, R. A., & Whitten, W. B. (1974). Recency-sensitive retrieval processes in long-  
626 term free recall. doi: 10.1016/0010-0285(74)90009-7
- 627 Blanca, M. J., Alarcon, R., Arnau, J., Bono, R., & Bendayan, R. (2017). Non-normal  
628 data: Is ANOVA still a valid option? *Psicothema*, *29*(4), 552-557.  
629 doi:10.7334/psicothema2016.383Clayton, N. S., Bussey, T. J., & Dickinson, A.  
630 (2003). Can animals recall the past and plan for the future? *Nat Rev Neurosci*,  
631 *4*(8), 685-691. doi:10.1038/nrn1180
- 632 Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery  
633 by scrub jays. *Nature*, *395*(6699), 272-274.
- 634 Clayton, N. S., & Dickinson, A. (1999). Scrub jays (*Aphelocoma coerulescens*)  
635 remember the relative time of caching as well as the location and content of their  
636 caches. *Journal of Comparative Psychology*, *113*(4), 403-416.
- 637 Clayton, N. S., Yu, K. S., & Dickinson, A. (2001). Scrub jays (*Aphelocoma*  
638 *coerulescens*) form integrated memories of the multiple features of caching  
639 episodes. *Journal of Experimental Psychology: Animal Behavior Processes*,  
640 *27*(1), 17-29.
- 641 Colgin, L. L., Moser, E. I., & Moser, M. B. (2008). Understanding memory through  
642 hippocampal remapping. *Trends in Neurosciences*, *31*(9), 469-477. doi:S0166-  
643 2236(08)00167-7 [pii]10.1016/j.tins.2008.06.008
- 644 Danjo, T., Toyozumi, T., & Fujisawa, S. (2018). Spatial representations of self and  
645 other in the hippocampus. *Science*, *359*(6372), 213-218.  
646 doi:10.1126/science.aao3898
- 647 Davis, K. E., Easton, A., Eacott, M. J., & Gigg, J. (2013). Episodic-like memory for  
648 what-where-which occasion is selectively impaired in the 3xTgAD mouse model  
649 of Alzheimer's disease. *J Alzheimers Dis*, *33*(3), 681-698. doi:10.3233/JAD-  
650 2012-121543T060134J4386234W [pii]
- 651 de Kort, S. R., Dickinson, A., & Clayton, N. S. (2005). Retrospective cognition by  
652 food-caching western scrub-jays. *Learning and Motivation*, *36*(2), 159-176.  
653 doi:10.1016/j.lmot.2005.02.008

- 654 Diana, R. A., Van den Boom, W., Yonelinas, A. P., & Ranganath, C. (2011). ERP  
655 correlates of source memory: unitized source information increases familiarity-  
656 based retrieval. *Brain Research*, *1367*, 278-286.  
657 doi:10.1016/j.brainres.2010.10.030
- 658 Eacott, M. J., & Norman, G. (2004). Integrated memory for object, place, and context in  
659 rats: a possible model of episodic-like memory? *Journal of Neuroscience*, *24*(8),  
660 1948-1953. doi:10.1523/JNEUROSCI.2975-03.200424/8/1948 [pii]
- 661 Easton, A., Webster, L. A., & Eacott, M. J. (2012). The episodic nature of episodic-like  
662 memories. *Learn Mem*, *19*(4), 146-150. doi:10.1101/lm.025676.112
- 663 Eichenbaum, H. (2014). Time cells in the hippocampus: a new dimension for mapping  
664 memories. *Nat Rev Neurosci*, *15*(11), 732-744. doi:10.1038/nrn3827
- 665 Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2009). Memory for what, where, and  
666 when in the black-capped chickadee (*Poecile atricapillus*). *Animal Cognition*,  
667 *12*(6), 767-777. doi:DOI 10.1007/s10071-009-0236-x
- 668 Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2011). Mechanisms of what-where-  
669 when memory in black-capped chickadees (*Poecile atricapillus*): do chickadees  
670 remember "when"? *Journal of Comparative Psychology*, *125*(3), 308-316.  
671 doi:10.1037/a0023635
- 672 Ferbinteanu, J., & Shapiro, M. L. (2003). Prospective and retrospective memory coding  
673 in the hippocampus. *Neuron*, *40*(6), 1227-1239.
- 674 Friedman, W. J. (1987). A Follow-up to Scale Effects in Memory for the Time of  
675 Events - the Earthquake Study. *Memory & Cognition*, *15*(6), 518-520. doi:Doi  
676 10.3758/Bf03198386
- 677 Friedman, W. J. (1993). Memory for the Time of Past Events. *Psychological Bulletin*,  
678 *113*(1), 44-66.
- 679 Friedman, W. J. (2001). Memory processes underlying humans' chronological sense of  
680 the past. In C. Hoerl & T. McCormack (Eds.), *Time and memory: Issues in*  
681 *Philosophy and Psychology* (pp. 139-167). Oxford: Clarendon Press.
- 682 Howard, M. W., & Kahana, M. J. (2002). A distributed representation of temporal  
683 context. *Journal of Mathematical Psychology*, *46*(3), 269-299. doi:  
684 10.1006/jmps.2001.1388
- 685 Huttenlocher, J., Hedges, L. V., & Bradburn, N. M. (1990). Reports of Elapsed Time -  
686 Bounding and Rounding Processes in Estimation. *Journal of Experimental*  
687 *Psychology-Learning Memory and Cognition*, *16*(2), 196-213. doi:Doi  
688 10.1037/0278-7393.16.2.196
- 689 Janssen, S. M. J., Chessa, A. G., & Murre, J. M. J. (2006). Memory for time: How  
690 people date events. *Memory & Cognition*, *34*(1), 138-147. doi:Doi  
691 10.3758/Bf03193393
- 692 Jozet-Alves, C., Bertin, M., & Clayton, N. S. (2013). Evidence of episodic-like memory  
693 in cuttlefish. *Current Biology*, *23*(23), R1033-R1035.  
694 doi:10.1016/j.cub.2013.10.021
- 695 Kart-Teke, E., De Souza Silva, M. A., Huston, J. P., & Dere, E. (2006). Wistar rats  
696 show episodic-like memory for unique experiences. *Neurobiology of Learning*  
697 *and Memory*, *85*(2), 173-182. doi:S1074-7427(05)00108-5 [pii]  
698 10.1016/j.nlm.2005.10.002
- 699 Kennedy, P. J., & Shapiro, M. L. (2009). Motivational states activate distinct  
700 hippocampal representations to guide goal-directed behaviors. *Proceedings of*  
701 *the National Academy of Sciences*, *106*(26), 10805-10810.  
702 doi:10.1073/pnas.0903259106

703 Kraus, B. J., Robinson, R. J., White, J. A., Eichenbaum, H., & Hasselmo, M. E. (2013).  
704 Hippocampal "Time Cells": Time versus Path Integration. *Neuron*, 78(6), 1090-  
705 1101. doi:10.1016/j.neuron.2013.04.015

706 Lee, I., Griffin, A. L., Zilli, E. A., Eichenbaum, H., & Hasselmo, M. E. (2006). Gradual  
707 Translocation of Spatial Correlates of Neuronal Firing in the Hippocampus  
708 toward Prospective Reward Locations. *Neuron*, 51(5), 639-650.  
709 doi:10.1016/j.neuron.2006.06.033

710 Leutgeb, S., Leutgeb, J. K., Barnes, C. A., Moser, E. I., McNaughton, B. L., & Moser,  
711 M. B. (2005). Independent codes for spatial and episodic memory in  
712 hippocampal neuronal ensembles. *Science*, 309(5734), 619-623.  
713 doi:10.1126/science.1114037

714 MacDonald, Christopher J., Lepage, Kyle Q., Eden, Uri T., & Eichenbaum, H. (2011).  
715 Hippocampal "Time Cells" Bridge the Gap in Memory for Discontiguous  
716 Events. *Neuron*, 71(4), 737-749. doi:10.1016/j.neuron.2011.07.012

717 Mankin, E. A., Diehl, G. W., Sparks, F. T., Leutgeb, S., & Leutgeb, J. K. (2015).  
718 Hippocampal CA2 activity patterns change over time to a larger extent than  
719 between spatial contexts. *Neuron*, 85(1), 190-201.  
720 doi:10.1016/j.neuron.2014.12.001

721 Mankin, E. A., Sparks, F. T., Slayyeh, B., Sutherland, R. J., Leutgeb, S., & Leutgeb, J.  
722 K. (2012). Neuronal code for extended time in the hippocampus. *Proceedings of*  
723 *the National Academy of Sciences of the United States of America*, 109(47),  
724 19462-19467. doi:10.1073/pnas.1214107109

725 Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. (2010). Keeping track of time:  
726 evidence for episodic-like memory in great apes. *Animal Cognition*, 13(2), 331-  
727 340. doi:10.1007/s10071-009-0282-4

728 Mau, W., Sullivan, D. W., Kinsky, N. R., Hasselmo, M. E., Howard, M. W., &  
729 Eichenbaum, H. (2018). The Same Hippocampal CA1 Population  
730 Simultaneously Codes Temporal Information over Multiple Timescales. *Current*  
731 *Biology*, 28(10), 1499-1508 e1494. doi:10.1016/j.cub.2018.03.051

732 Morris, R. G., & Frey, U. (1997). Hippocampal synaptic plasticity: role in spatial  
733 learning or the automatic recording of attended experience? *Philos Trans R Soc*  
734 *Lond B Biol Sci*, 352(1360), 1489-1503. doi:10.1098/rstb.1997.0136

735 Muller, R. U., & Kubie, J. L. (1987). The effects of changes in the environment on the  
736 spatial firing of hippocampal complex-spike cells. *Journal of Neuroscience*,  
737 7(7), 1951-1968.

738 O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary  
739 evidence from unit activity in the freely moving rat. *Brain Research*, 34, 171-  
740 175.

741 Omer, D. B., Maimon, S. R., Las, L., & Ulanovsky, N. (2018). Social place-cells in the  
742 bat hippocampus. *Science*, 359(6372), 218-224. doi:10.1126/science.aao3474

743 Panoz-Brown, D., Iyer, V., Carey, L. M., Sluka, C. M., Rajic, G., Kestenman, J., . . .  
744 Crystal, J. D. (2018). Replay of Episodic Memories in the Rat. *Current Biology*,  
745 28(10), 1628-+. doi:10.1016/j.cub.2018.04.006

746 Pastalkova, E., Itskov, V., Amarasingham, A., & Buzsaki, G. (2008). Internally  
747 Generated Cell Assembly Sequences in the Rat Hippocampus. *Science*,  
748 321(5894), 1322-1327. doi:10.1126/science.1159775

749 Persson, B. M., Ainge, J. A., & O'Connor, A. R. (2016). Disambiguating past events:  
750 Accurate source memory for time and context depends on different retrieval  
751 processes. *Neurobiology of Learning and Memory*, 132, 40-48.  
752 doi:10.1016/j.nlm.2016.05.002 S1074-7427(16)30056-9 [pii]

- 753 Roberts, W. A. (2002). Are animals stuck in time? *Psychological Bulletin*, 128(3), 473-  
754 489. doi:10.1037//0033-2909.128.3.473
- 755 Roberts, W. A., & Feeney, M. C. (2009). The comparative study of mental time travel.  
756 *Trends in Cognitive Sciences*, 13(6), 271-277. doi:10.1016/j.tics.2009.03.003
- 757 Roberts, W. A., Feeney, M. C., Macpherson, K., Petter, M., McMillan, N., & Musolino,  
758 E. (2008). Episodic-like memory in rats: is it based on when or how long ago?  
759 *Science*, 320(5872), 113-115. doi:10.1126/science.1152709
- 760 Smith, D. M., & Mizumori, S. J. (2006). Learning-related development of context-  
761 specific neuronal responses to places and events: the hippocampal role in  
762 context processing. *Journal of Neuroscience*, 26(12), 3154-3163. doi:26/12/3154  
763 [pii] 10.1523/JNEUROSCI.3234-05.2006
- 764 Suddendorf, T. (2013). Mental time travel: continuities and discontinuities. *Trends in*  
765 *Cognitive Sciences*, 17(4), 151-152. doi:10.1016/j.tics.2013.01.011
- 766 Suddendorf, T., Addis, D. R., & Corballis, M. C. (2009). Mental time travel and the  
767 shaping of the human mind. *Philosophical Transactions of the Royal Society B-*  
768 *Biological Sciences*, 364(1521), 1317-1324. doi:10.1098/rstb.2008.0301
- 769 Suddendorf, T., & Busby, J. (2003). Mental time travel in animals? *Trends in cognitive*  
770 *sciences*, 7(9), 391-396.
- 771 Tell, Caroline. (2013, September 20). Step away from the phone! *The New York Times*,  
772 Retrieved from [https://www.nytimes.com/2013/09/22/fashion/step-away-from-](https://www.nytimes.com/2013/09/22/fashion/step-away-from-the-phone.html)  
773 [the-phone.html](https://www.nytimes.com/2013/09/22/fashion/step-away-from-the-phone.html)
- 774 Tsao, A., Sugar, J., Lu, L., Wang, C., Knierim, J. J., Moser, M. B., & Moser, E. I.  
775 (2018). Integrating time from experience in the lateral entorhinal cortex. *Nature*,  
776 561(7721), 57-+. doi:10.1038/s41586-018-0459-6
- 777 Tulving, E. (1983). *Elements of episodic memory*. Oxford: Clarendon Press.
- 778 Wood, E. R., Dudchenko, P. A., Robitsek, R. J., & Eichenbaum, H. (2000).  
779 Hippocampal neurons encode information about different types of memory  
780 episodes occurring in the same location. *Neuron*, 27(3), 623-633. doi:S0896-  
781 6273(00)00071-4 [pii]
- 782 Yonelinas, A. P. (1999). The contribution of recollection and familiarity to recognition  
783 and source-memory judgments: a formal dual-process model and an analysis of  
784 receiver operating characteristics. *Journal of Experimental Psychology.*  
785 *Learning, Memory, and Cognition*, 25(6), 1415-1434.
- 786 Yonelinas, A. P., Kroll, N. E., Dobbins, I. G., & Soltani, M. (1999). Recognition  
787 memory for faces: when familiarity supports associative recognition judgments.  
788 *Psychonomic Bulletin & Review*, 6(4), 654-661.
- 789 Zhou, W., & Crystal, J. D. (2009). Evidence for remembering when events occurred in a  
790 rodent model of episodic memory. *Proceedings of the National Academy of*  
791 *Sciences*, 106(23), 9525-9529. doi:10.1073/pnas.0904360106
- 792 Zinkivskay, A., Nazir, F., & Smulders, T. V. (2009). What-Where-When memory in  
793 magpies (*Pica pica*). *Animal Cognition*, 12(1), 119-125. doi:10.1007/s10071-  
794 008-0176-x

795 **Figure captions**

796 Figure 1. Temporal accuracy in the *when* and *HLA* conditions. (a) Mean unsigned  
797 temporal error for each episode using either a *when* or *HLA* strategy. (b) Mean signed  
798 temporal error across all three episodes. Negative values imply an underestimation of  
799 time. Error bars in all figures represent the standard error of the mean.

800

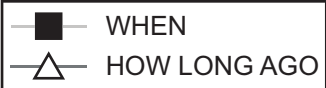
801 Figure 2. Performance on temporal accuracy by participants in either the free choice  
802 (either *when* or *HLA* time strategy) or fixed choice conditions (*when* versus *HLA* time  
803 strategy). Error bars in all figures represent the standard error of the mean. (a)  
804 Participants preferentially adopted a *HLA* temporal strategy for episodic recall in the  
805 free choice group. (b,d) Mean signed and unsigned temporal estimation errors in the  
806 free choice group and (c,e) forced choice groups. Mean temporal estimation errors  
807 follow a similar trend in both the free and forced choice groups with participants  
808 overestimating time of episodic events while using a *when* strategy at episode 3.

809

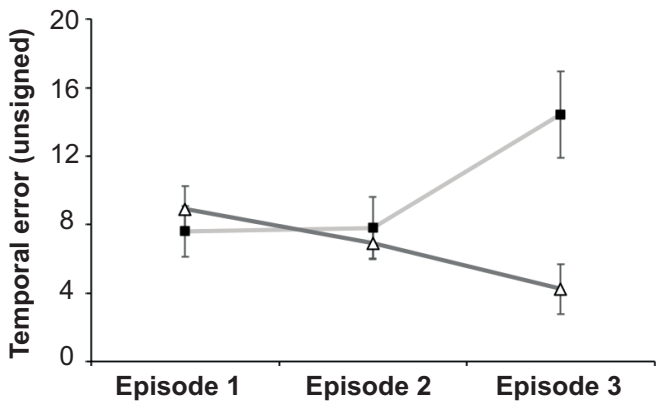
810 Figure 3. (a-c) Proportion of participants across the two temporal strategies who  
811 correctly recalled aspects of episodes (*what*, *where* and combined *what* and *where*).

812

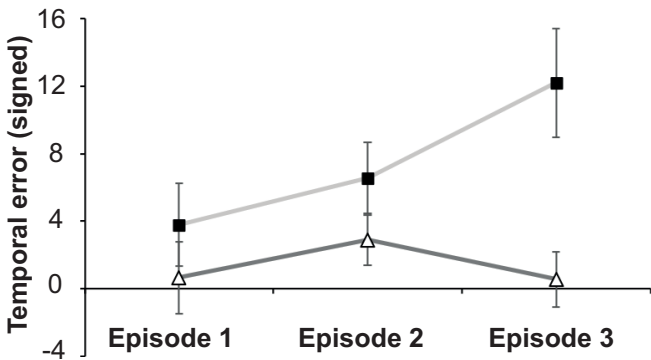
813 Figure 4: (a) Unsigned and (b) signed performance on temporal accuracy for correctly  
814 judged aspects of episodes (what, where and combined what and where) by participants  
815 using two different recall strategies.



a

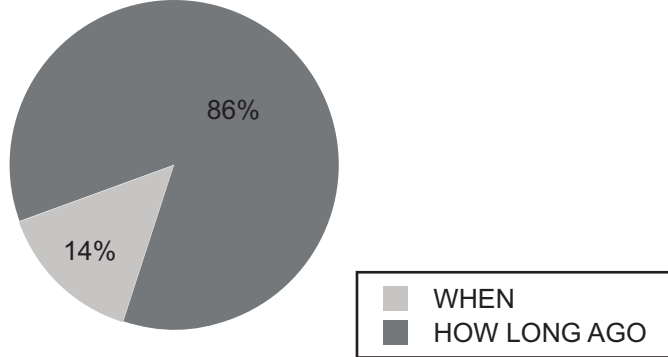


b



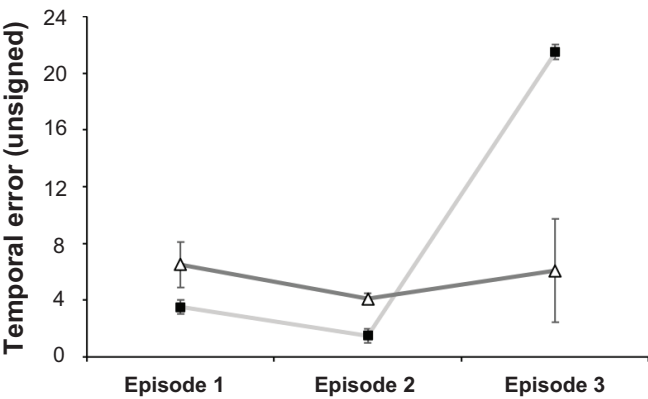


a



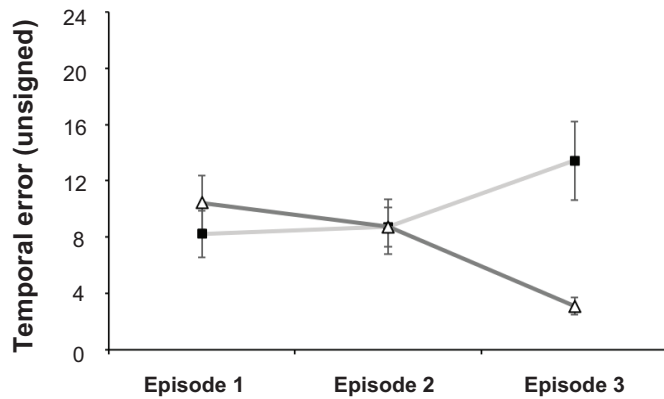
Free choice group

b

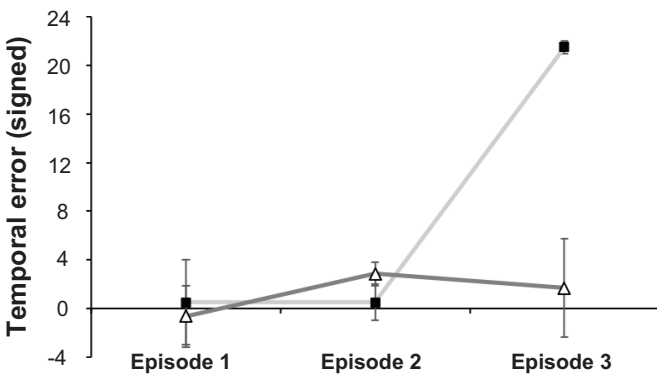


Forced choice group

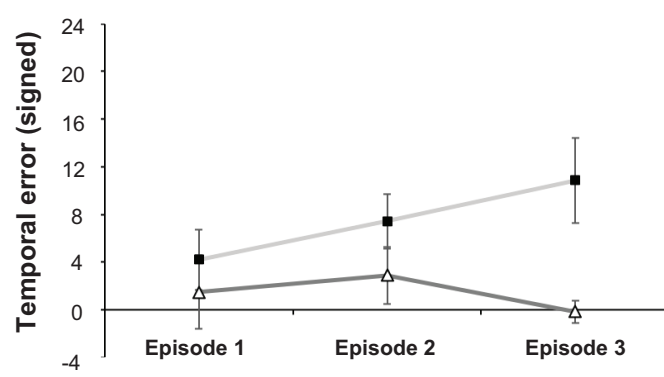
c

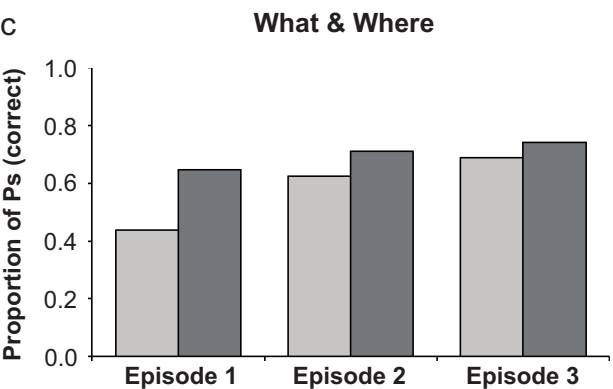
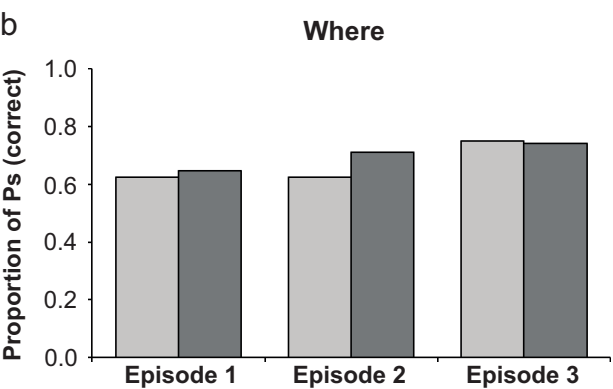
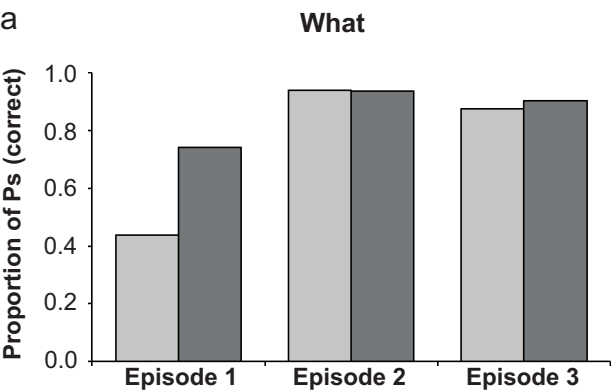
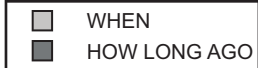


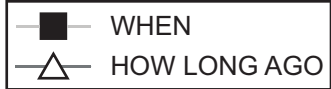
d



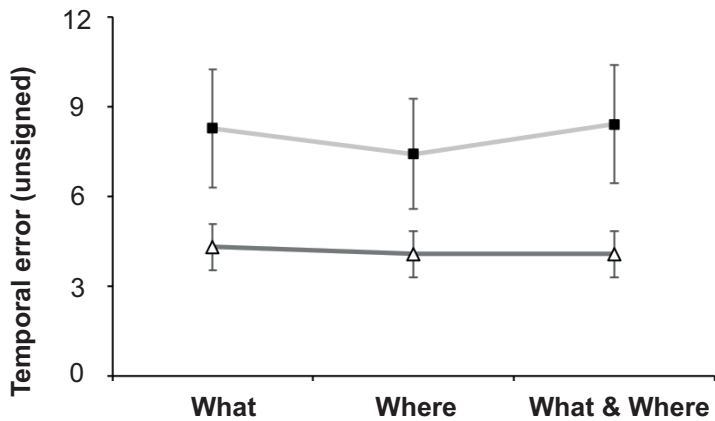
e



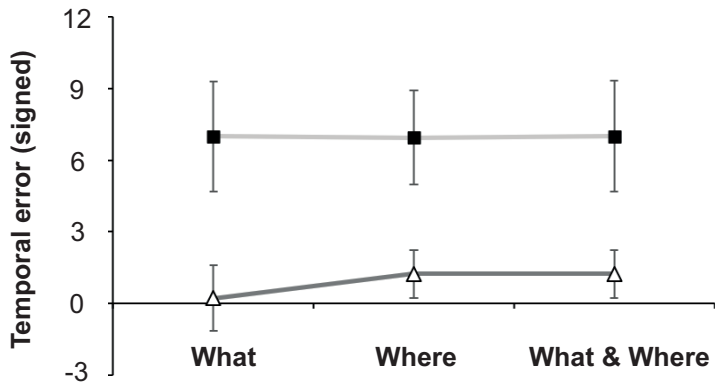


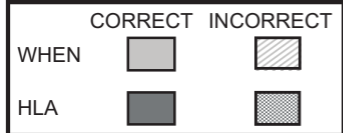


a



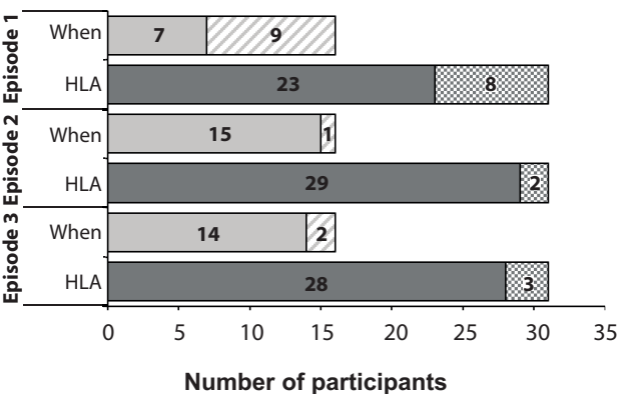
b





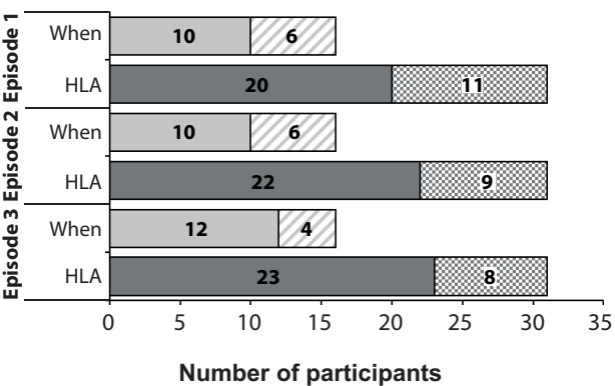
a

### What



b

### Where



c

### What & Where

