

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

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Amy Lewis ^{1,2,3}, Josep Call ^{1,2} and Dorte Berntsen ³

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

² Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany.

³ 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

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

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

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 *troglydites*; 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

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

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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

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

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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.

503 If the apes use contextual binding then performance in both conditions should be
504 poorer than in Experiment 2, due to a lack of distinctive cues. If the apes use associative
505 learning, then performance in the reinforced condition should be comparable to Experiment 2
506 (as the reinforcement value is the same), and better than the non-reinforced condition.

507

508 **Methods**

509 **Subjects**

510 All subjects from Experiment 2 took part in this experiment, with the exception of Kara,
511 Annett, Ulla, Riet and Dokana. In addition, four extra apes took part (Bimbo, Suaq, Natascha
512 and Kuno), resulting in 29 apes (see table 2); 16 chimpanzees (mean age =27.1 years), eight
513 bonobos (mean age= 20) and five orangutans (mean age =17).

514

515 **Apparatus**

516 The same apparatus from Experiment 1 was used in this experiment, except that the blue
517 containers were replaced with green ones (Length = 13 cm, Width = 7 cm, Height = 6 cm) to
518 minimize potential interference from the previous studies.

519

520 **Design**

521 Apes were allocated to one of two exposure conditions; reinforced (R) or non-reinforced
522 (NR). In most cases, subjects were assigned to the opposite condition they received in
523 Experiment 1; that is, reinforced to non-reinforced. Conditions were balanced in terms of age,
524 gender and species as much as possible.

525

526 **Procedure**

527 **Exposure phase.**

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

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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

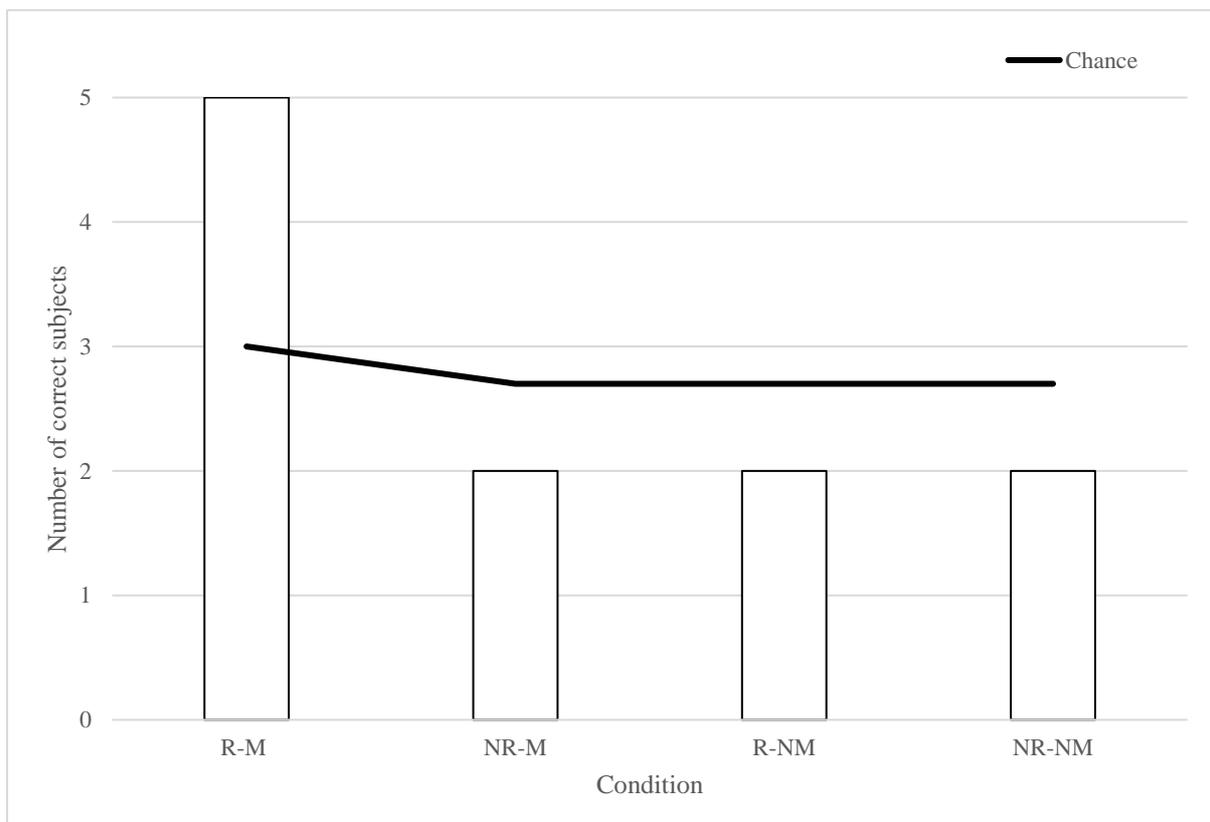


fig. 2: Number of correct subjects by condition. R-M = reinforced matching, NR-M = non-reinforced matching, R-NM = reinforced non-matching, NR-NM = non-reinforced non-matching. Chance shows number of subjects that would be correct if performing at chance.

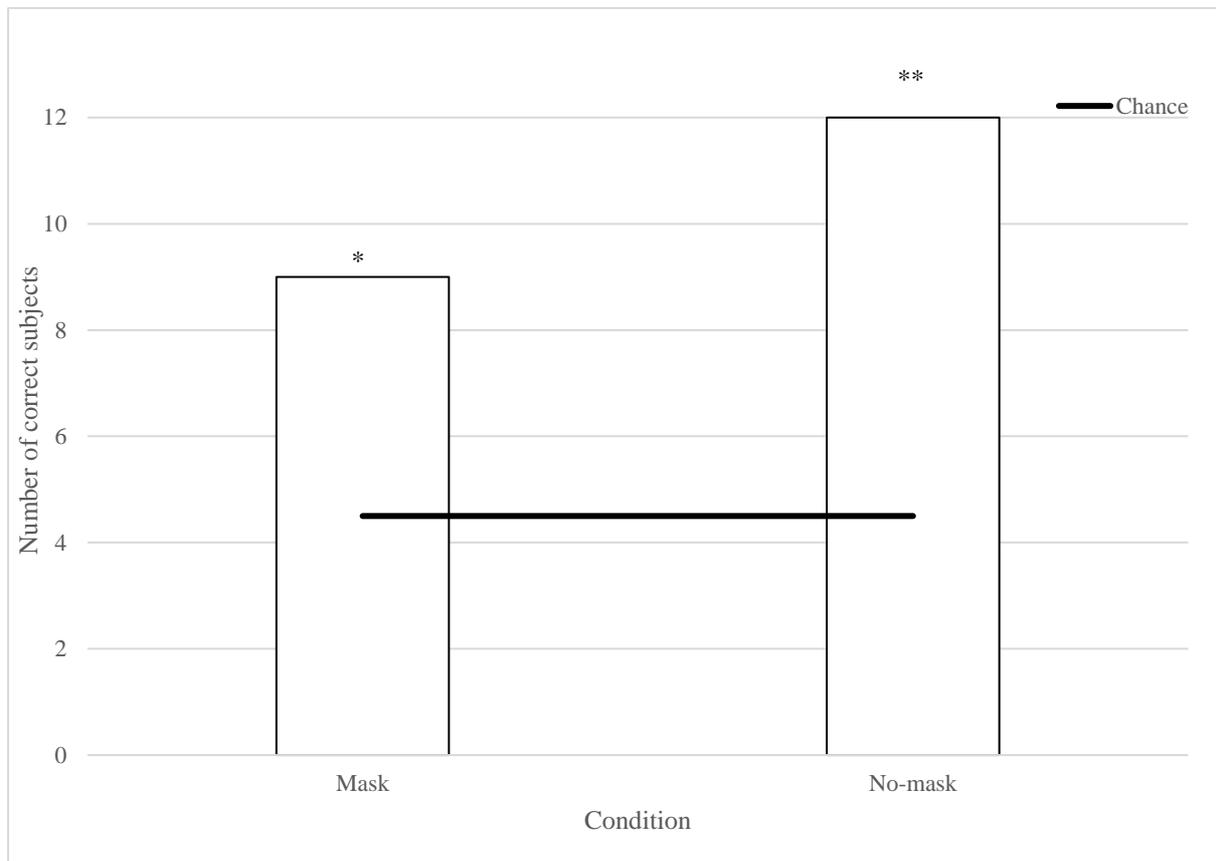


fig. 3 Number of correct subjects by each condition, chance shows number of subjects that would be correct if performing at chance. *= 0.05 **=<0.001.

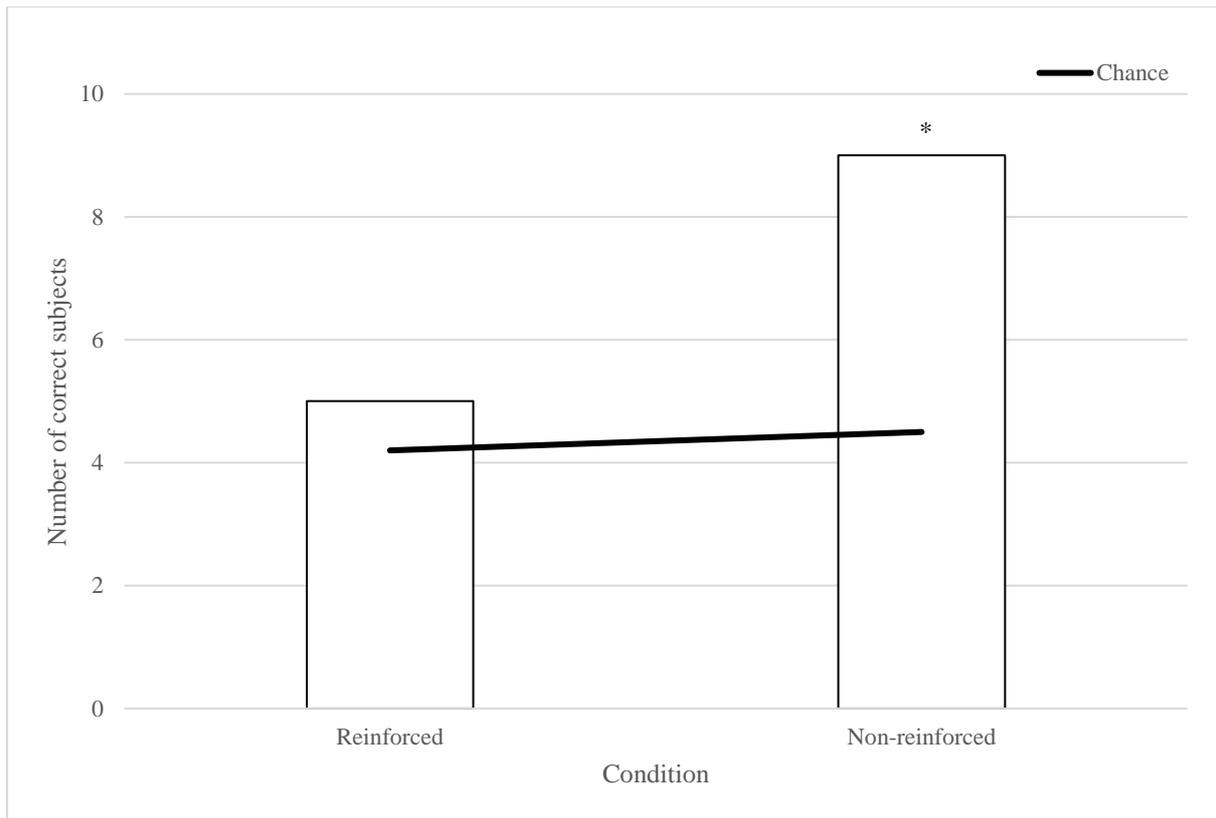


fig.4 Number of correct subjects by condition, chance shows number of subjects that would be correct if performing at chance. * = 0.05