

**Distinctiveness enhances long-term event memory in non-human primates,  
irrespective of reinforcement.**

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25

Amy Lewis <sup>1,2,3</sup>, Josep Call <sup>1,2</sup> and Dorte Berntsen <sup>3</sup>

<sup>1</sup> School of Psychology and Neuroscience, University of St Andrews, St Mary's Quad, South Street, St Andrews, Fife, KY16 9JP.

<sup>2</sup> Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany.

<sup>3</sup> Center on Autobiographical Memory Research, Bartholins Allé 9, 8000 Århus C, Denmark.

Short title: Distinctiveness and memory in primates

Corresponding author:

Amy Lewis

Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig, 04103, Germany

[amy\\_lewis@eva.mpg.de](mailto:amy_lewis@eva.mpg.de)

26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50

### **Abstract**

Non-human primates are capable of recalling events that occurred as long as three years ago, and are able to distinguish between similar events; akin to human memory. In humans, distinctiveness enhances memory for events, however, it is unknown whether the same occurs in non-human primates. As such, we tested three great ape species on their ability to remember an event that varied in distinctiveness. Across three experiments, apes witnessed a baiting event in which one of three identical containers was baited with food. After a delay of two weeks, we tested their memory for the location of the baited container. Apes failed to recall the baited container when the event was un-distinctive (Experiment 1), but were successful when it was distinctive (Experiment 2), although performance was equally good in a less-distinctive condition. A third experiment (Experiment 3) confirmed that distinctiveness, independent of reinforcement, was a consistent predictor of performance. These findings suggest that distinctiveness may enhance memory for events in non-human primates in the same way as in humans, and provides further evidence of basic similarities between the ways apes and humans remember past events.

Key words: Long-term memory, primates, binding, distinctiveness, event memory.

## 51 Introduction

52 Humans remember past events on a regular basis. Such episodic memories serve important  
53 social and instrumental functions [e.g. Pillemer, 2003]. Until recently, most research on  
54 memory of non-human primates (hereafter primates) has focused on short term memory  
55 [Menzel, 1973; Robbins and Bush, 1973; Mishkin and Delacour, 1975; Fujita and  
56 Matsuzawa, 1990; MacDonald and Agnes, 1999; Beran, Beran and Menzel, 2005; Hoffman  
57 and Beran, 2006; Inoue and Matsuzawa, 2007; Rodriguez et al. , 2011], with primate episodic  
58 memory research coming into fruition over the past decade [Menzel, 1999; Schwartz and  
59 Evans, 2001; Schwartz et al. , 2002; Schwartz, Hoffman and Evans, 2005; Hoffman, Beran  
60 and Washburn, 2009; Martin-Ordas, Haun, Colmenares and Call, 2010; Dekleva et al. , 2011;  
61 Noser and Byrne, 2015]. However, comparative studies on episodic memory have been  
62 hampered by the definition of the phenomenon [Tulving, 1972; 2001], in terms of the  
63 recollection of personal past events involving auto-noetic consciousness; an awareness that the  
64 event happened to oneself. Since such awareness is hard, if not impossible, to test in animals,  
65 researchers have turned to other more objective operationalizations [see Clayton, Griffiths,  
66 Emery and Dickinson, 2001; Dere, Kart-Teke, Huston and De Souza Silva, 2006; Crystal,  
67 2009; Templer and Hampton, 2013 for reviews].

68 Despite the progress being made here, there is still controversy over what ‘counts’ as  
69 episodic memory [Suddendorf and Busby, 2003; Suddendorf, 2007; Basile, 2015], due in part  
70 to the many stringent as well as changing criteria that arise from Tulving’s [1972; 1983;  
71 1984; 1985; 2002; 2005] definitions. In an attempt to overcome some of these conceptual  
72 problems, Rubin and Umanath [2015] recently proposed an alternative conceptualization for  
73 memory for events, which removes some of the restrictive criteria imposed by the  
74 consciousness based conception of episodic memory and enables researchers to have simpler  
75 and more measurable criteria that also can be applied to non-human animals. Rubin and

76 Umanath (2015) refer to memory for events as ‘event memory’, which is defined as “the  
77 mental construction of a scene, real or imagined, for the past or the future” [p.1]. Unlike  
78 episodic memory, auto-noetic consciousness is not required. The only criteria required is the  
79 construction of a scene from an egocentric vantage point. As such, event memory involves  
80 fewer requirements than episodic memory, but still involves the process of remembering an  
81 event or scene, as opposed to remembering solely spatial information or knowledge.

82         Scene construction is defined as the mental generation of a scene or event, which is  
83 achieved by binding multiple informational elements into a coherent and spatially organized  
84 representation [Hassabis and Maguire, 2007; Raffard et al. , 2010; Lind, Williams, Bowler  
85 and Peel, 2014; Rubin and Umanath, 2015]. As such, to show that one’s recall is of an event  
86 memory, one needs to show evidence of scene construction, that is, the binding of  
87 information in a spatial context (hereafter contextual binding). Such contextual binding is  
88 thought to be an essential characteristic of episodic memory [Moscovitch, 1994; Chalfonte  
89 and Johnson, 1996; Raj and Bell, 2010], and it has even been argued that impairments in  
90 episodic memory, such as source memory failure, are a result of difficulties with binding  
91 stimuli or reconstructing the bound information at retrieval [Schacter, Norman and Koutstaal,  
92 1998; Schacter and Addis, 2007]. Additionally, Rubin and Umanath [2015] refer to evidence  
93 that the hippocampus is not merely responsible for spatial memory in animals but is also  
94 involved in contextual binding. For instance, damage to the hippocampus can leave spatial  
95 memory intact but lacking in detail [Winocur et al. , 2005]. As such, they argue that the  
96 function of the hippocampus in animals shares some properties with human episodic  
97 memory, and goes beyond spatial processing. Consequently, if an animal has an intact  
98 hippocampus it would likely be capable of contextual binding and, thus, event memory.

99         Evidence of contextual binding has already been shown in primates, corvids and rats  
100 [Clayton, Yu and Dickinson, 2001; Crystal, Alford, Zhou and Hohmann, 2013; Martin-Ordas,

101 Berntsen and Call, 2013; Crystal and Alford, 2014; Crystal and Smith, 2014; Panoz-Brown et  
102 al. , 2016]. For instance, Martin-Ordas, Berntsen and Call [2013] showed that when exposed  
103 to various contextual information, apes were able to recall the location of a tool three years  
104 after they had witnessed it being hidden. In order to remember where the tool was hidden the  
105 apes had to bind the relevant contextual features together and ignore a number of irrelevant  
106 associative links, such as other tasks with the same experimenter, other experiments  
107 involving tool use, other tests in the same location and so forth. In this case, only by binding  
108 the relevant contextual cues were the apes able to distinguish between events that shared  
109 many of the same contextual features, and subsequently, were able to correctly recall the  
110 event in which a tool was hidden. Furthermore, in a second experiment, apes were able to  
111 distinguish between two very similar tool hiding events in order to successfully recall the  
112 location of a tool, thus providing additional evidence of binding. Similarly, Crystal and  
113 Smith [2014] showed that rats were able to find food in a maze under conditions that required  
114 them to bind multiple disparate features, related to location, activity, and spatial cues, in  
115 order to successfully search at the relevant place. Such studies show contextual binding in  
116 action, and provide some evidence for event memory in animals.

117         In humans, the ability to remember an event is dependent upon the interaction  
118 between encoding and retrieval. Tulving [1974] described remembering as the product of  
119 both encoding and retrieval; “we remember an event if it has left behind a trace *and* if  
120 something reminds us of it” [p.74]. Furthermore, not all retrieval cues are equally effective.  
121 The encoding specificity principle [Tulving and Thomson, 1973] states that a retrieval cue is  
122 only effective in so far that it was encoded with the memory trace.

123         The effectiveness of the retrieval cue also depends on the number of memory traces to  
124 which it is associated; referred to as cue overload [Watkins and Watkins, 1975]. The more  
125 traces the cue is associated with the less likely that the cue will generate the target memory to

126 be recalled. Subsequently, the more distinctive the cue is the less likely it will be overloaded.  
127 Distinctiveness is defined by [Hunt and Worthen, 2006] as difference in the context of  
128 similarity, meaning that distinctive cues share fewer features with other cues that are either in  
129 the immediate context, referred to as primary distinctiveness, or that are stored in memory,  
130 referred to as secondary distinctiveness [Eysenck, 1979; Schmidt, 1991; Hunt and Worthen,  
131 2006]. A cue which shares fewer commonalities with other memory traces is less likely to  
132 become overloaded. From these two theories we can predict that successful recall of an event  
133 will be maximized when the memory trace and retrieval cue match (encoding specificity),  
134 and when the retrieval cue is distinct from other memory traces [Nairne, 2002; 2007]. These  
135 mechanisms also operate when retrieval is spontaneous and thus requires little effort  
136 [Berntsen, Staugaard and Sorensen, 2013].

137         As with retrieval, encoding can be enhanced depending upon the type of information  
138 to be remembered. In particular, distinctive information captures attentional resources,  
139 resulting in better encoding, regardless of reinforcement [Jenkins and Postman, 1948;  
140 Schmidt, 1991; Hunt and Worthen, 2006]. Likewise, emotion captures attentional resources  
141 in a similar manner, leading to greater memory for emotional material [Cahill and McGaugh,  
142 1995; Kensinger, 2004], often at the detriment to peripheral information [Easterbrook, 1959;  
143 Burke, Heuer and Reisberg, 1992; Schmidt, 2007; Kensinger, 2009; Nashiro and Mather,  
144 2011].

145         In animal research, encoding and retrieval processes have mainly been investigated in  
146 rodents and birds [see Shettleworth, 2010], with a few studies investigating the role of  
147 distinctiveness, where it has been found that distinctive items are recalled better than non-  
148 distinctive items [Roberts, 1980; Zentall, Hogan, Edwards and Hearst, 1980; Reed and  
149 Richards, 1996]. With regards to primate research only a handful of studies exist that  
150 examine encoding and retrieval processes. It has been shown that memory performance is

151 good when the information to be encoded is relevant [Martin-Ordas, Atance and Call, 2014]  
152 and distinctive [Beran, 2011; Martin-Ordas, Berntsen and Call, 2013 experiment 2; Mendes  
153 and Call, 2014], and that emotion enhances recognition memory for pictures [Kano, Tanaka  
154 and Tomonaga, 2008], possibly due to better encoding as a result of increased attention to  
155 emotional material [Kano and Tomonaga, 2010]. Furthermore, Kano and Hirata [2015]  
156 showed that apes are able to encode and retrieve information embedded in a distinctive event.  
157 Here, apes watched a film of an actor dressed in a King Kong suit performing an aggressive  
158 act. The following day, when watching the same film again, the apes were able to predict  
159 what would happen next through use of anticipatory looks; i.e. they looked at the location in  
160 which King Kong would appear before he appeared. Thus, the apes retrieved the information  
161 previously encoded in anticipation of what was coming next.

162         As these primate studies have either investigated distinctiveness over very short  
163 retention intervals [i.e. Kano, Tanaka and Tomonaga, 2008; Beran, 2011; Martin-Ordas,  
164 Atance and Call, 2014], or have not provided a control condition in which a distinctive cue is  
165 absent [i.e. Martin-Ordas, Berntsen and Call, 2013; Kano and Hirata, 2015], we still know  
166 very little about the role of distinctiveness in long term event memory. As such, the aim of  
167 the current study was to investigate the effect of distinctiveness on long term memory for  
168 simple events in great apes.

169         We originally began with one experiment in mind, however, additional experiments  
170 were needed to clarify the results we obtained. For ease of reading and clarity, we present the  
171 baseline Experiment first (Experiment 1), so that the reader can see the progression of a  
172 standard procedure to a distinctive procedure. The original chronological order of the  
173 Experiments was Experiment 2, Experiment 1, Experiment 3 (see table 1 for an overview of  
174 each Experiment). We refer to Rubin and Umanath's [2015] definition of event memory, in  
175 which evidence of contextual binding is indicative of recall of a memory of an event. We also

176 consider an alternative memory account, associative spatial memory, in which memory  
177 performance may be a result of learning to associate a particular spatial location with a food  
178 reward. We contrast these two explanations, since the use of associative memory is a concern  
179 that is often raised when researching episodic memory in animals [see Zentall, 2006]. We  
180 predict that distinctiveness will enhance memory only in the case of contextual binding. That  
181 is, distinctiveness will only enhance memory recall if the distinctive feature(s) are bound to  
182 the target location. In the case of associative learning, we predict that only reinforcement of  
183 the target location will improve recall. In the present experiments we use the term  
184 distinctiveness to refer to secondary distinctiveness (rather than primary distinctiveness),  
185 which refers to the presence of an unusual feature(s) in comparison to features in stored  
186 memory [Eysenck, 1979; Schmidt, 1991; Hunt and Worthen, 2006].

187 Table 1

188 Title: Overview of the experimental design for the three experiments

### 189 **Experiment 1: Baseline**

190  
191 The aim of this experiment was to establish a baseline level of memory performance by using  
192 a standard and undistinctive baiting procedure. We presented the apes with a platform task in  
193 which one of three containers was baited. Previous research using a similar experimental  
194 task has shown that apes can recall the location of a baited container after 24 hours [Martin-  
195 Ordas and Call, 2011], but it is unknown if they can recall for longer periods in this type of  
196 task. As such, we chose to use a two week delay period, replicating the delay used by  
197 Martin-Ordas, Berntsen and Call [2013] who showed good recall for a distinctive hiding  
198 event after two weeks. However, we expected performance to be poorer in this task, as the  
199 platform task was not distinctive.

200 Additionally, we manipulated whether the experimenter identification (ID) at encoding  
201 and retrieval was matched (the same person) or non-matched (different people) and whether



202 the apes were reinforced or not at encoding. This manipulation aimed to help distinguish  
203 between a contextual binding account and associative learning account. If the apes'  
204 performance is explained by event memory, then contextual binding would predict that  
205 performance in conditions in which the experimenter ID is matching will be better than  
206 conditions in which it is non-matching; if the apes bind the baited container's location to the  
207 contextual features present at encoding, then the more of these contextual features that are  
208 present at retrieval the more likely the correct memory is to be recalled (in line with encoding  
209 specificity theory). If performance is explained by associative learning, we would predict  
210 performance in conditions in which the apes are rewarded at encoding should be better than  
211 those which are not rewarded.

212

213

### Methods

214 This research adhered to the American Society of Primatologists principles for the ethical  
215 treatment of primates, and was ethically approved by an internal committee at the Max  
216 Planck Institute for Evolutionary Anthropology and the University of St Andrews. Animal  
217 husbandry and research complies with the "EAZA Minimum Standards for the  
218 Accommodation and Care of Animals in Zoos and Aquaria", the "EEP Bonobo Husbandry  
219 Manual", the "WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos  
220 and Aquariums" and the "Guidelines for the Treatment of Animals in Behavioral Research  
221 and Teaching" of the Association for the Study of Animal Behavior (ASAB). The research  
222 was collected during July 2015 – February 2016 at the Wolfgang Kohler Primate Research  
223 Center at Leipzig Zoo (Leipzig, Germany).

224

225 **Subjects**

226 Thirty-seven apes participated in this experiment (see table 2); 24 chimpanzees (*Pan*  
227 *troglydytes*; mean age =24 years), seven bonobos (*Pan paniscus*; mean age 14) and six  
228 orangutans (*Pongo abelii*; mean age = 19). None of the apes were food or water deprived,  
229 and all received a healthy and balanced diet during the testing period.

230 Table 2:

231 Title: Subject demographics

232

### 233 **Apparatus**

234 Three opaque red containers (Length= 7cm, width = 10cm, Height =10cm) were positioned  
235 on a sliding platform roughly 16cm apart. The sliding platform was positioned in-front of a  
236 Plexiglas panel frame with three circular holes, which allowed the subjects to point at the  
237 desired container and for the experimenter to pass the food reward through (see figure 1). A  
238 plastic occluder was placed on top of the sliding platform, the experimenter baited the  
239 container behind the occluder ensuring the subject could not see which container was baited;  
240 this is a common procedure for baiting containers.

241

242 Fig.1

243

### 244 **Design**

245 Apes were allocated to one of two exposure conditions; reinforced (R) or non-reinforced  
246 (NR) and one of two test conditions; matching experimenter (M), or non-matching  
247 experimenter (NM); a 2x2 between subjects' design. Conditions were balanced in terms of  
248 age, gender and species as much as possible, this was to minimize any potential effect these  
249 variables may have on performance.

250

### 251 **Procedure**

252 **Exposure phase.**

253 The experimenter (E) sat facing the subject behind the sliding platform. On the platform were  
254 the three red opaque containers, one to the left, center and right, respectively, roughly equal  
255 distance apart. E covered the containers with the occluder so that the subject could no longer  
256 see the containers nor E's hands. E then baited one of the containers with one piece of banana  
257 (here-after, the baited container). The occluder was then removed, and E lifted the baited  
258 container to reveal its contents. The container was then placed back over the food, and the  
259 two empty containers were simultaneously lifted and replaced. E then pushed the platform  
260 toward the subject and waited for them to make a choice. The outcome of the choice differed  
261 depending on the condition:

262         *Reinforced:* If the subject chose the correct container, the food was revealed and given  
263 to the subject. The contents of the empty containers were then shown to the subject.

264         *Non reinforced:* If the subject chose the correct container, the food was revealed but  
265 was not given to the subject and was thrown away into an opaque bucket. The apes could see  
266 the bucket and the throwing of the food into the bucket. The contents of the empty containers  
267 were then shown to the subject.

268         Each subject received two trials on the same day, with one additional trial if an  
269 incorrect choice was made. Two incorrect choices led to the subject being dropped from the  
270 study. This was to ensure that the apes understood what was required of them (to point to the  
271 baited container), and that they were paying attention and not simply picking the correct one  
272 by chance. The position of the baited container was the same in each trial and was  
273 counterbalanced between subjects.

274         **Test phase.**

275 The test took place two weeks later (13-15 days). The experimenter ID differed depending on  
276 the condition:

277         *Matching:* The experimenter ID was the same as at exposure.

278           *Non-matching*: The experimenter ID was different to that at exposure.  
279 The procedure then followed the exposure procedure, except now E did not reveal the  
280 location of the baited container before the subject made a choice. Additionally, if the subject  
281 made a correct choice they received the food regardless of which exposure condition they  
282 were in. Subjects only received one trial.

283

## 284 **Data Analysis**

285 A correct response was defined as choosing the baited container. As there were three  
286 containers, chance was set to 0.33. We were interested in whether performance was above  
287 chance in each condition, we analyzed this for each condition separately using two tailed  
288 binomial tests. Alpha level was set to 0.05 and all analysis was conducted using R studio  
289 version 0.98.109 (as was the case for all subsequent experiments).

290

## 291 **Results**

292 All subjects required only two trials during the exposure phase, except for Daza and Ulla who  
293 failed three and were subsequently dropped from the experiment.

294           Binomial tests revealed that performance was not above chance in any of the  
295 conditions (figure 2); reinforced matching (binomial test:  $N= 10$ ,  $P = 0.31$ ), non-reinforced  
296 matching (binomial test:  $N= 9$ ,  $P = 0.73$ ), reinforced non-matching (binomial test:  $N =9$ ,  $P =$   
297  $0.73$ ) non-reinforced non-matching (binomial test:  $N = 9$ ,  $P= 0.73$ ). As performance was  
298 numerically better in the reinforced matching compared to the other three conditions (in  
299 which performance was identical), we ran an additional analysis to compare performance  
300 between the reinforced matching and the remaining three conditions pooled together. A fisher  
301 exact test revealed no significant difference ( $df= 1$ ,  $P = 0.13$ ), indicating that performance  
302 was not significantly better in this condition.

303

304

Fig. 2

305

306

### Discussion

307

Subjects failed to recall the location of the baited container after two weeks. None of the

308

conditions differed from each other, suggesting that reinforcement and contextual binding

309

had little to no effect on memory performance. However, it is important to note that

310

contextual binding may not have had an effect here due to the nature of the baiting event, that

311

is, the event was designed to be undistinctive. The cue that we chose to manipulate was the

312

experimenter ID. As the apes are tested by numerous experimenters, and often multiple times

313

per day, it may be that this particular cue is overloaded. As such, the experimenter may not

314

have been an effective cue in triggering a specific, single episode at retrieval. Additionally,

315

the other relevant cues may also have been overloaded; the location has been used for many

316

other tasks [e.g. Call, 2006], platform tasks have been done many other times [e.g. Call,

317

2004], and similar containers have been used in other tasks [e.g. Call, 2006], thus, even if

318

contextual binding took place, there was nothing distinctive about the bound representation to

319

lead to the recall of this specific baiting event. This is consistent with Eysenck's theory of

320

distinctiveness [Eysenck, 1979], in which "performance is assumed to depend far more on

321

distinctive than non-distinctive overlap" [ p.94]. As such, the failure to recall the baited

322

location is not necessarily a result of a failure of contextual binding, but rather a lack of

323

distinct or diagnostic information in the bound representation to retrieve a specific memory,

324

resulting in the recall of a 'gist' like memory [Schacter, Norman and Koutstaal, 1998;

325

Schacter and Addis, 2007].

326

With regards to the associative account, it may be that the reinforcement was not great

327

enough to influence performance. As the apes only received one piece of banana per trial, and

328

only two trials during the exposure phase, this may not have been a large enough

329 reinforcement to learn the association between the food and the spatial location of the  
330 container after a long delay. During training, when a delay period was not implemented, the  
331 apes were successful at choosing the correct container (except for two subjects who were not  
332 included in the analysis), thus they were able to learn where the food was, but failed to recall  
333 the information after a long delay.

334

### 335 **Experiment 2: Distinctiveness**

336 Experiment 1 revealed that the apes failed to remember the location of the baited container  
337 after two weeks, as such the aim of this experiment was to improve memory performance by  
338 making the event more distinctive. This was achieved by baiting the container outside the  
339 testing room and by increasing the amount of banana. Both manipulations are very rare, if not  
340 completely novel, in our lab for this type of task, and thus are distinctive in comparison to  
341 standard baiting tasks.

342         Additionally, we further investigated the impact of distinctiveness by including a  
343 surprising feature in one condition and not in another; a facial mask worn by the  
344 experimenter depicting the face of the apes' keeper. Four different masks were used, one for  
345 each species. The masks were made using high quality head-shots of four of the keepers; a  
346 bonobo keeper, an orangutan keeper and two chimpanzee keepers (the chimpanzees were  
347 housed in two separate groups and thus had separate keepers). Previous research has shown  
348 that apes are capable of recognizing human faces in the form of 2D photographic images  
349 [Tomonaga, 1999; Martin-Malivel and Okada, 2007; Sliwa, Duhamel, Pascalis and Wirth,  
350 2011]. Thus, a photographic mask depicting the keepers face should be recognizable to the  
351 apes. The apes only saw the mask of their own keeper; for example, bonobos only saw the  
352 mask of the bonobo keeper. We chose to use masks of the keepers for two reasons. Firstly,  
353 we wanted to surprise the apes. The apes are very familiar with their keepers and thus should

354 be surprised when they see the keeper's face on the body of a person that is not their keeper.  
355 Furthermore, it is likely they will also recognise the keeper by sound in addition to sight [e.g.  
356 see Martinez and Matsuzawa, 2009], thus, the configuration of the keeper's facial features  
357 with the body and voice of another experimenter should be surprising. Secondly, although we  
358 wanted to surprise the apes, we did not want to frighten them. Using faces of familiar keepers  
359 should not be frightening to the apes.

360 If the apes' performance is explained by event memory, then contextual binding  
361 would predict better memory recall in this experiment as opposed to Experiment 1, and better  
362 recall performance in the more distinctive mask condition than the non-mask condition.  
363 Likewise, if the apes' performance is due to associative learning this would also predict better  
364 performance in this experiment as opposed to Experiment 1; this is because the food reward  
365 (amount of banana) is larger, thus strengthening the reinforcement. However, this account  
366 would predict no difference between the mask and no mask condition, as the reinforcement  
367 value does not differ.

368

369

## Methods

### 370 Subjects

371 The same subjects from Experiment 1 participated here, with the exception of (Kuno, Swela,  
372 Natascha, Bimbo) and the addition of (Joey, Daza, Ulla, Robert, Frederike), resulting in a  
373 total of thirty apes (see table 2); Nineteen chimpanzees (mean age = 26.8), four orangutans  
374 (mean age = 18) and seven bonobos (mean age = 16).

375

### 376 Apparatus

377 The apparatus and set-up was the same as Experiment 1, except the red opaque containers  
378 were replaced with blue opaque containers, measuring the same dimensions (see figure 1).

379 The reason we replaced the containers was to minimize proactive interference [Anderson and  
380 Neely, 1996]. Additionally, a tray was included on which the containers were placed (see  
381 figure 1), and a cardboard laminated mask was present for half of the subjects. There were  
382 four masks, depicting a colour photograph of each keeper associated with each species (with  
383 two keepers for the chimpanzees). Each species only saw the mask of their keeper. The mask  
384 covered the entire face of the experimenter, except for the eyes.

385

### 386 **Design**

387 The apes were allocated to one of two conditions; mask (two orang-utans, four bonobos and  
388 nine chimpanzees, age range 10-41 years, mean 22 years) no-mask (three bonobos, two  
389 orang-utans, ten chimpanzees, age range 7-49 years, mean 23 years).

390

### 391 **Procedure**

#### 392 **Exposure phase.**

#### 393 *Mask condition.*

394 The three blue containers were positioned on the tray, one to the left, one to the center and  
395 one to the right. Half a sliced banana was placed under one of the containers outside of the  
396 testing room and out of sight of the subject. The experimenter (E), wearing the mask of the  
397 keeper, entered the testing room carrying the tray and placed it onto the sliding platform. E,  
398 sat facing the subject behind the sliding platform, called the subject's name and made eye  
399 contact with them (ensuring the subject looked at the mask). E then lifted up the baited  
400 container so that the banana was visible, and replaced it again once the subject had seen it. E  
401 then simultaneously lifted up the remaining two containers, and replaced them once the  
402 subject had seen that there was no banana there.



403 E then pushed the sliding platform towards the subject and waited for them to make a  
404 choice (by pointing/reaching through one of the holes). If the subject chose the baited  
405 container (correct choice) they received the banana, and the two empty containers were lifted  
406 to show the subject that they were empty. If the subject chose one of the empty containers,  
407 the container was lifted, then the remaining two containers were lifted to reveal their  
408 contents. No banana was received in this case. Each subject received two trials; if an  
409 incorrect choice was made, they received one additional trial. If the subject chose incorrectly  
410 in two trials, they were dropped from the experiment. The position of the baited container  
411 was the same in each trial and was different to Experiment 1 (to minimize interference). The  
412 location of the baited container was counterbalanced between subjects.

413 ***No-mask condition.***

414 The no-mask condition was identical to the mask condition, except that E did not wear a  
415 mask of the keeper.

416 **Test phase**

417 The test took place two weeks (13-17 days) later. Following the same procedure as before,  
418 and in the same testing room, E baited one of the containers (the same one previously baited)  
419 and the subject made a choice. Crucially, E did not reveal the location of the banana to the  
420 subject before they made a choice. Subjects from the mask condition saw E wearing the same  
421 mask as they saw previously. Subjects from the no-mask condition saw E wearing no mask.  
422 All subjects received only one trial.

423

424 **Data analysis**

425 The data were analysed in the same way as Experiment 1. In addition, to see if performance  
426 was better than in Experiment 1, we compared overall performance in Experiment 1 to  
427 overall performance in Experiment 2 using a two (response) by two (Experiment) Fisher

428 exact test.

429

430

### Results

431 All subjects required only two trials during the exposure. As we were interested in whether  
432 the apes remembered the baited container significantly above chance, we compared the  
433 number of correct choices per condition to chance (exact binomial, two tailed). Both the  
434 mask (binomial test:  $N=15$ ,  $P = 0.05$ ) and no-mask condition (binomial test:  $N=15$ ,  $P <$   
435  $0.001$ ) were significantly above chance, and were not different to each other (Fisher exact  
436 test:  $df= 1$ ,  $P = 0.4$ ) (see figure 3). Thus, subjects in both conditions were able to correctly  
437 recall the baited location from two weeks previously, with neither condition showing better  
438 performance than the other. Additionally, performance was better than Experiment 1 (Fisher  
439 exact test:  $df=1$   $P = 0.004$ ).

440

Fig. 3

441

442

### Discussion

443 The results indicate that subjects were able to recall the location of the baited container after  
444 a delay of two weeks. Additionally, performance was extremely high across conditions. This  
445 was somewhat surprising given the difficulty of the task; the apes had to distinguish this task  
446 from many similar tasks [e.g. Call, 2004], to distinguish these containers from other similar  
447 containers [e.g. Call, 2006], and also to recall the exact location of the baited container in an  
448 array in which the containers were extremely close together (see figure 1). These findings add  
449 to existing evidence that apes are capable of remembering past encounters over long time  
450 intervals [ e.g. Martin-Ordas, Berntsen and Call, 2013]

451

452 The better performance in comparison to Experiment 1 supports both contextual  
binding and associative learning. With regards to contextual binding, none of the cues were

453 distinctive in Experiment 1 (the task, experimenter, location and baiting procedure were  
454 common to many other tasks), even the loss of small amount of food upon a correct choice  
455 had occurred before to the same apes [e.g. Vlamings, Uher and Call, 2006; Uher and Call,  
456 2008], making it difficult to distinguish between similar memories even when bound  
457 [Schacter, Norman and Koutstaal, 1998; Schacter and Addis, 2007]. Conversely, in the  
458 current experiment, the baiting procedure and food amount were distinctive in both  
459 conditions, and when bound to the other features (e.g. experimenter, room, baited container)  
460 may have led to a distinctive, un-overloaded [i.e Watkins and Watkins, 1975; Rubin, 1995]  
461 and highly specific (i.e. encoding specificity) cue at retrieval, facilitating successful recall.  
462 This interpretation would be consistent with the findings from Martin-Ordas, Berntsen and  
463 Call [2013]. In the case of the associative learning, the better performance can be explained  
464 by the larger reinforcement (larger food reward) strengthening the association between the  
465 baited container's location and the presence of a food reward.

466         Performance between the two conditions did not differ, which is supportive of the  
467 associative learning account, given that reinforcement value was the same in both conditions.  
468 However, it is not in support of contextual binding, in which performance should have been  
469 better in the mask condition; the more distinctive features that are bound the more unique and  
470 specific the retrieval cue becomes, and thus, the more effective it is at recalling the correct  
471 memory. However, there are multiple reasons why this may not have been the case. Firstly,  
472 as performance was high in both conditions, it may be that any potential enhancement of an  
473 additional distinctive feature was not seen, although this seems unlikely as performance was  
474 better (but not significantly) in the no-mask condition. Secondly, the mask was intended to  
475 elicit surprise, and indeed, a number of individuals produced a physical reaction to the mask  
476 (prolonged looking, wariness, aggression). In both the human and animal literature emotion  
477 enhances memory, however, the effect seems to be a focal one; memory for the emotional

478 material is enhanced at the cost of peripheral material [Easterbrook, 1959; Burke, Heuer and  
479 Reisberg, 1992; Schmidt and Saari, 2007; Kensinger, 2009]. In this case the mask may have  
480 captured attention, resulting in less attentional resources to encode other information, such as  
481 the experimenter, the location and the baited container. Similarly, the same effect has been  
482 found for distinctive material, that is, that distinctive items are recalled at the expense of  
483 peripheral non-distinctive items [Ellis et al. , 1971; Schulz, 1971]; [but see Schmidt, 1985].

484

### 485 **Experiment 3: Reinforcement and distinctiveness**

486 Performance was better in Experiment 2 compared with Experiment 1. However, it is less  
487 clear whether the better performance can be attributed to the larger reinforcement (associative  
488 learning) or by distinctiveness (contextual binding). As such, Experiment 3 aimed to  
489 distinguish between the two accounts. First, to investigate whether distinctiveness could  
490 account for the better memory performance, we kept the food amount the same as in  
491 Experiment 2, but changed the baiting procedure to the traditional method used in  
492 Experiment 1. Thus, the difference between Experiment 2 and Experiment 3 became one of  
493 distinctiveness, in which Experiment 3 was less distinctive due to the use of a standard  
494 baiting procedure and the large amount of food no-longer being distinctive. The large food  
495 amount was no longer distinctive because it occurred in Experiment 2, and thus the apes now  
496 had experience of receiving large food amounts in this type of task. To assess whether  
497 reinforcement influenced performance, we included a reinforced and non-reinforced  
498 condition (as with Experiment 1). Therefore, if the performance from Experiment 2 was a  
499 result of the larger food amount (reinforcement) we should see poorer performance in  
500 Experiment 3 in the non-reinforced compared with the reinforced condition. In short,  
501 Experiment 3 differed from Experiment 2 in terms of being less distinctive and included a  
502 non-reinforced condition. It remained the same in terms of the amount of food used.



528 The procedure was identical to the exposure procedure from Experiment 1, with the  
529 exception that the amount of banana under the baited container was larger (half a banana); the  
530 same amount as in Experiment 2. The position of the baited container was the same in each  
531 trial, but different from the previous two experiments.

### 532 **Test phase.**

533 The test took place two weeks (13-14 days) later. The procedure was the same as the  
534 exposure procedure, except that E did not reveal the location of the baited container before  
535 the subject made a choice. Additionally, if the subject made a correct choice they received the  
536 food regardless of which exposure condition they were in. Subjects only received one trial.

537

### 538 **Data analysis**

539 The data were analysed in the same way as the previous two Experiments. Additionally, we  
540 compared whether performance in the R condition was the same as performance in  
541 Experiment 2 (conditions from Experiment 2 were pooled due to not being statistically  
542 different) using a 2 (Experiment 2, R) by 2 (response) Fisher exact test. We also compared  
543 performance in the NR condition to Experiment 2; 2 (Experiment 2, NR) by 2 (response)  
544 Fisher exact text.

545

546

### 546 **Results**

547 All subjects required only two trials during the exposure procedure, except for Frederike who  
548 required three. Performance was above chance in the NR condition (binomial test:  $N=15$ ,  $P =$   
549  $0.05$ ) but not in the R condition (binomial test:  $N=14$ ,  $P = 0.78$ ), thus, subjects remembered  
550 the baited location in the NR but not the R condition (see figure 4). With regards to  
551 performance between this Experiment and Experiment 2, performance in the R condition was  
552 worse (Fisher exact test:  $df=1$ ,  $P = 0.05$ ) and not significantly different in the NR condition  
553 (Fisher exact test:  $df=1$ ,  $P = 0.52$ ).

554

555

Fig. 4

556

557

### Discussion

558

Apes only successfully recalled the location of the baited container when they were not

559

reinforced during the initial exposure phase. This is surprising as it goes against any law of

560

reinforcement, strongly contradicting an associative learning account.

561

With regards to contextual binding, such results appear to be un-supportive. However,

562

it may be that our original prediction was misguided; as with baiting the container outside the

563

testing room, ‘throwing’ away a *large* amount of food is not a common occurrence, and is

564

therefore distinctive (different in comparison to the standard procedure). The crucial

565

difference between the throwing away of food in Experiment 1 and this experiment is the

566

amount of food that was thrown away. As the apes rarely receive such large food amounts, it

567

is highly unlikely they have experienced such a large amount being thrown away. In contrast,

568

they have had experience of small amounts being discarded, such as in reverse contingency

569

tasks [Vlamings, Uher and Call, 2006; Uher and Call, 2008]. Thus, even though we did not

570

intend to include a distinctive feature to the event, the act of throwing away a large amount of

571

food may have been distinctive, resulting in enhanced performance. Indeed, the finding that

572

performance in this condition was comparable to performance in Experiment 2 suggests that

573

distinctiveness may be the common explanatory variable.

574

Such a finding is consistent with distinctiveness effects in human memory, in which

575

distinctiveness enhances memory regardless of reinforcement [Hunt and Worthen, 2006;

576

Guitart-Masip et al. , 2010]. Furthermore, research with primates suggests that a novel

577

stimulus attracts attention even when it is associated with a negative outcome [Foley,

578

Jangraw, Peck and Gottlieb, 2014], which is consistent with our finding that a novel event

579

leads to memory enhancement even when the event is negative. In the human literature, this

580 effect is referred to as an “attention magnet” [Laney, Campbell, Heuer and Reisberg, 2004],  
581 in which negatively arousing stimuli capture attention and subsequently are remembered very  
582 well.

583         However, it could be argued that the difference between the conditions is simply a  
584 result of whether food was received or not at encoding. We believe this is not the case for two  
585 reasons. Firstly, if we explain the performance by the giving or not giving of food before the  
586 test, then the results from Experiment 2 and Experiment 3 should differ; they should perform  
587 above chance when they did not receive food (as we see here in the NR condition), but not  
588 when they receive the food, this is not what we see in Experiment 2. Secondly, performance  
589 in the NR condition of Experiment 1 was at chance, whereas in this experiment it was above  
590 chance. Therefore, the common explanatory variable cannot be the receiving or not receiving  
591 of food at encoding.

592         An alternative explanation for the good performance in the NR condition here could  
593 be the role of experience. At the time of this experiment the apes had already been tested on  
594 two very similar tasks (i.e. Experiments 1 and 2), both with a two-week retention period. As  
595 such, the apes may have anticipated that they would be tested on the location of the baited  
596 container. However, if this were the case then performance in the R condition should also be  
597 good, yet here they perform at chance. Furthermore, if the apes are simply learning that they  
598 will be tested after a delay, performance should be as good, if not better than, the first  
599 experiment they received (Experiment 2), which is not the case for the R condition.

600         The finding that performance in the R condition was poorer than in Experiment 2 is  
601 supportive of contextual binding. The R condition had no distinctive features; although the  
602 large food amount was distinctive in Experiment 2, here it was no longer distinctive due to  
603 the very fact it had recently occurred in Experiment 2. That is, a large food amount was no  
604 longer novel to the apes due to past experience of large food amounts in this type of task.



605 Thus, just like Experiment 1, contextual binding may not have led to successful recall due to  
606 lack of distinct information in the bound representation, resulting in ‘gist’ like memory rather  
607 than recall of the specific event [Schacter, Norman and Koutstaal, 1998; Schacter and Addis,  
608 2007]. In contrast, this finding contradicts associative learning, in which performance should  
609 increase as reinforcement value increases; here the condition with the high reward (R  
610 condition) was at chance, whereas the condition with no reward (NR) was above chance.  
611 Additionally, performance in the R condition was poorer than in Experiment 2, even though  
612 the reinforcement amount was identical. Such results strongly contradict an associative  
613 memory account.

614

615

### **General Discussion**

616 The purpose of this study was to investigate the influence of distinctiveness on long-term  
617 event memory in great apes. In order to address the common concern that animals may use  
618 associative memory to recall information, we generated differing predictions based on two  
619 accounts; event memory, as shown by contextual binding, and associative memory.

620 Experiment 1 used a standard baiting procedure in which the apes were rewarded with  
621 a regular amount of food for a correct choice. This baseline experiment allowed for us to  
622 assess whether apes could recall an event that occurred only twice after a two-week delay,  
623 using a standard and undistinctive procedure. Additionally, we assessed whether performance  
624 could be hindered or enhanced from this baseline by manipulating reinforcement and by  
625 matching contextual features at encoding and retrieval. The results indicated that the apes  
626 failed to remember the location of the baited container in any of the conditions, suggesting  
627 that neither associative learning nor contextual binding had an effect on memory  
628 performance. However, the poor performance could be explained by both the cues being  
629 overloaded and undistinctive, resulting in binding having no beneficial effect, and by the

630 reinforcement value being too small for associative learning to occur and be retained over a  
631 two-week delay.

632         An alternative explanation could be that the apes simply did not assume that the same  
633 container would be baited after a two-week delay. As the apes are tested on many similar  
634 tasks, which are often unrelated to one another, the apes' experimental history may  
635 predispose them to assume that tasks separated in time are not related to one another.  
636 However, we believe this is not the case for two reasons. Firstly, the apes successfully  
637 assumed that food was in the same location in Experiments 2 and 3, as shown by selecting  
638 the correct container above chance. Secondly, previous research from our lab using a similar  
639 design has shown that apes can successfully select the location of a container baited 24 hours  
640 previously [Martin-Ordas and Call, 2011]. Instead, we believe that the lack of any distinctive  
641 diagnostic cues made it very difficult for the apes to distinguish between one platform baiting  
642 experiment and another. That is to say, the apes did not fail to assume they should look in the  
643 location in which the food was hidden last, rather, that they did not have enough distinctive  
644 diagnostic information to correctly recall where it was hidden last.

645         In Experiment 2 we showed that by making elements of the event distinctive and by  
646 increasing the reinforcement value (larger amount of food), performance could be greatly  
647 enhanced. However, it was unclear as to whether distinctiveness (contextual binding) or  
648 reinforcement (associative learning) accounted for the improved performance. Experiment 3  
649 aimed to distinguish between the two accounts. We found that by using the standard baiting  
650 procedure (removing distinctiveness) and using a large food reward (high reinforcement),  
651 performance was at chance, contradicting associative learning. When the apes were not  
652 reinforced for a correct choice and a large amount of food was thrown away (a distinctive  
653 event), performance was again comparable to Experiment 2, providing support for contextual  
654 binding and strongly contradicting associative learning.

655           The results from Experiment 3 show that memory performance was enhanced for  
656 distinctive events, irrespective of reinforcement, thus showing commonalities with human  
657 memory [Hunt and Worthen, 2006]. Such a finding is consistent with contextual binding; by  
658 binding distinct and specific features to the baited container's location, the apes could  
659 distinguish between other highly similar baiting events. The more distinctive the event, the  
660 more unique this bound representation became, and thus, the more likely the correct memory  
661 was recalled. In contrast, associative learning would not make use of distinctive material in  
662 the same way, indeed, associative learning would only improve as the strength of the  
663 association increases, which here was manipulated by increasing the amount of food that was  
664 baited in the location.

665           One could argue that a contextual binding account would predict enhanced  
666 performance in conditions in which encoding and retrieval cues are highly matched (i.e.  
667 encoding specificity), contradicting our findings in Experiment 1. However, this ignores the  
668 importance of the cue-overload theory, in which a cue is only effective if it is not associated  
669 to many memory traces [Watkins and Watkins, 1975]. In Experiment 1, all the cues were  
670 common and un-distinctive, and thus highly overloaded. Even when bound, the combination  
671 of cues was still not distinct and specific enough to generate a specific memory [e.g. see  
672 Eysenck, 1979], and more likely to result in the recall of a gist memory [e.g. Schacter,  
673 Norman and Koutstaal, 1998; Schacter and Addis, 2007]. Thus, when taking account of both  
674 the encoding specificity and cue overload theories, a contextual binding account is consistent  
675 with the results from all three experiments.

676           Although our findings are more consistent with a distinctiveness effect, as opposed to  
677 associative learning by reinforcement, we acknowledge that we cannot rule out other  
678 alternative explanations. The distinctiveness account does not always directly follow from  
679 our data, for instance, a distinctiveness account would predict enhanced performance for the

680 mask condition in Experiment 2, and better performance in the matching condition compared  
681 to the non-matching condition of Experiment 1. However, we believe that when accounting  
682 for other well-known memory conceptions, such as cue-overload in Experiment 1 and  
683 attention magnets in Experiment 2, our data remain consistent with a distinctiveness account.  
684 Thus, although there may be other viable explanations, we favor a distinctiveness account.

685         In addition to the findings on distinctiveness and contextual binding, surprise may  
686 also have had an effect in Experiments 2 and 3. In Experiment 2, the element of surprise may  
687 have led to attention being focused on the surprising element (the mask) and consequently  
688 drawn away from the peripheral elements, including baiting of the container. This focusing of  
689 attention at the detriment to peripheral information occurs in human memory [Easterbrook,  
690 1959; Burke, Heuer and Reisberg, 1992; Schmidt, 2007; Kensinger, 2009] and shares  
691 parallels with divided attention which has been shown in rodents [Zentall, 1985]. With  
692 regards to Experiment 3, the throwing away of a large amount of food upon a correct choice  
693 may also have been surprising due to its unexpectedness. But here, and unlike the mask in  
694 Experiment 2, the location of the baited container is the focal point, as it is the baited  
695 container from which the food is thrown away. Thus, the location of the baited container may  
696 benefit from additional attention and thus be remembered to a greater extent than containers  
697 with no surprising element. Indeed, this result is consistent with the von-Restorff effect [von  
698 Restorff, 1933], in which an item that is different (isolated) from a series of similar items is  
699 remembered better than other items. In this situation, the surprising container is remembered  
700 better than the non-surprising containers. However, as we did not collect data on emotional  
701 responses, such as surprise, we can only speculate on this.

702         According to Rubin and Umanath [2015] definition of event memory, a memory of a  
703 past event requires mentally reconstructing a scene, with scene construction defined as the  
704 ability to bind various informational features into a coherently organized spatial

705 representation [Hassabis and Maguire, 2007; Raffard et al. , 2010; Lind, Williams, Bowler  
706 and Peel, 2014; Rubin and Umanath, 2015]. The reconstruction of a scene can occur  
707 voluntary or involuntary and can be of a single episode or multiple events. Our results are  
708 consistent with this; the apes were able to successfully recall the spatial location of one of  
709 three identical containers only when distinctive features were present, suggesting that these  
710 distinctive features were bound to the specific spatial location of the container. Although are  
711 findings are consistent with binding, we acknowledge that mechanisms other than binding  
712 may have been at work, and as such further research is needed to clarify these underlying  
713 mechanisms. Performance was not predicted by the amount of reinforcement (food reward),  
714 and thus strongly contradicts an associative learning account.

715

### 716 **Summary**

717 Our results suggest that great apes can bind distinctive information to spatial locations in  
718 order to distinguish between very similar events, providing evidence of event memory in apes  
719 [as defined by Rubin and Umanath, 2015]. These results add to the growing literature on  
720 contextual binding in animals [Clayton, Yu and Dickinson, 2001; Crystal, Alford, Zhou and  
721 Hohmann, 2013; Martin-Ordas, Berntsen and Call, 2013; Crystal and Smith, 2014], and  
722 shows parallels with human memory, in which distinctiveness enhances memory for events  
723 independent of reinforcement [Hunt and Worthen, 2006].

724

725

### 726 **Acknowledgements**

727 The authors wish to thank the staff at Leipzig Zoo, with special thanks to the ape keepers. We  
728 thank Evelyn Kanzler, Robert Eisenberg, Nicole Romanowsky and Nico Schenk for their  
729 self-portrait photographs and Johannes Grossman for taking the photographs. We also thank

730 Cristina Zickert for transforming the photographs into masks. This research was funded by  
731 the Danish National Research Foundation (DNRF89).

732

733

734

735

### References

736 Anderson MC, Neely JH. 1996. Interference and inhibition in memory retrieval. In: EL B,

737 RA B, editors. Handbook of perception and cognition. San Diego: Academic Press. p

738 237-313.

739 Basile BM. 2015. Rats remind us what actually counts in episodic memory research. Front

740 Psychol 6:75.

741 Beran MJ. 2011. Chimpanzees (*Pan troglodytes*) Show the Isolation Effect During Serial List

742 Recognition Memory Tests. *Animal Cognition* 14(5):637-645.

743 Beran MJ, Beran MM, Menzel CR. 2005. Spatial memory and monitoring of hidden items

744 through spatial displacements by chimpanzees (*Pan troglodytes*). *Journal of*

745 *Comparative Psychology* 119(1):14-22.

746 Berntsen D, Staugaard SR, Sorensen LM. 2013. Why am I remembering this now? Predicting

747 the occurrence of involuntary (spontaneous) episodic memories. *J Exp Psychol Gen*

748 142(2):426-44.

749 Burke A, Heuer F, Reisberg D. 1992. Remembering emotional events. *Memory & Cognition*

750 20(3):227-290.

751 Cahill L, McGaugh JL. 1995. A novel demonstration of enhanced memory associated with

752 emotional arousal. *Conscious Cogn* 4(4):410-421.

753 Call J. 2004. Inferences about the location of food in the great apes (*Pan paniscus*, *Pan*

754 *troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*). *Journal of Comparative*

755 *Psychology* 118(2):232-41.

- 756 Call J. 2006. Inferences by exclusion in the great apes: the effect of age and species. *Animal*  
757 *Cognition* 9(4):393-403.
- 758 Chalfonte B, Johnson M. 1996. Feature memory and binding in young and older adults.  
759 *Memory & Cognition* 24(4):403-416.
- 760 Clayton NS, Griffiths DP, Emery NJ, Dickinson A. 2001. Elements of episodic-like memory  
761 in animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*  
762 356(1413):1483-1491.
- 763 Clayton NS, Yu KS, Dickinson A. 2001. Scrub Jays (*Aphelocoma coerulescens*) Form  
764 Integrated Memories of the Multiple Features of Caching Episodes. *Journal of*  
765 *Experimental Psychology Animal Behavior Processes* 27(1):17-29.
- 766 Crystal JD. 2009. Elements of episodic-like memory in animal models. *Behavioral Processes*  
767 80(3):269-77.
- 768 Crystal JD, Alford WT. 2014. Validation of a rodent model of source memory. *Biol Lett*  
769 10(3):20140064.
- 770 Crystal JD, Alford WT, Zhou W, Hohmann AG. 2013. Source memory in the rat. *Curr Biol*  
771 23(5):387-91.
- 772 Crystal JD, Smith AE. 2014. Binding of episodic memories in the rat. *Current Biology*  
773 24(24):2957-61.
- 774 Dekleva M, Dufour V, de Vries H, Spruijt BM, Sterck EH. 2011. Chimpanzees (*Pan*  
775 *troglodytes*) fail a what-where-when task but find rewards by using a location-based  
776 association strategy. *PLoS One* 6(2):e16593.
- 777 Dere E, Kart-Teke E, Huston JP, De Souza Silva MA. 2006. The case for episodic memory in  
778 animals. *Neuroscience & Biobehavioral Reviews* 30(8):1206-24.
- 779 Easterbrook JA. 1959. The effect of emotion on cue utilization and the organization of  
780 behavior. *Psychological Review* 66:183-201.

- 781 Ellis NR, Detterman DK, Runcie D, McCarver RB, Craig EM. 1971. Amnesic effects in  
782 short-term memory. *Journal of Experimental Psychology* 89(2):357-61.
- 783 Eysenck M. 1979. Depth, elaboration, and distinctiveness. In: Cermak LS, Craik FIM,  
784 editors. *Levels of processing in human memory*: Hillsdale, NJ: Erlbaum. p 89-118.
- 785 Foley NC, Jangraw DC, Peck C, Gottlieb J. 2014. Novelty enhances visual salience  
786 independently of reward in the parietal lobe. *Journal of Neuroscience* 34(23):7947-57.
- 787 Fujita K, Matsuzawa T. 1990. Delayed Figure Reconstruction by a Chimpanzee (*Pan*  
788 *troglodytes*) and Humans (*Homo sapiens*). *Journal of Comparative Psychology*  
789 104(4):345-351.
- 790 Guitart-Masip M, Bunzeck N, Stephan KE, Dolan RJ, Duzel E. 2010. Contextual novelty  
791 changes reward representations in the striatum. *Journal of Neuroscience* 30(5):1721-6.
- 792 Hassabis D, Maguire EA. 2007. Deconstructing episodic memory with construction. *Trends*  
793 *in cognitive sciences* 11(7):299-306.
- 794 Hoffman ML, Beran MJ. 2006. Chimpanzees (*Pan troglodytes*) remember the location of a  
795 hidden food item after altering their orientation to a spatial array. *Journal of*  
796 *Comparative Psychology* 120(4):389-93.
- 797 Hoffman ML, Beran MJ, Washburn DA. 2009. Memory for "what", "where", and "when"  
798 information in rhesus monkeys (*Macaca mulatta*). *Journal of Experimental*  
799 *Psychology: Animal Behavioral Processes* 35(2):143-52.
- 800 Hunt RR, Worthen JB. 2006. *Distinctiveness and Memory*: Oxford University Press, USA.
- 801 Inoue S, Matsuzawa T. 2007. Working Memory of Numerals in Chimpanzees. *Current*  
802 *Biology* 17(23):R1004-R1005.
- 803 Jenkins WO, Postman L. 1948. Isolation and spread of effect in serial learning. *American*  
804 *Journal of Psychology* 61:214-221.



- 805 Kano F, Hirata S. 2015. Great Apes Make Anticipatory Looks Based on Long-Term Memory  
806 of Single Events. *Current Biology* 25(19):2513-7.
- 807 Kano F, Tanaka M, Tomonaga M. 2008. Enhanced recognition of emotional stimuli in the  
808 chimpanzee (*Pan troglodytes*). *Animal Cognition* 11(3):517-24.
- 809 Kano F, Tomonaga M. 2010. Attention to emotional scenes including whole-body  
810 expressions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*  
811 124(3):287-94.
- 812 Kensinger EA. 2004. Remembering emotional experiences: the contribution of valence and  
813 arousal. *Annual Review of Neuroscience* 15(4):241-51.
- 814 Kensinger EA. 2009. Remembering the Details: Effects of Emotion. *Emotion Review*  
815 1(2):99-113.
- 816 Laney C, Campbell HV, Heuer F, Reisberg D. 2004. Memory for thematically arousing  
817 events. *Memory and Cognition* 32(7):1149-59.
- 818 Lind SE, Williams DM, Bowler DM, Peel A. 2014. Episodic memory and episodic future  
819 thinking impairments in high-functioning autism spectrum disorder: an underlying  
820 difficulty with scene construction or self-projection? *Neuropsychology* 28(1):55-67.
- 821 MacDonald SE, Agnes MM. 1999. Orangutan (*Pongo pygmaeus abelii*) Spatial Memory and  
822 Behavior in a Foraging Task. *Journal of Comparative Psychology* 113(2):213-217.
- 823 Martin-Malivel J, Okada K. 2007. Human and chimpanzee face recognition in chimpanzees  
824 (*Pan troglodytes*): role of exposure and impact on categorical perception. *Behavioral*  
825 *Neuroscience* 121(6):1145-55.
- 826 Martin-Ordas G, Atance CM, Call J. 2014. Remembering in tool-use tasks in children and  
827 apes: the role of the information at encoding. *Memory* 22(1):129-44.
- 828 Martin-Ordas G, Berntsen D, Call J. 2013. Memory for distant past events in chimpanzees  
829 and orangutans. *Current Biology* 23(15):1438-41.

- 830 Martin-Ordas G, Call J. 2011. Memory processing in great apes: the effect of time and sleep.  
831 Biol Lett 7(6):829-32.
- 832 Martin-Ordas G, Haun D, Colmenares F, Call J. 2010. Keeping track of time: evidence for  
833 episodic-like memory in great apes. *Animal Cognition* 13(2):331-40.
- 834 Martinez L, Matsuzawa T. 2009. Auditory-visual intermodal matching based on individual  
835 recognition in a chimpanzee (*Pan troglodytes*). *Anim Cogn* 12 Suppl 1:S71-85.
- 836 Mendes N, Call J. 2014. Chimpanzees form long-term memories for food locations after  
837 limited exposure. *American Journal of Primatology* 76(5):485-95.
- 838 Menzel CR. 1999. Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan*  
839 *troglodytes*) after extended delays. *Journal of Comparative Psychology* 113(4):426-  
840 34.
- 841 Menzel EW. 1973. Chimpanzee spatial memory organization. *Science* 182(4115):943-5.
- 842 Mishkin M, Delacour J. 1975. An analysis of short-term visual memory in the monkey.  
843 *Journal of Experimental Psychology: Animal Behavior Processes* 1(4):326-34.
- 844 Moscovitch M. 1994. Memory and working with memory: Evaluation of a component  
845 process model and comparisons with other models. *Memory systems*. D. L. Schacter  
846 & E. Tulving ed: Cambridge, MA: MIT Press. p 269-310.
- 847 Nairne JS. 2002. The myth of the encoding-retrieval match. *Memory* 10(5-6):389-95.
- 848 Nairne JS. 2007. *The foundations of remembering: Essays in honor of Henry L. Roediger,*  
849 *III.*: New York, NY, US: Psychology Press.
- 850 Nashiro K, Mather M. 2011. How arousal affects younger and older adults' memory binding.  
851 *Experimental Aging Research* 37(1):108-28.
- 852 Noser R, Byrne RW. 2015. Wild chacma baboons (*Papio ursinus*) remember single foraging  
853 episodes. *Animal Cognition* 18(4):921-9.

- 854 Panoz-Brown D, Corbin HE, Dalecki SJ, Gentry M, Brotheridge S, Sluka CM, Wu JE,  
855 Crystal JD. 2016. Rats Remember Items in Context Using Episodic Memory. *Curr*  
856 *Biol* 26(20):2821-2826.
- 857 Pillemer D. 2003. Directive functions of autobiographical memory: The guiding power of the  
858 specific episode. *Memory* 11(2):193-202.
- 859 Raffard S, D'Argembeau A, Bayard S, Boulenger JP, Van der Linden M. 2010. Scene  
860 construction in schizophrenia. *Neuropsychology* 24(5):608-15.
- 861 Raj V, Bell MA. 2010. Cognitive processes supporting episodic memory formation in  
862 childhood: The role of source memory, binding, and executive functioning.  
863 *Developmental Review* 30(4):384-402.
- 864 Reed P, Richards A. 1996. The von Restorff Effect in Rats (*Rattus norvegicus*). *Journal of*  
865 *Comparative Psychology* 110(2):193-198.
- 866 Robbins D, Bush CT. 1973. Memory in Great Apes. *Journal of Experimental Psychology*  
867 *General* 97(3):344-348.
- 868 Roberts WA. 1980. Distribution of trials and intertrial retention in delayed matching to  
869 sample with pigeons. *Journal of Experimental Psychology: Animal Behavior*  
870 *Processes* 6(3):217-237.
- 871 Rodriguez JS, Zurcher NR, Bartlett TQ, Nathanielsz PW, Nijland MJ. 2011. CANTAB  
872 delayed matching to sample task performance in juvenile baboons. *Journal of*  
873 *Neuroscience Methods* 196(2):258-63.
- 874 Rubin DC. 1995. *Memory in oral traditions. The cognitive psychology of epic, ballads, and*  
875 *counting-out rhymes*: New York. Oxford University Press.
- 876 Rubin DC, Umanath S. 2015. Event memory: A theory of memory for laboratory,  
877 autobiographical, and fictional events. *Psychological Review* 122(1):1-23.

- 878 Schacter DL, Addis DR. 2007. The cognitive neuroscience of constructive memory:  
879 remembering the past and imagining the future. *Philosophical Transactions of the*  
880 *Royal Society of London B Biological Sciences* 362(1481):773-86.
- 881 Schacter DL, Norman KA, Koutstaal W. 1998. The cognitive neuroscience of constructive  
882 memory. *Annual Review of Psychology* 49:289-318.
- 883 Schmidt SR. 1985. Encoding and retrieval processes in the memory for conceptually  
884 distinctive events. *Journal of Experimental Psychology: Learning, Memory, and*  
885 *Cognition* 11(3):565-78.
- 886 Schmidt SR. 1991. Can we have a distinctive theory of memory?
- 887 Schmidt SR. 2007. Unscrambling the Effects of Emotion and Distinctiveness on Memory.  
888 *The foundations of remembering: Essays in honor of Henry L Roediger, III*: New  
889 York, NY, US: Psychology Press, xi. p 141-158.
- 890 Schmidt SR, Saari B. 2007. The emotional memory effect: Differential processing or item  
891 distinctiveness? *Memory & Cognition* 35(8):1905-1916.
- 892 Schulz L. 1971. Effects of High-Priority Events on Recall and Recognition of Other Events.  
893 *Journal of verbal learning and verbal behaviour* 10:322-330.
- 894 Schwartz BL, Colon MR, Sanchez IC, Rodriguez IA, Evans S. 2002. Single-Trial Learning of  
895 “What” and “Who” Information in a Gorilla (*Gorilla gorilla gorilla*): Implications for  
896 Episodic Memory. *Animal Cognition* 5(2):85-90.
- 897 Schwartz BL, Evans S. 2001. Episodic Memory in Primates. *American Journal of*  
898 *Primatology* 55(2):71-85.
- 899 Schwartz BL, Hoffman ML, Evans S. 2005. Episodic-like memory in a gorilla: A review and  
900 new findings. *Learning and Motivation* 36(2):226-244.
- 901 Shettleworth S. 2010. *Cognition, Evolution and Behavior*: Oxford University Press, New  
902 York. .

- 903 Sliwa J, Duhamel JR, Pascalis O, Wirth S. 2011. Spontaneous voice-face identity matching  
904 by rhesus monkeys for familiar conspecifics and humans. *Proceedings of the National*  
905 *Academy of Sciences of the United States of America* 108(4):1735-40.
- 906 Suddendorf T. 2007. The evolution of foresight: what is mental time travel, and is it unique to  
907 humans. *Journal of Behavioral and Brain Science* 30:299-313.
- 908 Suddendorf T, Busby J. 2003. Mental Time Travel in Animals? *Trends in cognitive sciences*  
909 7(9):391-396.
- 910 Templer VL, Hampton RR. 2013. Episodic memory in nonhuman animals. *Current Biology*  
911 23(17):R801-6.
- 912 Tomonaga M. 1999. Inversion effect of perception of human faces in a chimpanzee. *Primates*  
913 40(3):417-438.
- 914 Tulving E. 1972. Episodic and semantic memory. In: Donaldson ETaW, editor. *Organization*  
915 *of Memory*: New York: Academic Press. p 381-402.
- 916 Tulving E. 1974. Cue-Dependent Forgetting. *American Scientist* 62(1):74-82.
- 917 Tulving E. 1983. *Elements of episodic memory*. Oxford, England: Clarendon Press.
- 918 Tulving E. 1984. *Précis of elements of episodic memory*. *Behavioral and Brain Sciences*  
919 7:223-268.
- 920 Tulving E. 1985. How Many Memory Systems Are There? *American Psychologist*  
921 40(4):385-398.
- 922 Tulving E. 2001. *Chronesthesia: awareness of subjective time. The Age of the Frontal Lobes*.  
923 New York: Oxford University Press. p 311-325.
- 924 Tulving E. 2002. Episodic memory: From mind to brain. *Annual Review of Psychology* 53:1-  
925 25.

- 926 Tulving E. 2005. Episodic Memory and Autonoesis: Uniquely Human? In: Terrace HS,  
927 Metcalfe J, editors. *The Missing Link in Cognition: Origins of Self-Reflective*  
928 *Consciousness*. Oxford: Oxford University Press. p 3-56.
- 929 Tulving E, Thomson D. 1973. Encoding specificity and retrieval processes. *Psychological*  
930 *Review* 80(5):352-373.
- 931 Uher J, Call J. 2008. How the great apes (*Pan troglodytes*, *Pongo pygmaeus*, *Pan paniscus*,  
932 *Gorilla gorilla*) perform on the reversed reward contingency task II: transfer to new  
933 quantities, long-term retention, and the impact of quantity ratios. *Jouranal of*  
934 *Comparative Psychology* 122(2):204-12.
- 935 Vlamings PH, Uher J, Call J. 2006. How the great apes (*Pan troglodytes*, *Pongo pygmaeus*,  
936 *Pan paniscus*, and *Gorilla gorilla*) perform on the reversed contingency task: the  
937 effects of food quantity and food visibility. *Journal of Experimental Psychology:*  
938 *Animal Behavioural Processes* 32(1):60-70.
- 939 von Restorff H. 1933. Über die Wirkung von Bereichsbildungen im Spurenfeld. *Psychol*  
940 *Forsch* 18:299–342.
- 941 Watkins OC, Watkins MJ. 1975. Buildup of Proactive Inhibition as a Cue-Overload Effect.  
942 *Journal of Experimental Psychology: Human Learning and Memory* 1(4):1-15.
- 943 Winocur G, Moscovitch M, Fogel S, Rosenbaum RS, Sekeres M. 2005. Preserved spatial  
944 memory after hippocampal lesions: effects of extensive experience in a complex  
945 environment. *Nature Neuroscience* 8(3):273-5.
- 946 Zentall TR. 1985. Selective and divided attention in animals. *Behav Processes* 69(1):1-15.
- 947 Zentall TR. 2006. Mental time travel in animals: a challenging question. *Behav Processes*  
948 72(2):173-83.

- 949 Zentall TR, Hogan DE, Edwards CA, Hearst E. 1980. Oddity learning in the pigeon as a  
950 function of the number of incorrect alternatives. *Journal of Experimental Psychology:*  
951 *Animal Behavior Processes* 6:278-299.  
952

Table 1: Variables included in each of the three experiments. Empty cells indicate that the variable in question was not included.

Experiment	Condition	No. Subjects	Distinctive baiting procedure	Large food amount	Non-reinforced	Matching Experimenter	Mask
1	Reinforced Matching	10				✓	
	Non-reinforced Matching	9			✓	✓	
	Reinforced Non-Matching	9					
	Non-reinforced Non-matching	9			✓		
2	Mask	15	✓	✓		✓	✓
	No mask	15	✓	✓		✓	
3	Reinforced	14		✓		✓	
	Non-reinforced	15		✓	✓	✓	



Table 2: Age (at time of Experiment 1), sex, species and tasks participated in for each subject.

Subject	Species	Age (years)	Sex	Tasks participated in
Fimi	Bonobo	7	Female	1,2,3
Gemena	Bonobo	9	Female	1,2,3
Luiza	Bonobo	10	Female	1,2,3
Lexi	Bonobo	15	Female	1,2,3
Yasa	Bonobo	17	Female	1,2,3
Kuno	Bonobo	19	Male	1,3
Jasango	Bonobo	24	Male	1,2,3
Joey	Bonobo	32	Male	2,3
Bangolo	Chimpanzee	7	Male	1
Kara	Chimpanzee	10	Female	1,2
Lobo	Chimpanzee	11	Male	1,2,3
Kofi	Chimpanzee	11	Male	1
Tai	Chimpanzee	12	Female	1,2,3
Kisha	Chimpanzee	12	Female	1
Lome	Chimpanzee	13	Male	1,2,3
Alex	Chimpanzee	14	Male	1,2,3
Alexandra	Chimpanzee	15	Female	1,2,3
Annett	Chimpanzee	15	Female	1,2
Bambari	Chimpanzee	16	Female	1
Swela	Chimpanzee	20	Female	1
Frodo	Chimpanzee	21	Male	1,2,3
Sandra	Chimpanzee	22	Female	1,2,3
Jahaga	Chimpanzee	22	Female	1,2,3
Hope	Chimpanzee	26	Female	1
Daza	Chimpanzee	29	Female	2,3
Dorien	Chimpanzee	34	Female	1,2,3
Natascha	Chimpanzee	35	Female	1,3
Riet	Chimpanzee	37	Female	1,2,3
Corrie	Chimpanzee	38	Female	1,2,3
Ulla	Chimpanzee	38	Female	2
Fraukje	Chimpanzee	39	Female	1,2,3
Robert	Chimpanzee	39	Male	1,2,3
Frederike	Chimpanzee	41	Female	1,2,3
Jeudi	Chimpanzee	49	Female	1,2,3
Suaq	Orangutan	6	Male	1,3
Raja	Orangutan	11	Female	1,2,3
Pini	Orangutan	17	Female	1,2,3
Padana	Orangutan	19	Female	1,2,3
Dokana	Orangutan	26	Female	1,2
Bimbo	Orangutan	34	Male	1,3

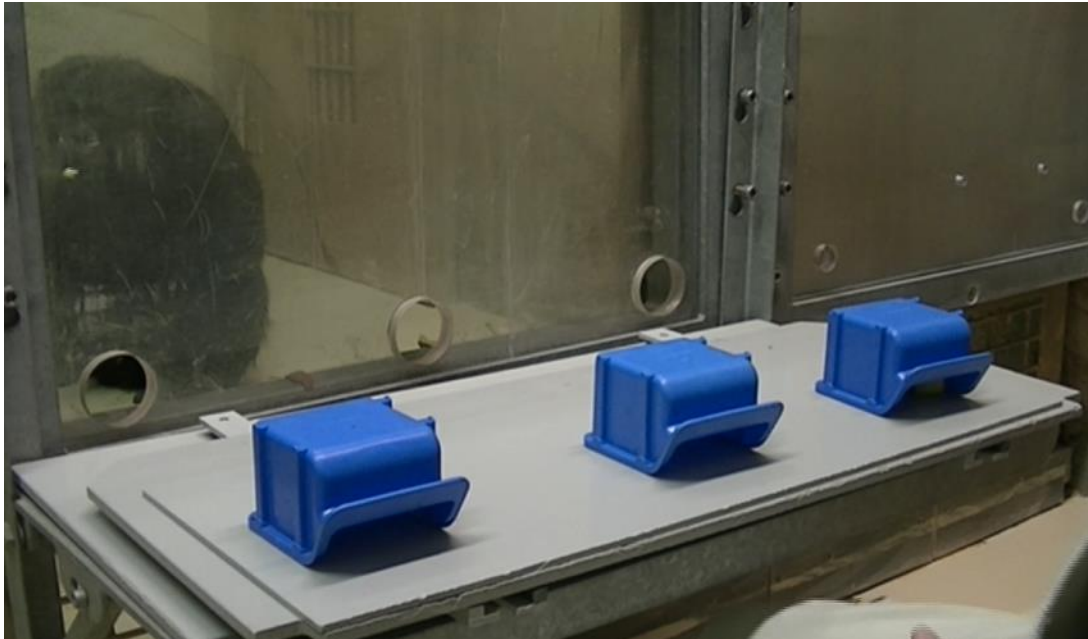


Fig.1. Set-up of the apparatus in Experiment 2. In Experiments 1 and 3 the tray on which the containers are on was not used (only the sliding platform that the tray is on) and an occluder was used

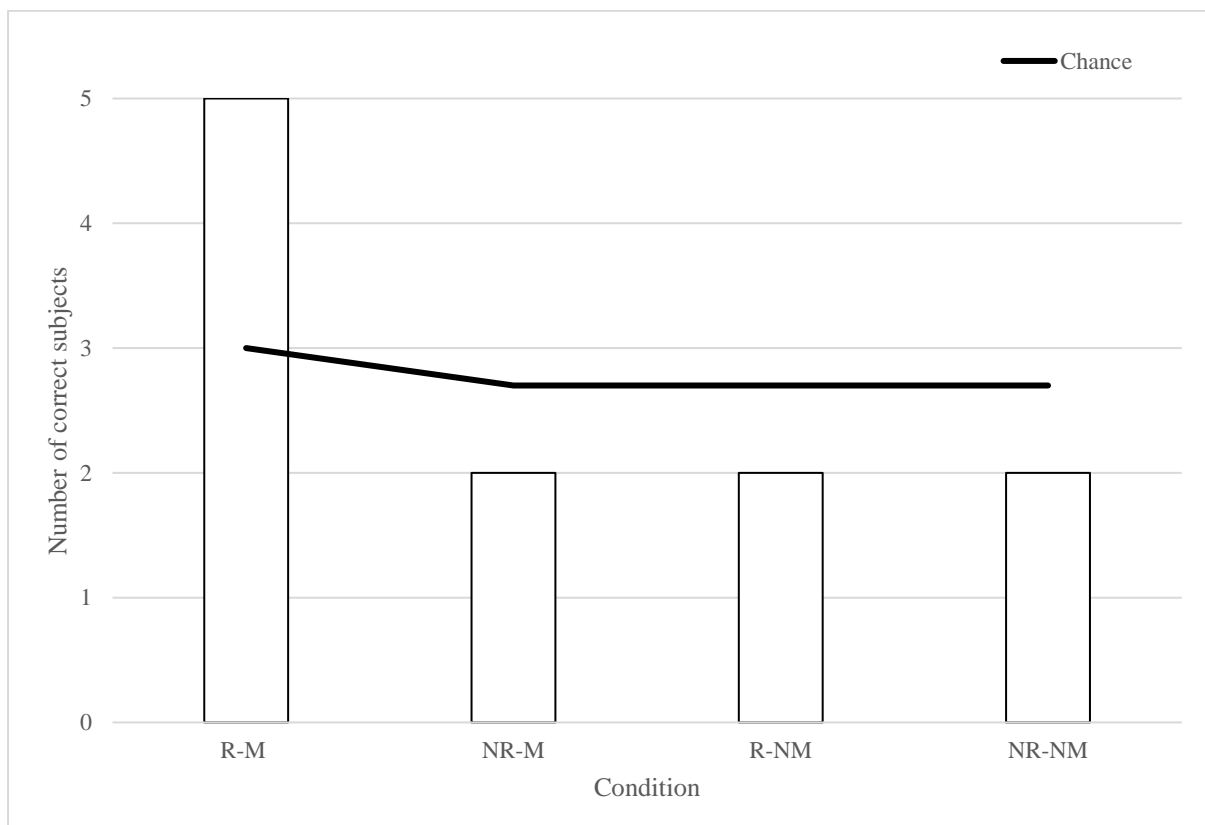


fig. 2: Number of correct subjects by condition. R-M = reinforced matching, NR-M = non-reinforced matching, R-NM = reinforced non-matching, NR-NM = non-reinforced non-matching. Chance shows number of subjects that would be correct if performing at chance.

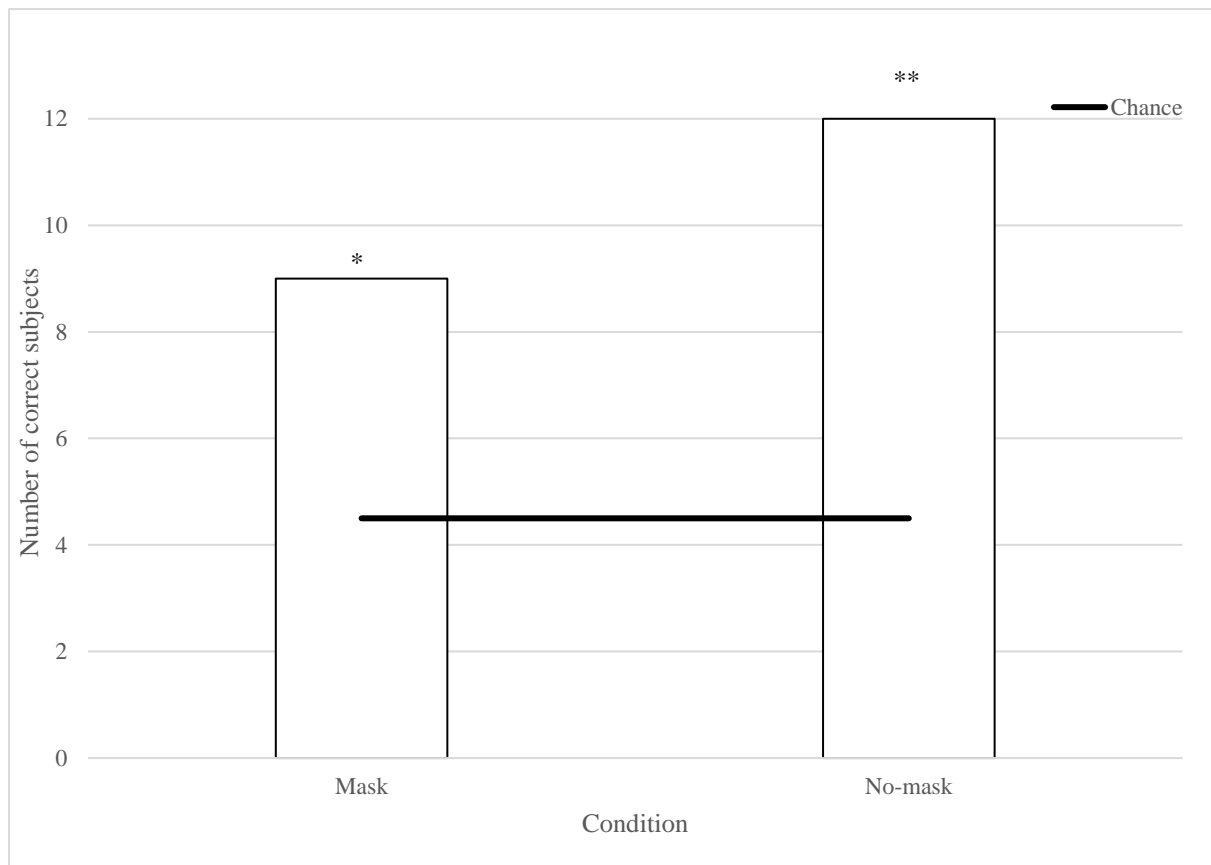


fig. 3 Number of correct subjects by each condition, chance shows number of subjects that would be correct if performing at chance. \*= 0.05 \*\*= $<0.001$ .

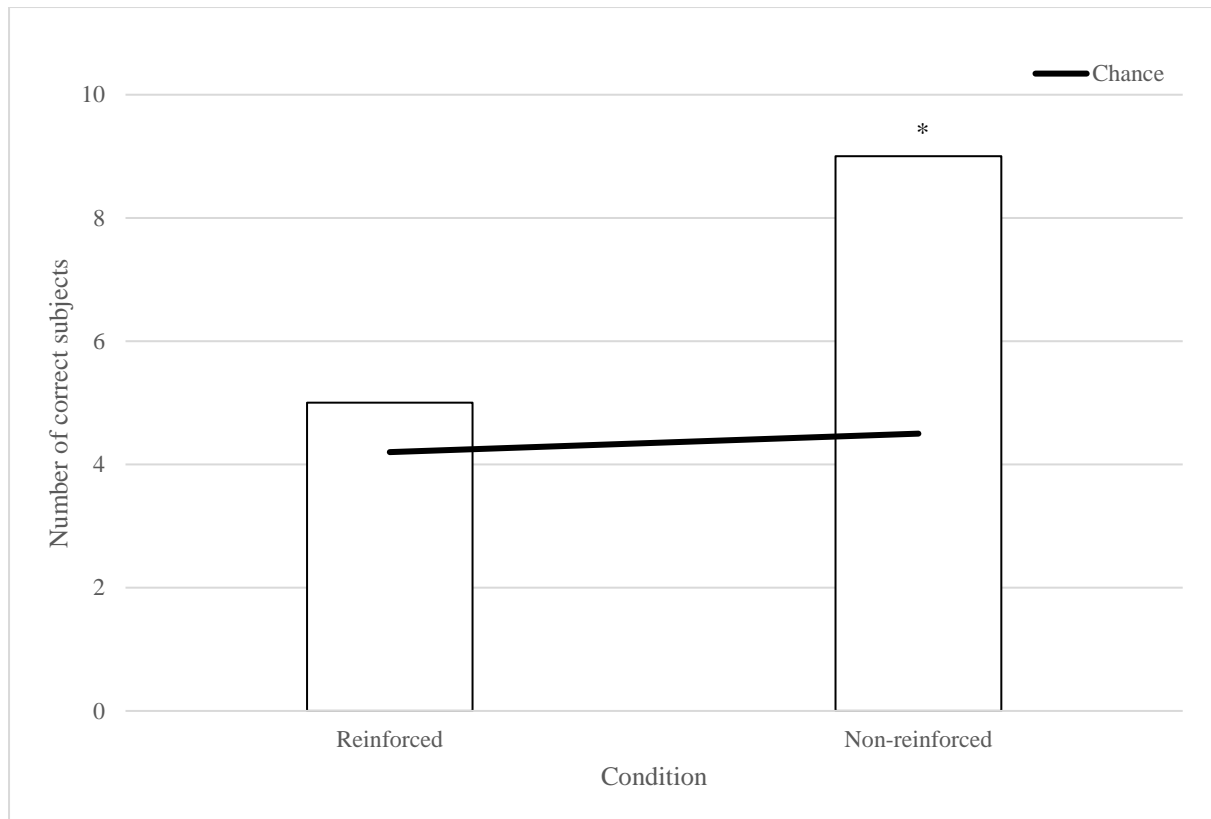


fig.4 Number of correct subjects by condition, chance shows number of subjects that would be correct if performing at chance. \* = 0.05