1   **Distinctiveness enhances long-term event memory in non-human primates,**

2   **irrespective of reinforcement.**

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11   Short title: Distinctiveness and memory in primates

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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 autonoetic 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 measureable 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, autonoetic 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 preforming 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

190 **Experiment 1: Baseline**

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   *troglodytes;* 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   The better performance in comparison to Experiment 1 supports both contextual

452   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

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   **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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732
733
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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
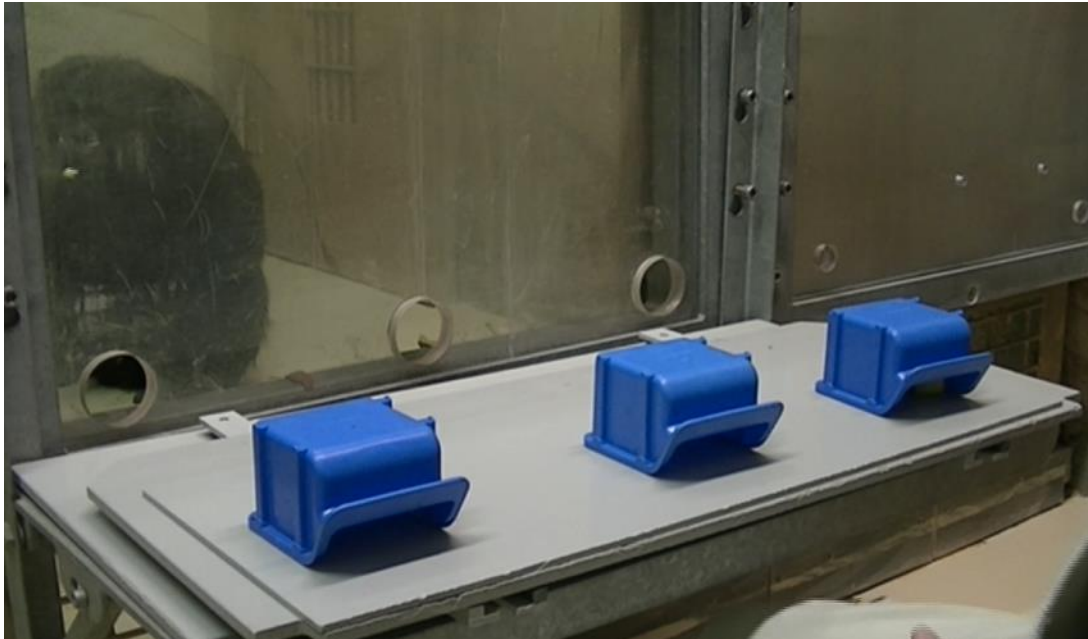
Fig.1. Set-up of the apparatus in Experiment 2. In Experiments 1 and 3 the tray on which the containers are on was not used (only the sliding platform that the tray is on) and an occluder was used
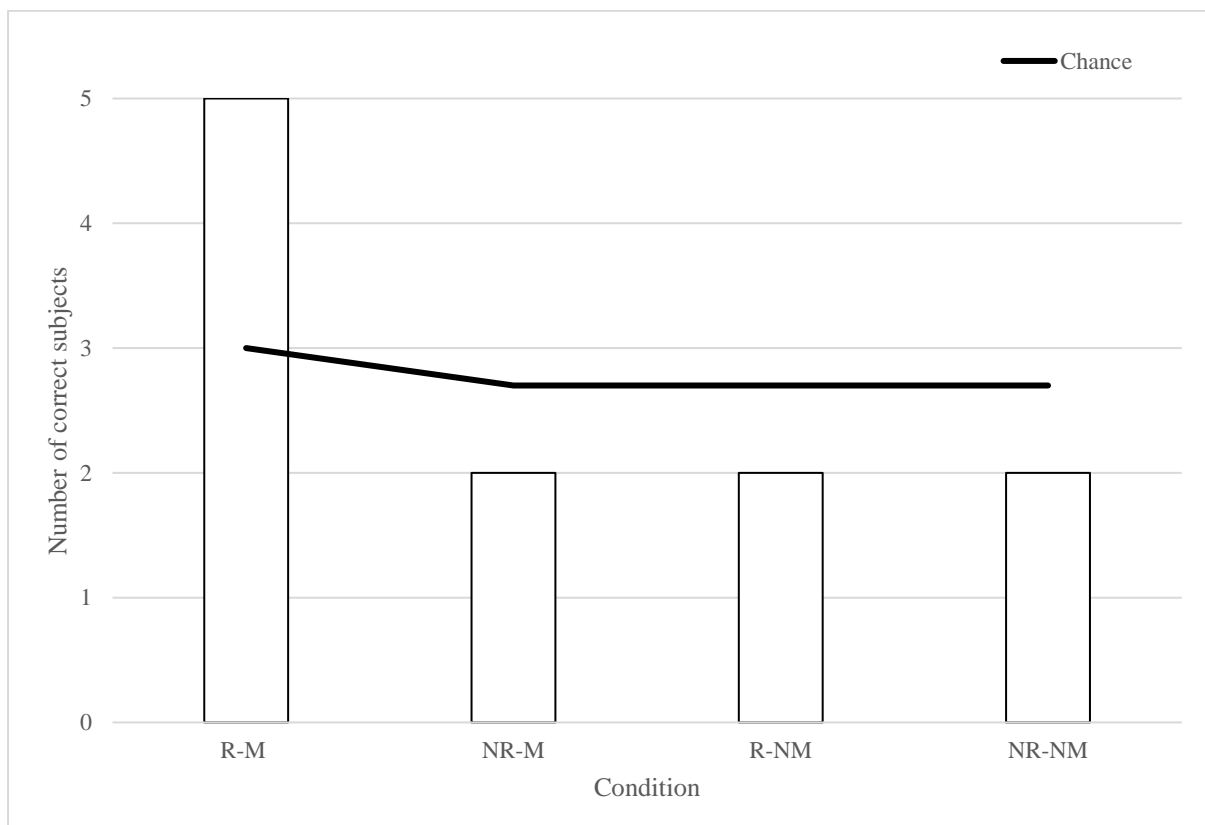

fig. 2: Number of correct subjects by condition. R-M = reinforced matching, NR-M = non-reinforced matching, R-NM = reinforced non-matching, NR-NM = non-reinforced non-matching. Chance shows number of subjects that would be correct if performing at chance.
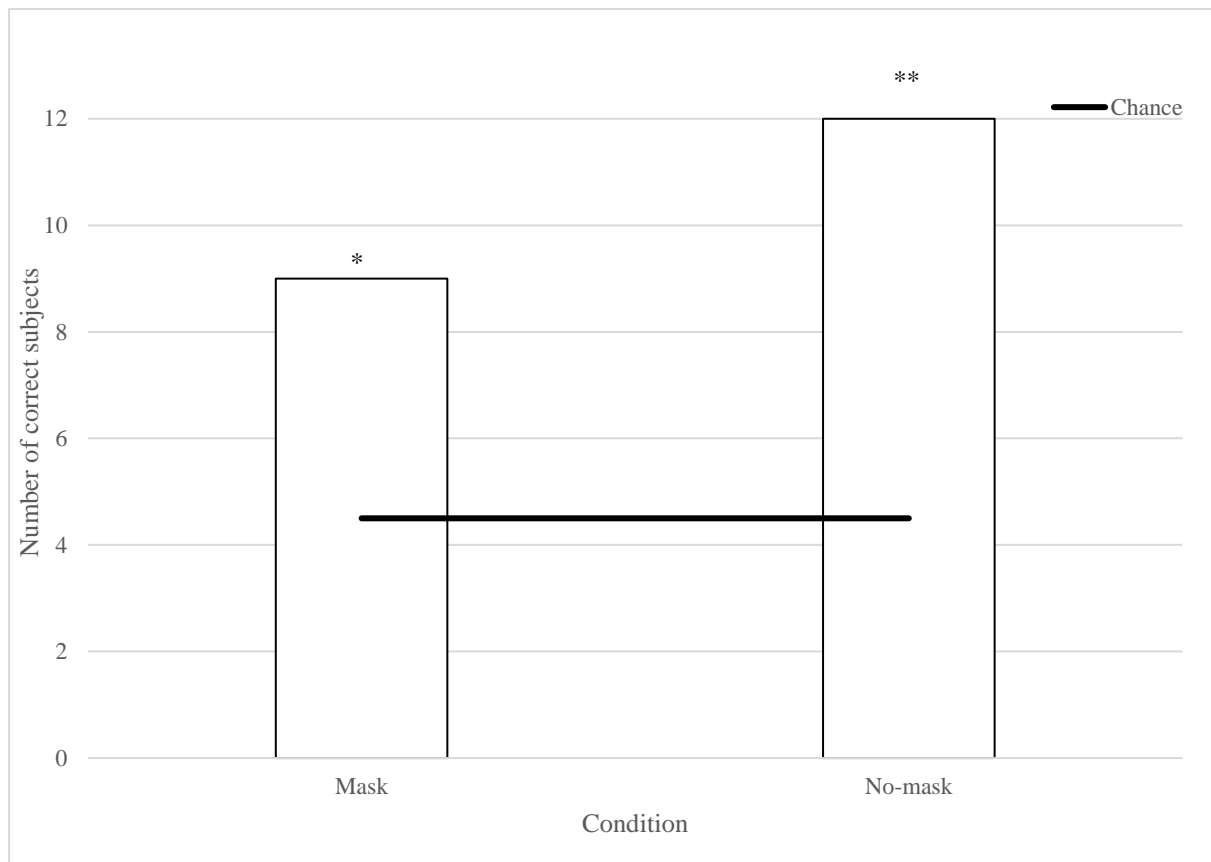
fig. 3 Number of correct subjects by each condition, chance shows number of subjects that would be correct if performing at chance. *= 0.05 **=<0.001.
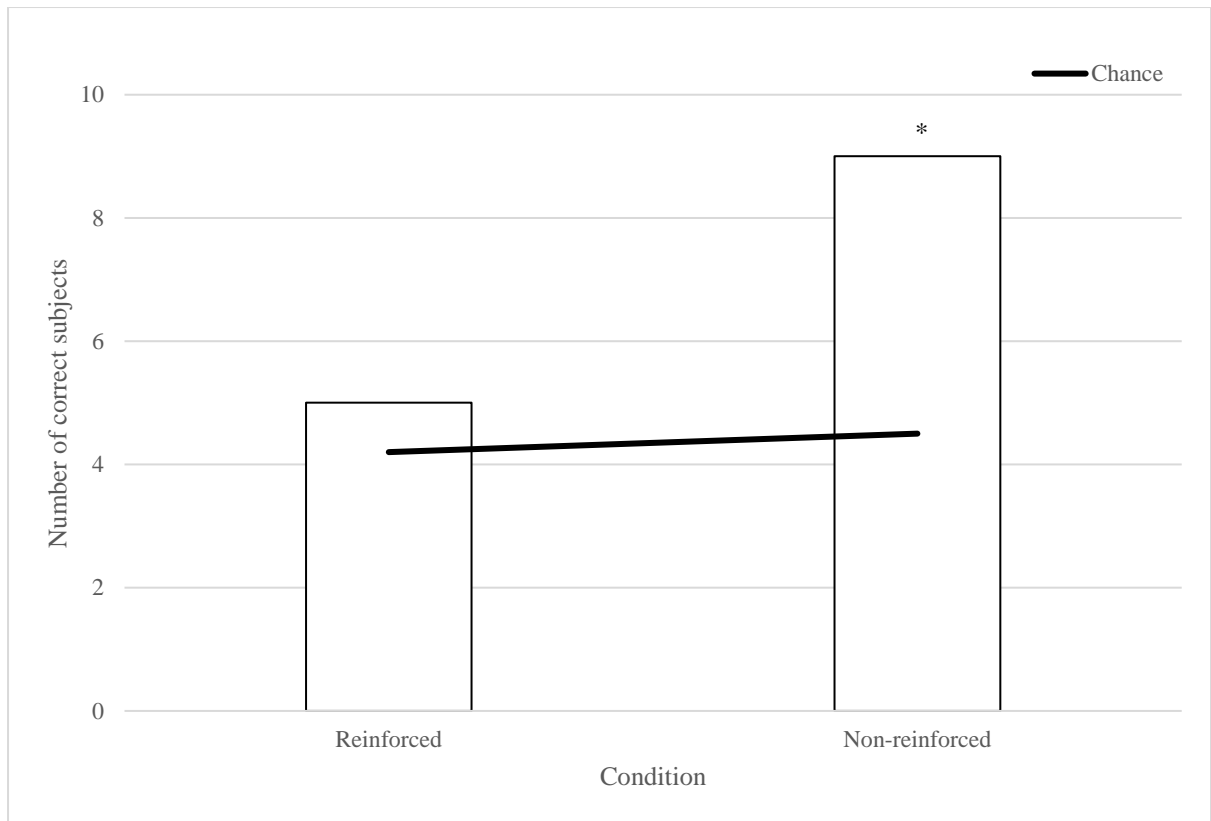
fig.4 Number of correct subjects by condition, chance shows number of subjects that would be correct if performing at chance. * = 0.05