Eurasian jays do not copy the choices of conspecifics, but they do show evidence of stimulus enhancement

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Corvids (birds in the crow family) are hypothesised to have a general cognitive tool-kit because they show a wide range of transferrable skills across social, physical and temporal tasks, despite differences in socioecology. However, it is unknown whether relatively asocial corvids differ from social corvids in their use of social information in the context of copying the choices of others, because only one such test has been conducted in a relatively asocial corvid. We investigated whether relatively asocial Eurasian jays (*Garrulus glandarius*) use social information (i.e., information made available by others). Previous studies have indicated that jays attend to social context in their caching and mate provisioning behaviour; however, it is unknown whether jays copy the choices of others. We tested the jays in two different tasks varying in difficulty, where social corvid species have demonstrated social information use in both tasks. Firstly, an object-dropping task was conducted requiring objects to be dropped down a tube to release a food reward from a collapsible platform, which corvids can learn through explicit training. Only one rook and one New Caledonian crow have learned the task using social information from a demonstrator. Secondly, we tested the birds on a simple colour discrimination task, which should be easy to solve, because it has been shown that corvids can make colour discriminations. Using the same colour discrimination task in a previous study, all common ravens and carrion crows copied the demonstrator. After observing a conspecific demonstrator, none of the jays solved the object-dropping task, though all jays were subsequently able to learn to solve the task in a non-social situation through explicit training, and jays chose the demonstrated colour at chance levels. Our results suggest that social and relatively asocial corvids differ in social information use, indicating that relatively asocial species may have secondarily lost this ability due to lack of selection pressure from an asocial environment.

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2 **enhancement**

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13 **ABSTRACT**

14 Corvids (birds in the crow family) are hypothesised to have a general cognitive tool-kit because

15 they show a wide range of transferrable skills across social, physical and temporal tasks, despite

16 differences in socioecology. However, it is unknown whether relatively asocial corvids differ

17 from social corvids in their use of social information in the context of copying the choices of

18 others, because only one such test has been conducted in a relatively asocial corvid. We

19 investigated whether relatively asocial Eurasian jays (*Garrulus glandarius*) use social

20 information (i.e., information made available by others). Previous studies have indicated that jays

21 attend to social context in their caching and mate provisioning behaviour; however, it is

22 unknown whether jays copy the choices of others. We tested the jays in two different tasks

23 varying in difficulty, where social corvid species have demonstrated social information use in

24 both tasks. Firstly, an object-dropping task was conducted requiring objects to be dropped down

25 a tube to release a food reward from a collapsible platform, which corvids can learn through

26 explicit training. Only one rook and one New Caledonian crow have learned the task using social

27 information from a demonstrator. Secondly, we tested the birds on a simple colour

28 discrimination task, which should be easy to solve, because it has been shown that corvids can

29 make colour discriminations. Using the same colour discrimination task in a previous study, all

30 common ravens and carrion crows copied the demonstrator. After observing a conspecific

31 demonstrator, none of the jays solved the object-dropping task, though all jays were

32 subsequently able to learn to solve the task in a non-social situation through explicit training, and

33 jays chose the demonstrated colour at chance levels. Our results suggest that social and relatively

34 asocial corvids differ in social information use, indicating that relatively asocial species may

35 have secondarily lost this ability due to lack of selection pressure from an asocial environment.

36 **Introduction**

37   A wide range of corvid species (e.g., crows, ravens, jays) are known for their complex

38 cognitive abilities, which are hypothesised to have been present in their common ancestor, thus

39 forming a 'general cognitive tool-kit' across this taxa (Emery & Clayton, 2004). For example,

40 even though rooks (*Corvus frugilegus*) do not make or use tools in the wild, they are able to

41 spontaneously innovate these behaviours in the lab (Bird & Emery, 2009b). Further, there is

42 evidence that some corvid species show cognitive competence across a wide range of social,

43 physical and temporal tasks. For instance, California scrub-jays (*Aphelocoma californica)* show

44 proficiency in cognitive tasks relating to memory (Clayton & Dickinson, 1998), future planning

45 (Clayton, Emery & Dickinson, 2006; Raby et al. 2007), and social cognition through cache

46 protection tactics (Clayton, Dally & Emery, 2007). As another example, rooks, in addition to

47 their tool abilities, cooperate with each other to solve novel problems (Seed et al. 2008) and

48 appear to understand support relationships because they look longer at impossible scenarios (e.g.,

49 a ball suspended in mid-air rather than sitting on a table; Bird & Emery 2010). Additionally,

50 New Caledonian crows reason about hidden causal agents (Taylor, Miller & Gray 2012), reason

51 by exclusion (Jelbert et al. 2015), and learn socially about novel foraging problems (Logan et al.

52 2016).

53   It is unknown whether this cognitive tool-kit includes the ability to use social information

54 specifically in the form of copying the choices of others, which is distinct from changing

55 behaviour when solving problems in different social contexts (several examples are given

56 below). The corvid common ancestor is hypothesised to have been social (Clayton & Emery,

57 2007). If this assumption is correct, rather than the common ancestor being asocial with sociality

58 having evolved several times in extant lineages, then there is reason to expect that relatively

59 asocial corvids could have retained the capacity to use social information. For example, it could

60 be adaptive by improving foraging and mate searching efficiency (e.g., Valone & Templeton,

61 2002). Alternatively, this ability could have been secondarily lost because of the lack of selection

62 pressure from an asocial environment, in a similar manner to the secondary loss of caching (food

63 hiding) in jackdaws (de Kort & Clayton, 2006). For example, in the absence of conspecifics for

64 most of the year, there might have been an increased selection pressure to rely solely on personal

65 information when foraging.

66   Most studies of corvid social information use, in the form of copying the choices of others,

67 have occurred in social species (species that live in groups of at least pairs year-round), which

68 makes it difficult to determine whether this ability is part of their general cognitive tool-kit.

69 Evidence of social information use, specifically copying the choices of others, has been found in

70 social corvid species, including pinyon jays (*Gymnorhinus cyanocephalus*; Templeton, Kamil &

71 Balda, 1999), rooks (Dally, Clayton & Emery, 2008), jackdaws (*Corvus monedula*; Schwab,

72 Bugnyar & Kotrschal, 2008a), common ravens (*Corvus corax*; Fritz & Kotrschal, 1999; Schwab

73 et al., 2008b), carrion crows (*Corvus corone corone*, *C. c. cornix*; Miller, Schwab & Bugnyar,

74 2016) and New Caledonian crows (*Corvus moneduloides*; Logan et al., 2016). Social species are

75 predicted to be better at acquiring new skills in a social context than in a non-social context

76 (Lefebvre & Giraldeau 1996), because they may attend more to conspecifics than asocial species

77 (Balda, Kamil & Bednekoff, 1997).

78   However, we are aware of only two tests of social information use in the form of copying

79 the choices of others in a relatively asocial corvid. Clark's nutcrackers (*Nucifraga columbiana*)

80 did not learn a motor or a discrimination task faster in a social learning condition than in an

81 individual learning condition, indicating that they did not use social information (Templeton,

82   Kamil & Balda, 1999). This was in contrast with highly social pinyon jays that did learn faster in

83   the social learning conditions (Templeton, Kamil & Balda, 1999). Additionally, Clark's

84   nutcrackers more accurately recovered caches they made rather than caches they observed others

85   make, in contrast with social Mexican jays that were accurate in both conditions (Bednekoff &

86   Balda 1996). These results suggest that relatively asocial corvids attend less to social information

87   than social corvids.

88   Outside of corvids, social learning in the form of copying conspecifics has been found in a

89   number of asocial species including red-footed tortoises (*Geochelone carbonaria*; Wilkinson et

90   al. 2010), black river stingrays (*Potamotrygon falkneri*; Thonhauser et al. 2013; Garrone Neto &

91   Uieda 2012), bearded dragons (*Pogona vitticeps*; Kis, Huber & Wilkinson 2014), and in juvenile,

92   but not adult, golden hamsters (*Mesocricetus auratus*; Lupfer, Frieman & Coonfield 2003) and

93   eastern water skinks (*Eulamprus quoyii*; Noble, Byrne & Whiting 2014). These non-corvid

94   species are likely to have had asocial ancestors, which suggests that social cues are not costly to

95   attend to and can evolve outside of a social context in these taxa. However, at present, the sample

96   size of the relatively asocial corvid species is too small to draw general conclusions about the

97   influence of a corvid's social system on their use of social information.

98   We addressed this gap by investigating whether the relatively asocial Eurasian jays

99   (*Garrulus glandarius*) used social information provided by a conspecific. Eurasian jays do not

100 live in social groups except during the breeding season when mated pairs defend a territory

101 (Goodwin 1951; Snow & Perrins, 1997; Clayton & Emery, 2007). There is evidence that socially

102 housed Eurasian jays attend to social context to modify their caching and mate provisioning

103 (courtship feeding) behaviour. For example, they prefer to cache in quiet rather than noisy

104 substrates when in the presence of conspecifics that could hear but not see the subject (Shaw &

105   Clayton, 2013); they attend to spatial and auditory cues when competitors are caching to later

106   pilfer those caches (Shaw & Clayton, 2014); and subordinates inhibit caching in front of

107   dominants and prefer to cache in less exposed areas (Shaw & Clayton, 2012). They also adjust

108   their behaviour appropriately depending on whether they are caching or pilfering (Shaw &

109   Clayton 2014), and whether they compete with a dominant or subordinate (Shaw & Clayton

110   2012). Furthermore, they prefer to cache out-of-sight behind an opaque barrier and at a distance

111   when observed by conspecifics (Legg & Clayton, 2014; Legg, Ostojić & Clayton, 2016). During

112   the breeding season, males are attentive to which foods their mates might prefer based on how

113   much of which foods she has already eaten (Ostojić et al., 2013; Ostojić et al., 2014).

114   These jays were socially raised and housed, which differs from their relatively asocial

115   system in the wild. The artificially social environment likely enhances their utilisation of any

116   innate social skills because these skills will have been given the opportunity to develop from an

117   early age. Therefore, if social skills are found in these conditions, it demonstrates the potential

118   flexibility of this species to use social cues (if social cues are used). As such, the social capacities

119   shown by socially raised and housed jays might differ from wild individuals. Despite the

120   evidence that socially housed Eurasian jays can respond to social context in caching and mate

121   provisioning paradigms, no study has yet tested whether this species uses social information to

122   copy the choices of others, which could be useful for learning about foraging opportunities even

123   in a relatively asocial species.

124   We tested whether socially housed Eurasian jays would use social information from a

125   conspecific demonstrator when learning to solve a novel problem – an object-dropping task

126   where an object must be dropped into a tube to release a food reward from a collapsible platform.

127   Further, if the birds did not use social information to solve the task, we tested whether there was

128   any evidence that they had attended to the demonstrator (as indicated by differences between

129   groups with differing levels of social learning opportunities), and what they might have learned

130   during this exposure. The object-dropping task has been used previously during pre-test training

131   for Aesop's Fable tasks in this species (Cheke, Bird & Clayton, 2011) as well as in a number of

132   other bird species (rooks: Bird & Emery, 2009a; New Caledonian crows: Jelbert et al., 2014;

133   Logan et al., 2014; Californian scrub-jays, Logan et al., 2016; great-tailed grackles, *Quiscalus*

134   *mexicanus*, Logan 2016). Aesop's Fable tasks require subjects to insert objects into water-filled

135   tubes to obtain out-of-reach floating rewards.

136   In the corvids that have been tested using this object-dropping task so far, we see a common

137   pattern, irrespective of whether they are habitual tool users. Namely, they are capable of learning

138   the object-dropping task, but only once they have experienced an object falling into a tube,

139   which usually occurs when they accidentally knock an object off the ledge into the tube. This

140   finding suggests that the birds need to see the object fall, and once they have, they can learn to

141   solve the rest of the task. This raises the question of whether they need direct experience of

142   manipulating the objects and observing them fall into the tube or whether witnessing another

143   individual's solution to the problem will suffice in learning the task. So far, only two birds have

144   solved the object-dropping task after observing a conspecific demonstrator: one rook (Bird &

145   Emery, 2009b) and one New Caledonian crow (Mioduszewska, Auersperg & von Bayern, 2015),

146   though only the latter study aimed to explicitly test for influences of social information use on

147   learning this task. New Caledonian crows are habitual tool users in the wild (Hunt, 1996), whilst

148   rooks - like Eurasian jays - are not, though rooks have shown tool-use and manufacture

149   proficiency in the lab (Bird & Emery, 2009b). Both rooks and crows are more social than jays, in

150   that rooks form large flocks for breeding, foraging and roosting, while New Caledonian crows

151   tend to form extended family groups that are fairly tolerant of their neighbours (Goodwin, 1986;

152   St Clair et al., 2015).

153   We also investigated whether Eurasian jays would choose the colour that was demonstrated

154   to be rewarded in a two-choice colour discrimination test. Unlike the object-dropping task, this is

155   a fairly simple task and corvids, including Eurasian jays, have been shown to be capable of

156   making colour discriminations (ravens: Range, Bugnyar & Kotrschal, 2008; Eurasian jays:

157   Clayton & Krebs, 1994; Davidson et al., Under Review). Furthermore, this test has explicitly

158   been used previously to demonstrate use of social information in other corvids, namely common

159   ravens and carrion crows, where all the individuals that were tested chose the demonstrated

160   colour (Miller, Schwab & Bugnyar, 2016). Ravens and crows are social species with high

161   fission-fusion dynamics, being highly social in non-breeding season, and territorial in the

162   breeding season (Goodwin, 1986). We conducted the task in a comparable manner to Miller,

163   Schwab & Bugnyar (2016) to allow for direct comparison between these two corvid studies. The

164   inclusion of both tasks in the present study allowed us to compare jay performances with social

165   corvid species that have been shown to use social information on the same tasks. Furthermore,

166   the use of both tasks enabled us to control for potential influences of task affordances, such as

167   difficulty. Namely, even if the object-dropping task was too difficult to learn socially, we would

168   still be able to detect whether the jays use social information in the simpler colour-discrimination

169   task.

170   The general tool-kit hypothesis (Emery & Clayton, 2005) may predict that relatively asocial

171   jays, like the more social New Caledonian crows, rooks, ravens and crows, would use the

172   information provided by the demonstrator, as they may have retained the capacity to use social

173   information (i.e., information made available by others). Alternatively, jays may differ from the

174 more social corvids in their use of social information, as they may have secondarily lost this

175 ability due to lack of selection pressure from an asocial environment.

176

177 **Methods**

178 **Subjects**

179   The subjects were 16 hand-reared juvenile Eurasian jays (8 females, 8 males) hatched in

180 May 2015. The birds were hand-reared as a group in 2015, and socially housed within a large

181 outdoor aviary (9x16.5x6m) at the Sub-department of Animal Behaviour in Madingley,

182 Cambridge. Birds were sourced from wild nests at 10 days old by a registered breeder under a

183 Natural England License to NSC (20140062). The subjects consisted of 5 sibling groups (one

184 pair, three groups of 3 birds, and one group of 4 birds), with 1 individual that had no siblings.

185 Testing took place in indoor test compartments (2x2x1m), with which the birds were familiar, as

186 they were fed their daily diet within these compartments and had constant access to them outside

187 of testing sessions. The birds could be separated individually, in pairs or sub-groups within these

188 compartments as required. One female bird ('Sjoika') did not participate in either experiment, as

189 she could not reliably be separated individually in the compartments. Subjects were identifiable

190 using unique colour leg-ring combinations. Prior to and during testing, subjects had access to

191 their daily diet, which consisted of soaked dog pellet and boiled vegetables, and water. Rewards

192 for both experiments were live mealworms, which are a highly valued food item, reserved only

193 for training and testing. Experiment 1 was conducted in October 2015 and Experiment 2 in

194 November 2015.

195

196 **EXPERIMENT 1: Object dropping task**

197 **Materials**

198   The testing apparatus was a clear Perspex 'object insertion' apparatus (total height=13cm)

199 consisting of a tube and a box (height=10.5cm, depth=6.5cm, width=11cm) containing a

200 collapsible platform (based on the design in Bird & Emery 2009b). Objects could be inserted into

201 a tube (length=8cm, diameter=5cm), causing the collapsible platform at the bottom of the tube to

202 release from a small magnet holding it in place. Once released from the magnet, a food reward

203 was dispensed to the subject (Figure 1). Several clear, plastic rings and one additional removable

204 platform (length=13cm, width=13cm) that attached to the exterior of the tube were used for the

205 earlier training stages. A blue ring was added to the top of the tube to increase the salience of this

206 area. Only one object was required to drop the collapsible platform and release the reward.

207 Spherical, black metal, hollow objects were used (measuring 2cm in diameter and weighing 4-

208 5g; Figure 1), with 3 thin pieces of black plastic string woven through the middle of each object

209 and tied in a knot on each side, to allow the birds to pick up the object more easily and prevent

210 them from rolling away.

211

212 **Procedure**

213   Subjects were separated into 3 groups: a trained group that had no prior experience with the

214 apparatus and had never seen another solve it, but were trained to correctly solve it by the

215 experimenter (3 males, 3 females); an observer group that observed a trained conspecific solve

216 the task (3 males, 3 females); and a control group that received no training on the task and did

217 not see any bird interact with the task (2 males, 1 female).

218

219 **Habituation and spontaneous object dropping**

220   All subjects were habituated to the apparatus and the object separately by presenting them

221   with small food rewards on top and beside the apparatus and object. Subjects were first presented

222   with a baited object on the table until they retrieved the reward in 5 consecutive trials. They were

223   then presented with the object insertion apparatus in the stages outlined in Table 1 and Figure 1.

224   Namely, the apparatus was presented in three scenarios to aid in learning how to correctly solve

225   the apparatus. 1. The removable platform was placed at the top of the tube (Figure 1a) to allow

226   the object to be placed on the rim of the tube so the bird could easily accidentally knock the

227   object into the tube by nudging it when attempting to obtain bait from under the object. 2. The

228   removable platform was placed at the bottom of the tube (Figure 1b) to encourage the bird to

229   pick up the object and lift it up to the top of the tube to insert it. 3. The removable platform was

230   removed (i.e., final stage apparatus; Figure 1c) so the bird had to pick up the object from the

231   table to insert it into the top of the tube. Rewards were placed on the apparatus, as well as

232   underneath it, with the collapsible platform in the dropped position, until subjects retrieved all

233   available rewards per trial in 5 consecutive trials.

234   All subjects were then given one 5 min test trial to determine whether they would

235   spontaneously pick up and drop the object into the tube prior to being allocated to a group.

236   During this test, the final stage apparatus (Figure 1c) was presented to each subject with the

237   object placed on the table beside the apparatus. No birds spontaneously solved the apparatus

238   within the 5 min, therefore they were randomly assigned to one of three groups: trained, observer

239   or control. Birds were allocated to groups by choosing names from a container: one 'male only'

240   and one 'female only' container ensured a balanced sex ratio in each group (3 males, 3 females

241   for the trained and observer groups; 2 males, 1 female for the control group).

242

243 **Trained group**

244   We first trained birds in the 'trained group' to successfully solve the task by inserting

245 objects from the table into the tube and obtaining the reward. We used the training stages

246 outlined in Table 1 and Figure 1 to gradually increase their proficiency from accidentally

247 inserting baited objects balanced on the rim of the tube to nudging objects down the tube with

248 the use of a removable platform attached to the outside of the tube (stages 1-2; Table 1), until

249 they picked up objects from the table to insert into the tube without the removable platform

250 present (stage 3; Table 1). In training stage 1, the object was baited with an insect on intermittent

251 insertions for the first 1-2 training sessions (3-21 insertions, mean=11 insertions). A session for

252 the trained group lasted 5-10 minutes and was not restricted to a specific number of object

253 insertions, but rather determined by the subject's motivation and performance in that particular

254 session. A maximum of 2 training sessions were run per day. An object insertion was considered

255 proficient if it was nudged or dropped directly into the tube, as opposed to being knocked in

256 accidentally by removing the baited insect, or first pushing it around on the platform or dropping

257 it onto the table from the platform.

258   Subjects moved from stage 1 to stage 2 when they had accidentally knocked the object into

259 the tube on 10 consecutive insertions (Figure 1a). The removable platform was then gradually

260 moved down the tube during stage 2 until the subject inserted the object from the platform when

261 it was placed at the bottom of the tube on 10 consecutive insertions (Figure 1b). If subjects

262 struggled with progression to the next stage (e.g., stopped inserting the object), they returned to

263 the previous stage, with the aim for each training session to 'end on a high' (i.e., with a reward

264 for inserting the object). A bird was considered to have solved the task when they had inserted

265   the object from the table into the final stage apparatus and obtained the reward in 10 consecutive

266   insertions (Figure 1c).

267   We then selected one bird from the trained group (Homer) to demonstrate how to solve the

268   apparatus to the observer group. This bird was selected to be the demonstrator because he was

269   motivated and reliable during training (e.g., he was easy to call into the test compartments and

270   comfortable being close to humans), and solved the task during training fairly quickly. Homer

271   was 100% accurate when he demonstrated for observers; therefore observers never saw failed

272   attempts.

273

274   **Observer group**

275   Observers saw the demonstrator successfully solve the apparatus 40 times per stage, using

276   the following stage order: 3-1-2-3 (e.g., observers saw 40 demonstrations of stage 3, then 40

277   demonstrations of stage 1, etc.; Table 1). This resulted in a total of 160 observations of

278   successful solves per observer bird. Observers were given 4 demonstration sessions of 10 solves

279   per session per stage. The stages were the same as those used for the trained group (Table 1;

280   Figure 1). As these stages facilitated the training of the trained group to solve the task, we might

281   expect that aspects of these stages are helpful for learning the task, hence including

282   demonstrations of each stage. Each demonstration session lasted approx. 3 min, with a maximum

283   of 2 sessions run per day. The demonstrations took place on a table in one compartment, with the

284   observers located in an adjacent, but separate compartment with free visual access between

285   compartments via mesh panels. There were 3-4 observer birds per adjacent compartment and

286   there were sufficient perches for all observers to view the demonstrations at the same time. The

287   observer group was split into 2 smaller sub-groups of 3 birds per group for observations to

288   ensure each bird had sufficient visual access of the demonstrator and to reduce crowding within

289   the test compartments. Each observer subject had the opportunity to watch 16 demonstration

290   sessions, with one or two sessions per day, ensuring that each observer had ample opportunities

291   to observe demonstrations.

292   Immediately after an observer saw 40 demonstrated solves of a particular stage, observer

293   were visually isolated and presented with the object insertion apparatus at the final stage (i.e., no

294   removable platform and with the object on the table). They were then given one 5-min test trial

295   to determine whether they had learnt to solve the task. Observer subjects received five 5-min test

296   trials: one pre-demonstration test trial that all birds received to determine whether they

297   spontaneously solve the task, and observer birds received four test trials immediately after

298   observing demonstrations at each stage (stages 3-1-2-3; Table 1). Each test trial therefore took

299   place on a separate day, over a period of 15 days. During all test trials, the observer subject was

300   presented with the final stage apparatus with the object on the table. To solve the task, the

301   subject was required to pick up the object from the table and insert it into the tube to release the

302   collapsible platform and obtain the reward. The longest time that any subject waited between

303   observing the last demonstration session of each stage and their own test trial was 10 minutes.

304

305   **Control group**

306   The control group did not receive any object insertion apparatus training or demonstrations,

307   and were presented with the 'final stage' object insertion apparatus the same number of times

308   that the observer group received the apparatus (i.e., 5 test trials). Test trials were run on the same

309   test days as the observer group to avoid any potential differences between the groups due to age

310   or other environmental factors.

311

312 **Data analysis**

313   All training and demonstration sessions and test trials were videotaped, as well as being live

314 coded. We recorded the number of (accidental and proficient) insertions required for the trained

315 group individuals to complete each training stage and solve the task (i.e., to insert an object from

316 the table into the tube at the final apparatus stage in 10 consecutive insertions). For the observer

317 and control groups, we recorded whether the subject solved the task (i.e., inserted an object from

318 the table into the tube at the final apparatus stage, and interacted with the apparatus or object).

319   To determine whether individuals in the observer group interacted with the apparatus and

320 object more than individuals in the control group during tests, we conducted a generalised linear

321 model (GLM) using a Poisson distribution with a log link in R v3.2.1 (function: glm; R Core

322 Team 2015). We combined the total number of times a bird touched the apparatus and object per

323 trial (response variable) to examine whether it varied by trial number or group (control or

324 observer; explanatory variables). We conducted a generalised linear mixed model (GLMM)

325 using a Poisson distribution with a log link (R package: lmerTest, function: glmer, Kuznetsova,

326 Brockhoff & Christensen, 2015) to determine whether the observer group interacted more with

327 particular parts of the apparatus or object after having seen the demonstrator solve the task. We

328 examined whether the number of touches (response variable) varied according to the location

329 that was touched (apparatus base, apparatus tube, or object) by group (control or observer;

330 explanatory variables) with bird ID as a random effect. To examine whether observer jays

331 touched the apparatus/object sooner than control jays, we conducted the same GLMM just

332 mentioned, but with a different response variable: the latency (in seconds) to touch the apparatus

333 or object per test trial per bird.

334   To examine the level of certainty associated with each model, the respective models were

335   compared with all model combinations and their Akaike weights, which sum to 1 across the

336   models, considered (R package: MuMIn, function: dredge; Bates, Maechler & Bolker, 2011). A

337   model was considered highly likely given the data if it had a high Akaike weight (>0.89) relative

338   to the other models (Burnham & Anderson, 2002).

339   Once Experiment 1 had been conducted, all of the birds in the control and observer groups

340   were trained to insert objects into the object insertion apparatus. We recorded the number of

341   (accidental and proficient) insertions required for the observer and control group to complete

342   each training stage and solve the task. We examined whether birds in the observer group solved

343   the task faster than birds in the trained or control groups using a GLM in R. The number of

344   object insertions required to complete stage 3 (insert the object from the table into the tube in 10

345   consecutive insertions; response variable) was compared across conditions (trained, observer,

346   control; explanatory variable) using a Poisson family with a log link.

347

348   **Results**

349   None of the jays solved the task spontaneously in the initial trial (i.e., prior to any training,

350   demonstrations or frequent exposure to the apparatus). In the trained group, all 6 jays learned to

351   drop objects over a period of 8 to 21 training sessions (4-11 days). In the observer group, 0 of 6

352   jays learned to drop objects by observing the demonstrator. In the control group, 0 of 3 jays

353   learned to drop objects without training or demonstrations. Only one bird ('Gizmo' – observer

354   bird), on her final test trial, lifted the object high up while standing near the tube, but she did not

355   insert it into the tube.

356   All observer and control subjects generally interacted with the apparatus and/or object

357   during test trials (in 44 of 45 test trials; with the apparatus in 39 trials and the object in 34 trials).

358   Individuals in the observer group did not touch the apparatus or object more than individuals in

359   the control group (mean touches=11 and 9, respectively; Table 2: Model 1). The Akaike weight

360   for this model was very low (0.11), and it was the third ranked model, indicating a high level of

361   uncertainty, therefore it is likely that there was not enough data for the model to draw strong

362   conclusions, or the effects were too small to detect.

363   While the number of interactions decreased with increasing trial number in control

364   individuals, there is weak evidence that observer individuals had relatively more interactions

365   with the apparatus and object in later trials than control individuals (Table 2: Model 1). There

366   was only weak evidence because the Akaike weight for the top-ranked model, which was the full

367   model, was only 0.46, indicating that there was a high degree of uncertainty in this model. There

368   was no evidence that birds in the observer group interacted more with particular parts of the

369   apparatus or object after seeing the demonstrator solve the task compared with control birds

370   (mean touches=4 and 3, respectively; Table 2: Model 2). When comparing the latency to the first

371   touch between control and observer groups, observer birds touched the apparatus/object

372   significantly sooner than control birds (mean=23 and 83 seconds, respectively; Table 2, Model 3;

373   Figure 3). This model was highly likely given the data because its Akaike weight was 0.99. The

374   data in Figure 3 shows that there was no initial difference in latencies between control and

375   observer groups during their spontaneous test trial (trial 1), which was before the observer group

376   had access to social information about the apparatus. The difference between the two groups

377   occurred in trials 2-5 where, after the social demonstrations, observer latencies stayed the same,

378   while the control group's latencies increased.

379   Following this experiment, all 9 jays in the observer and control groups underwent training

380   to drop objects over a period of 8-12 training sessions (5 to 7 days). Therefore, the number of

381 object insertions required to reach proficiency was compared between the trained, observer, and

382 control groups. Birds in the trained group required more insertions to solve the task (i.e., to insert

383 objects from the table into the tube of the final stage apparatus; mean insertions to solve=167,

384 GLM estimate=0.39, SE=0.06, z=6.26, p<0.001), than observer and control birds. Birds in the

385 observer (mean insertions to solve=114, GLM estimate=0.01, SE=0.07, z=0.20, p=0.84) and

386 control (mean insertions to solve=113, GLM [intercept] estimate=4.72, SE=0.05, z=86.86,

387 p<0.001) groups did not differ in the number of insertions (Figure 4; ESM1 Table S1).

388

389 **EXPERIMENT 2: Two-choice colour discrimination task**

390 **Materials**

391 This set up consisted of two plastic cups – one black and one white (diameter=6cm,

392 height=14.5cm). Cups were spaced 30cm apart on a wooden board (50cm x 15cm). Each cup

393 was attached to its own metal rod so they could move up and down independently, but they were

394 prevented from being removed entirely from the rod by a bolt. Cups could be lifted upwards to

395 reveal a hidden reward (Figure 2). Two live mealworms were placed underneath each cup.

396

397 **Procedure**

398 **Demonstrator training**

399 One bird acted as a demonstrator - ' Homer' - the same demonstrator as in Experiment 1. In

400 visual isolation from the observer group, Homer received 4 sessions (5-10 mins per session) of

401 10 trials per session, where only one cup - the white cup - was baited ('demonstrated' cup) and

402 the other cup - the black cup - was locked down using the bolt so it could not be lifted. To pass

403 demonstrator training, Homer had to consistently lift only the demonstrated cup in all 10

404 consecutive trials within a session and not touch or try to lift to other cup before he could move

405   on to the demonstrations for observers. Homer touched both cups in session 1 and 2, but passed

406   criterion in session 3. He was given 4 training sessions in total to ensure comparability with the

407   number of demonstrator training sessions used for the carrion crows and ravens in Miller,

408   Schwab & Bugnyar (2016). Homer chose the white cup 100% of the time during demonstrators

409   for observers; therefore observers did not see any incorrect choices.

410

411   **Demonstrations for observers**

412   The observer group consisted of 7 birds in order to be comparable with the sample size in

413   Miller and colleagues (2016): 4 females and 3 males. These individuals also participated in

414   Experiment 1: 3 from the trained group, 3 from the observer group, and 1 from the control group.

415   In an adjacent compartment with visual access to the observers, the demonstrator lifted the

416   demonstrated cup (white) and obtained the reward in 4 sessions, with 10 trials per session. Both

417   cups were baited and could potentially be lifted, though the demonstrator only lifted the

418   demonstrated cup. The demonstrated cup location (left or right) was counterbalanced across

419   trials. Each observer watched one session per day.

420

421   **Testing observers**

422   After observers had seen Homer lifting the demonstrator cup 40 times, they were tested in

423   visual isolation from the group. Each observer was presented with the cups, both cups were

424   baited out-of-sight of the observer and we recorded which cup they touched first. They were

425   given one test trial, which lasted up to 3 minutes (all subjects interacted with the cups within 3

426   minutes). They were allowed to touch both cups. The location of the demonstrated cup was

427   randomized across subjects. If they touched the demonstrated cup (white) first, we considered

428   this to be using social information from the demonstrator.

429

430   **Data analysis**

431   We recorded the colour and latency of the cup first touched by the demonstrator during

432   training and demonstration trials, and by the observers during the test. The data were analysed

433   using SPSS version 21 for the exact two-tailed Binomial tests, and R for the t-test. RM and KL

434   both coded 20% of all videos across both experiments, with KL acting as a naïve coder, and

435   inter-observer reliability was excellent (Cohen's kappa k=0.989, p <0.001).

436

437   **Results**

438   Jays did not choose the demonstrated colour above chance levels (Binomial test: p=0.453).

439   Two of 7 jays (1 male, 1 female) chose the same coloured cup (white) as the demonstrator (i.e.,

440   copied the demonstrator), while the other 5 jays (3 females, 2 males) chose the non-demonstrated

441   coloured cup (black; Table 3). In comparison, Miller, Schwab & Bugnyar (2016) found that 8 of

442   8 crows (5 females, 3 males) and 8 of 8 ravens (3 females, 5 males) copied the conspecific

443   demonstrator, which was significant (Binomial test: p=0.008 for each species). We additionally

444   examined whether there was a difference in the latency to make the first choice between the birds

445   that chose the demonstrated colour versus those that did not. The jays that chose the

446   demonstrated colour did not have shorter latencies to their first choice (Welch two-sample t-test:

447   t=0.88, p=0.47, n=7, 95% confidence interval=-36-57; data in ESM1 Table S1). We also

448   explored whether relatedness influenced likelihood to copy the demonstrator. 0 of 2 jays that

449   selected the demonstrated coloured cup (Binomial test: p=0.5, n=2) and 2 of 5 jays that did not

450   select the demonstrated coloured cup were siblings of the demonstrator bird (Binomial test:

451   p=1.00, n=5). The birds did not appear to show a group side bias because they did not select the

452   cup on the same side regardless of colour (Table 3: Binomial test: p=1.00, n=7).

453

454   **Animal ethics**

455   The study was conducted under approval from University of Cambridge Psychology

456   Research Ethics Committee (application number: pre.2013.109) and the European Research

457   Council Executive Agency Ethics Team (application: 339993-CAUSCOG-ERR).

458

459   **Video summary**

460   A video shows examples from both experiments: https://youtu.be/L3IQy8cbqUQ.

461   Experiment 1: Trained group, Solving Task ('Stuka'); Experiment 1: Observer Group, Test Trial

462   5 ('Gizmo'); Experiment 2: Observer Group, Test Trial (Gizmo).

463

464   **Discussion**

465   We found that relatively asocial Eurasian jays did not use social information (i.e.,

466   information made available by a conspecific) in the form of copying the choices of others in

467   either task. In Experiment 1 (object-dropping task), birds in the observer group first touched the

468   apparatus and object significantly sooner than birds in the control group, indicating a form of

469   social learning called stimulus enhancement. Stimulus enhancement attracts the attention of an

470   observer towards a specific object where the model acts (Giraldeau, 1997). However, observing a

471   conspecific demonstrator did not facilitate solving the object-dropping task in Experiment 1, or

472   result in colour choice copying in Experiment 2.

473   Although corvids, including Eurasian jays, can be trained in the object-dropping task, it is

474   possible that this task is too difficult for social learning to facilitate the solution, except for the

475   occasional individual (i.e., one rook: Bird and Emery, 2009b; and one New Caledonian crow:

476   Mioduszewska, Auersperg & von Bayern, 2015), thus masking whether Eurasian jays are able to

477   use social information by observing, and thus learning from, a demonstrator. In the present study,

478   solving this task required the observer birds to copy several actions of the demonstrator: lifting

479   the object from the table to insert into the tube to drop the collapsible platform and obtain the

480   reward, rather than just knocking an object into the tube from the tube ledge, which is typically

481   stage 1 of training. In further support of the suggestion that this task is difficult for birds to learn

482   is that only one bird has spontaneously solved the object-dropping task in a previous study (one

483   New Caledonian crow; Mioduszewska, Auersperg & von Bayern, 2015), without any

484   demonstrations or training. Additionally, birds, including corvids, typically require a relatively

485   large number of training trials to learn to solve this task, indicating that it is fairly difficult to

486   learn even with explicit training (e.g., 90-275 trials in present study; 135-362 trials in grackles:

487   Logan, 2016; 76-255 trials in scrub-jays: Logan et al., 2016 – though note that definitions for

488   reaching proficiency differ between these studies and the current study).

489   It is therefore possible that the jays obtained some information from the demonstrator, but

490   potentially this information was not sufficient to enable them to complete the task (i.e., to insert

491   the object from the table into the tube). Therefore, we assessed whether there was any evidence

492   that the jays attended to the demonstrator, despite not being able to solve the task following the

493   demonstrations, by measuring differences in the number of interactions with the apparatus and

494   object between the control and observer groups. Individuals in the observer group were not more

495   likely to touch the apparatus or object than individuals in the control group. Observer individuals

496 touched the apparatus and object in later trials more than control individuals, indicating that jays

497 may have been more persistent after having seen another bird solve the task. However, it should

498 be noted that the models showed only weak evidence for these two findings.

499   We also found that the observer group solved the object-dropping task significantly more

500 quickly than the trained group; however, there was no difference in the rate of learning (i.e., total

501 number of insertions required to solve the task) between the observer and control groups. The

502 strongest evidence of any form of social learning was in the form of stimulus enhancement:

503 observer birds that had seen a demonstrator interact with the apparatus and object first touched

504 these elements significantly sooner than control birds that had never observed another touching

505 the apparatus. It is possible that increased exposure to the apparatus may have facilitated learning

506 in both the observer and control groups, perhaps by removing neophobia of the apparatus

507 (although all birds were habituated to the apparatus prior to testing), and/or some social

508 facilitation of attraction or attention to the apparatus, as opposed to learning the actions to

509 perform the task. However, it is unclear whether observers attended to social information

510 provided by the conspecific or whether they would have learned about the task by observing a

511 'ghost control' where the object was inserted into the tube in the absence of a conspecific. Future

512 research incorporating ghost controls could distinguish between whether jays attend to social

513 information about what to attend to or whether they solely attend to the relevant object

514 movements and reward outcomes.

515   In Experiment 2, in comparison with the object-dropping task, the colour discrimination task

516 was relatively simple as corvids are capable of making colour discriminations (Clayton & Krebs,

517 1994; Range, Bugnyar & Kotrschal, 2008). For example, there is evidence that juvenile Eurasian

518 jays can discriminate between colours in similar two-choice discrimination tasks. Davidson and

519 colleagues (Under Review) trained half of a group of Eurasian jays to associate a yellow

520 coloured object with a reward and a green coloured object with no reward, and the other half to

521 associate the green object with a reward and the yellow object with no reward. The jays then

522 demonstrated proficiency by flying to the perch where the rewarded colour was located.

523   Further, the same task used in Experiment 2 was used previously in 8 ravens and 8 carrion

524 crows, and all birds chose the demonstrated colour (Miller, Schwab & Bugnyar, 2016). While the

525 methods have some limitations (e.g., no counterbalancing of rewarded cup color, using only one

526 demonstrator whose characteristics might have made him less likely for observers to attend to,

527 low statistical power from only one trial per bird), we ran this task in a comparable manner to

528 Miller, Schwab & Bugnyar (2016) to allow for direct comparison between these two studies,

529 including the use of one male, same-age conspecific demonstrator to an observer group and one

530 test trial. Additionally, all birds were hand-reared in species groups in a similar manner, tested by

531 the same experimenter (RM) and similar sample sizes were used (8 ravens, 8 crows, 7 jays). We

532 also similarly controlled for the influence of spatial location by randomizing the location of the

533 demonstrated cup across subjects, and we found no group-level bias for one location (right/left)

534 over the other (Table 3).

535   There were two notable differences between these studies. Firstly, the colour discrimination

536 task used different colours: blue and yellow cups in Miller, Schwab & Bugnyar (2016) compared

537 with white and black cups in the present study. The justification for this difference was the need

538 to avoid a possible overlap between this study and the prior experience of the jays with several

539 different colours in differing reward scenarios during previous studies (e.g., Davidson et al.,

540 Under Review). Furthermore, Shaw and colleagues (2015) suggest that colour discrimination

541 tasks should aim to use gray scale cues (e.g., light vs. dark gray) to avoid innate species-level

542   colour preferences. We cannot entirely rule out innate colour preferences, because we did not

543   transfer birds to novel colour combinations. However, innate preferences would likely have been

544   expressed at the species level, which did not occur here because jays randomly chose white and

545   black cups in their first trials.

546   Secondly, the jays were juveniles, whereas the ravens and crows were sub-adults. Therefore,

547   it is possible that social learning in the jays may not have developed by this early stage.

548   However, this is unlikely given that juveniles in other relatively asocial species exhibited social

549   learning whereas adults did not (Lupfer, Frieman & Coonfield 2003; Noble, Byrne & Whiting

550   2014). To our knowledge, no corvid studies have compared juvenile and adult social information

551   use. However, object permanence in Eurasian jays, which relates to caching development,

552   develops at a similar stage as in other corvids (ravens: Bugnyar, Stowe & Heinrich, 2007; scrub-

553   jays: Salwiczek et al., 2009). Specifically, jays reach a full (i.e., stage 6 Piagetian) understanding

554   of object permanence within their first few months of life (Zucca, Milos & Vallortigara, 2007).

555   As the jays we tested were more than a few months of age, we do not expect their behaviour to

556   differ from adult behaviour with regard to social learning. The finding that the jays behaved

557   differently from the more social carrion crows and ravens in the use of social information in this

558   task is important. It raises the question of whether these more social species - as with the more

559   social rook (Bird & Emery, 2009b) and New Caledonian crow (Mioduszewska, Auersperg & von

560   Bayern, 2015) - might be able to learn to copy the demonstrator in the object-dropping task

561   (Experiment 1).

562   Previous studies have indicated that Eurasian jays do attend to social context in caching and

563   mate provisioning (Shaw & Clayton, 2012; Shaw & Clayton, 2013; Ostojić et al., 2013; Shaw &

564   Clayton, 2014; Ostojić et al., 2014; Legg, Ostojić & Clayton, 2016). It is therefore still possible

565 that jays use social information, but not for copying others' choices, as none of the previous

566 studies required the birds to copy a demonstrator. Jays may also be more likely to pay attention

567 to and copy different demonstrators, such as an older, more affiliated or related individuals, as

568 model identity has been found to influence social learning in other corvids (ravens, jackdaws:

569 Schwab, Bugnyar & Kotrschal 2008a; Schwab et al., 2008b). For example, presence of siblings

570 enhances social learning in ravens (Schwab et al., 2008b). Our demonstrator was a sibling of

571 some of the observers, which suggests that there was no influence of relatedness to demonstrator

572 on likelihood of copying in Experiment 2. However, our study was not designed to test the

573 relationship between relatedness and social learning and we do not have the statistical power to

574 make a firm conclusion on this point.

575   The use of social information is a process with several stages, which are likely to be

576 sequential and distinct: acquisition (observing another), application (performing the observed

577 behaviour, not necessarily successfully) and exploitation (successfully performing the observed

578 behaviour in a way that gives the individual an advantage; Carter, Tico & Cowlishaw, 2016;

579 Guillette, Scott & Healy, 2016). For instance, in chacma baboons (*Papio ursinus*), the average

580 individual only acquired social information on <25% of occasions and exploited social

581 information on <5% of occasions, and information use was dependent on phenotypic constraints

582 such as network position and dominance status (Carter, Tico & Cowlishaw, 2016). The results of

583 Experiments 1 and 2 demonstrated that Eurasian jays did not appear to apply or exploit the social

584 information available even though they had the opportunity to acquire it. Though we reiterate

585 that social species also do not show a strong capacity to socially learn the object-dropping task in

586 Experiment 1.

587   In conclusion, Eurasian jays did not appear to use social information in the form of copying

588   the decisions of a conspecific in the object-dropping and colour discrimination tasks, which vary

589   in difficulty. However, their attention was drawn to the apparatus and object in the object-

590   dropping task as indicated by observers touching these components sooner than control birds. In

591   previous studies with social corvids, the birds have only been explicitly tested for influences of

592   social information on learning the object-dropping task in one study, with only one New

593   Caledonian crow learning the task following a conspecific demonstration (Mioduszewska,

594   Auersperg & von Bayern, 2015). We also know that, when tested using very similar procedures,

595   including the same lead experimenter, ravens and crows use social information in the colour

596   discrimination task, in contrast to the jays. These corvid species vary in sociality, but all are

597   more social than the jays. Our results from relatively asocial Eurasian jays are therefore

598   consistent with those from relatively asocial Clark's nutcrackers (Bednekoff & Balda 1996,

599   Templeton, Kamil & Balda, 1999) in that social and relatively asocial corvids appear to differ in

600   their use of social information with regard to copying the choices of others. The present study

601   may indicate that Eurasian jays secondarily lost the ability to copy social information provided

602   by a conspecific, at least in some contexts, while maintaining the ability to attend to the general

603   movements of others, due to lack of selection pressure from an asocial environment. However,

604   more comparisons between social and relatively asocial corvids are needed to confirm this

605   hypothesis.

606

607   **Data Availability**

608   Data for the social learning GLMMs is available at the KNB Data Repository at:

609   https://knb.ecoinformatics.org/#view/corina_logan.45.5 (Miller & Logan, 2016).

610

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616

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Stages of the object insertion apparatus.

Training stages: training the trained group, and subsequent to their tests, the observer and control groups, to insert objects into the tube to release the food reward. Training stages occurred in the following sequence: 1-2-3. Demonstrator stages: birds in the observer group watched the demonstrator solve the apparatus 40 times per stage before being presented with the final stage apparatus in a test trial. Demonstration stages occurred in the following sequence: 3-1-2-3.

1 Table 1. Stages of the object insertion apparatus. Training stages: training the trained group, and

2 subsequent to their tests, the observer and control groups, to insert objects into the tube to release

3 the food reward. Training stages occurred in the following sequence: 1-2-3. Demonstrator stages:

4 birds in the observer group watched the demonstrator solve the apparatus 40 times per stage

5 before being presented with the final stage apparatus in a test trial. Demonstration stages

6 occurred in the following sequence: 3-1-2-3.

Stage	Removable platform position		Object position		Figure 2 corresponding image
	Training	Demonstration	Training	Demonstration	
1	Top of the tube	Top of the tube	Platform. Object baited with insect and then not baited	Table	a
2	Gradually lowered down the tube using plastic rings until at the bottom of the tube	At the bottom of the tube	Platform or table	Table	b
3	No platform	No platform	Apparatus base or table	Table	c

Did observers learn what to attend to from the demonstrator?

Results from the GLM (Model 1) and GLMM (Model 2) examining whether individuals in the observer group **touched** the apparatus and object more than control individuals (Model 1) or whether they interacted more with particular parts of the apparatus (base or tube) or object (Model 2). Model 3 (GLMM) examined **latencies** to first touch per trial to determine whether individuals in the observer group first touched the apparatus/object sooner than control birds. SE: standard error, z: z value, p: p value, the rows in italics list the variance and standard deviation of the random effect.

1   Table 2. Results from the GLM (Model 1) and GLMM (Model 2) examining whether individuals

2   in the observer group **touched** the apparatus and object more than control individuals (Model 1)

3   or whether they interacted more with particular parts of the apparatus (base or tube) or object

4   (Model 2). Model 3 (GLMM) examined **latencies** to first touch per trial to determine whether

5   individuals in the observer group first touched the apparatus/object sooner than control birds. SE:

6   standard error, z: z value, p: p value, the rows in italics list the variance and standard deviation of

7   the random effect.

Model	Variable	Estimate	SE	z	p
1	Intercept (controls)	3.19	0.17	18.42	<0.001
	Trial	-0.37	0.07	-5.62	<0.001
	Observers	-0.17	0.21	-0.83	0.41
	Trial*Observers	0.16	0.08	2.06	0.04
2	Intercept (apparatus base, controls)	1.19	0.25	4.83	<0.001
	Object	-0.25	0.20	-1.12	0.23
	Tube	-0.32	0.21	-1.54	0.12
	Observers	0.44	0.29	1.50	0.13
	Observers*object	-0.37	0.24	-1.51	0.13
	Observers*tube	-0.14	0.24	-0.59	0.56
	Bird ID	*0.12*	*0.35*		
3	Intercept (controls)	4.32	0.21	20.88	<0.001
	Observers	-1.22	0.26	-4.78	<0.001
	Bird ID	*0.13*	*0.35*		

Two-choice colour discrimination task results

The birds observed the trained demonstrator Homer lifting the white cup to retrieve a mealworm on 40 consecutive trials.

1   Table 3. Two-choice colour discrimination task results. The birds observed the trained

2   demonstrator Homer lifting the white cup to retrieve a mealworm on 40 consecutive trials.

ID	Sex	Demonstrated colour	Chosen colour (first choice)	Location of chosen colour	Latency to first choice (s)
Dolci	F	White	Black	Left	19
Stuka	F	White	Black	Right	51
Horatio	M	White	White	Left	44
Booster	M	White	Black	Left	20
Lintie	F	White	Black	Right	12
Gizmo	F	White	White	Right	25
Roland	M	White	Black	Left	19

Figure 1

Experiment 1 set up: Stages of the object insertion apparatus.

a) The removable platform at the top of the tube, b) the removable platform at the bottom of the tube, and c) the final stage apparatus (no removable platform). Photo: Rachael Miller.
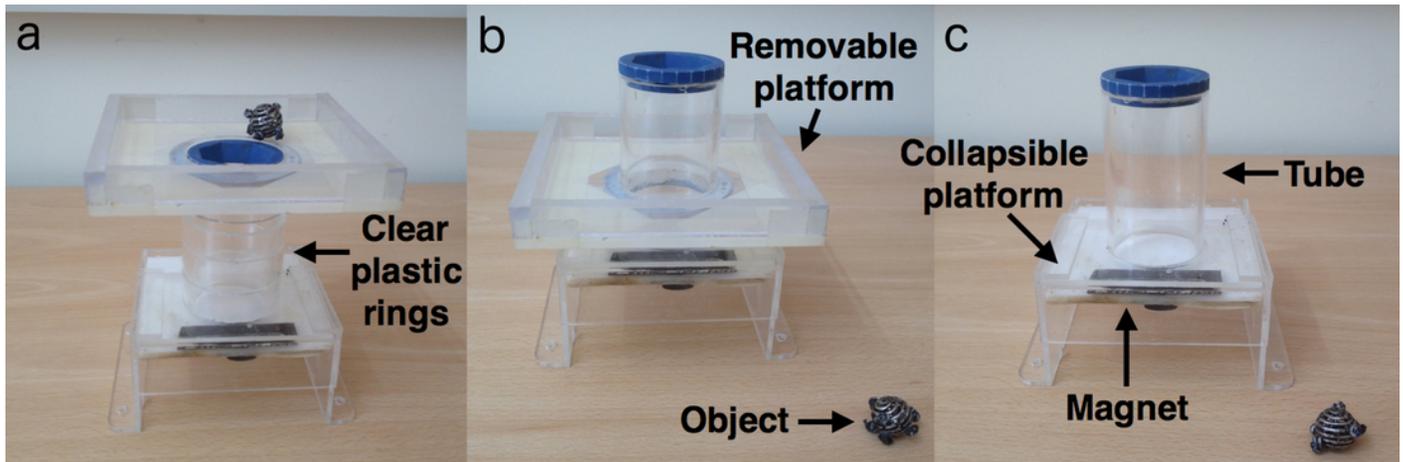
Figure 2

Experiment 2 set up.

Two-choice colour discrimination task where observers only saw a demonstrator find food under the white cup. Photo: Sarah Jelbert.
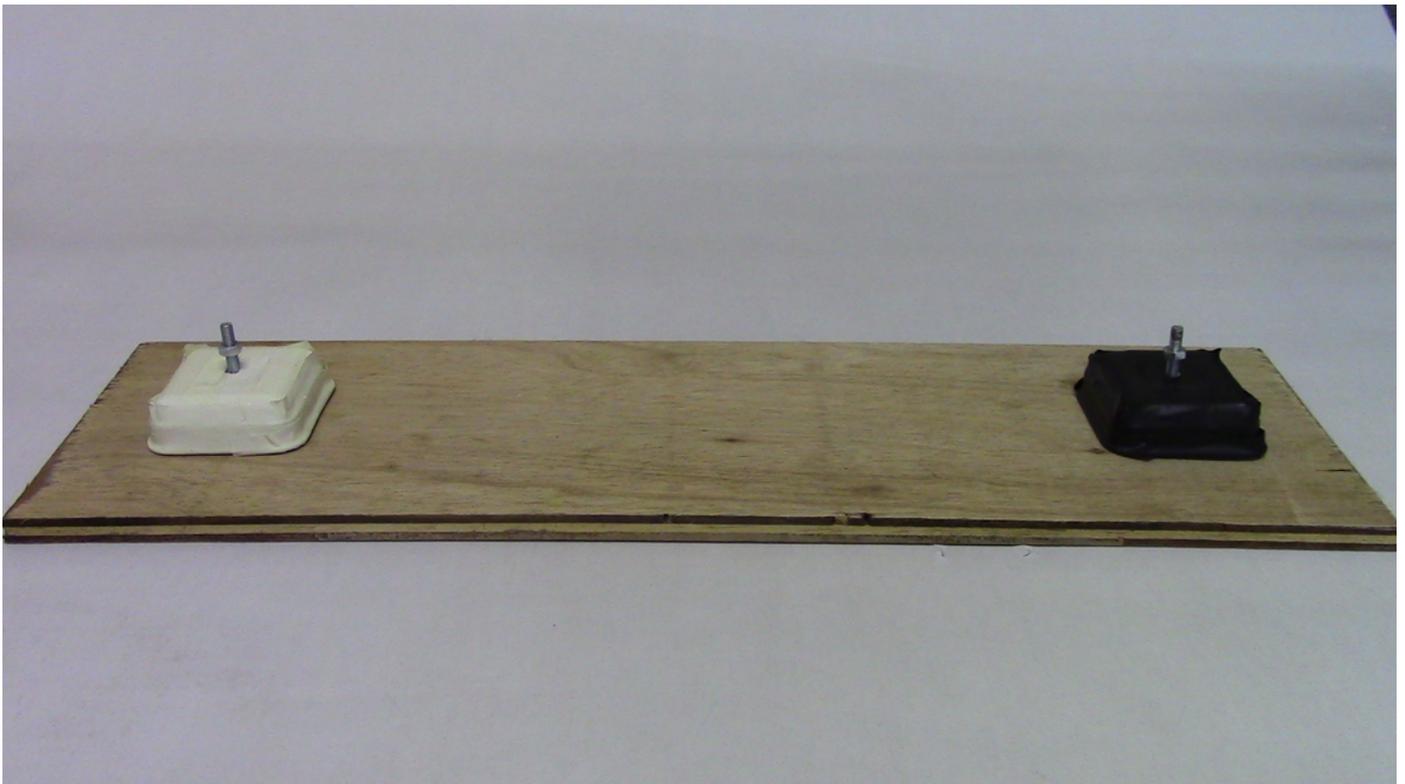
Figure 3

Experiment 1: Object dropping test trials for observer and control groups

Mean latency to first touch of the apparatus or object per trial for Observer (white boxplot) and Control (hatched boxplot) groups.
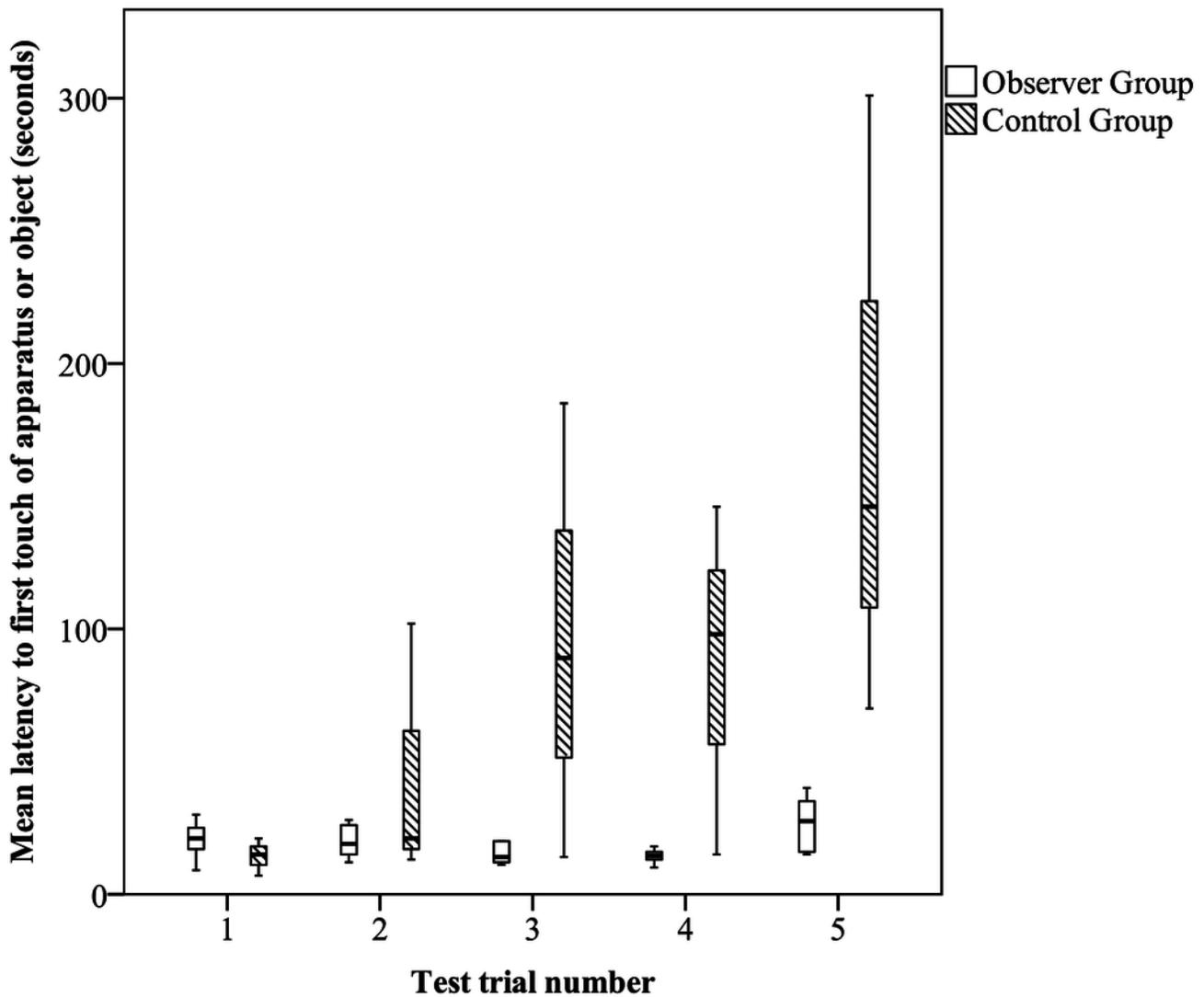
Figure 4

Experiment 1: number of object insertions to solve

Total number of object insertions to solve the object-dropping task per group