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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13 **ABSTRACT**

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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.

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 (*Corvus moneduloides*) reason about hidden causal agents (Taylor,

51   Miller & Gray 2012), reason by exclusion (Jelbert et al. 2015), and learn socially about novel

52   foraging problems (Logan et al. 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 (*Corvus monedula*; de Kort & Clayton, 2006). For example, in the absence

64   of conspecifics for most of the year, there might have been an increased selection pressure to rely

65   solely on personal 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 (Logan et al., 2016). Social species are predicted to be better

75   at acquiring new skills in a social context than in a non-social context (Lefebvre & Giraldeau

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

77   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; California 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 (eight females, eight males)

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

181 a large 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 five sibling groups (one

184 pair, three groups of three birds, and one group of four birds), with one individual that had no

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

186 familiar, as they were fed their daily diet within these compartments and had constant access to

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

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

189 experiment, as she could not reliably be separated individually in the compartments. Subjects

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

191 had access to their daily diet, which consisted of soaked dog pellet and boiled vegetables, and

192 water. Rewards for both experiments were live mealworms, which are a highly valued food item,

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

194 Experiment 2 in November 2015.

195

196 **Animal ethics**

197   These experiments were conducted under approval from University of Cambridge

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

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

200

201   **Video summary**

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

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

204   5 ('Gizmo'); Experiment 2: Observer Group, Test Trial (Gizmo).

205

206   **EXPERIMENT 1: Object dropping task**

207   **Materials**

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

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

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

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

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

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

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

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

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

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

218   5g; Figure 1), with three thin pieces of black plastic string woven through the middle of each

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

220   prevent them from rolling away.

221

Procedure

223   Subjects were separated into three groups: a trained group that had no prior experience with

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

225   experimenter (three males, three females); an observer group that observed a trained conspecific

226   solve the task (three males, three females); and a control group that received no training on the

227   task and did not see any bird interact with the task (two males, one female).

228

Habituation and spontaneous object dropping

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

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

232   with a baited object on the table until they retrieved the reward in five consecutive trials. They

233   were then presented with the object insertion apparatus in the stages outlined in Table 1 and

234   Figure 1. Namely, the apparatus was presented in three scenarios to aid in learning how to

235   correctly solve the apparatus. 1. The removable platform was placed at the top of the tube

236   (Figure 1a) to allow the object to be placed on the rim of the tube so the bird could easily

237   accidentally knock the object into the tube by nudging it when attempting to obtain bait from

238   under the object. 2. The removable platform was placed at the bottom of the tube (Figure 1b) to

239   encourage the bird to pick up the object and lift it up to the top of the tube to insert it. 3. The

240   removable platform was removed (i.e., final stage apparatus; Figure 1c) so the bird had to pick

241   up the object from the table to insert it into the top of the tube. Rewards were placed on the

242   apparatus, as well as underneath it, with the collapsible platform in the dropped position, until

243   subjects retrieved all available rewards per trial in five consecutive trials.

244   All subjects were then given one five min test trial to determine whether they would

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

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

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

248   within the five minutes, therefore they were randomly assigned to one of three groups: trained,

249   observer or control. Birds were allocated to groups by choosing names from a container: one

250   'male only' and one 'female only' container ensured a balanced sex ratio in each group (three

251   males, three females for the trained and observer groups; two males, one female for the control

252   group).

253

254   **Trained group**

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

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

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

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

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

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

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

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

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

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

265   session. A maximum of two training sessions were run per day. An object insertion was

266   considered proficient if it was nudged or dropped directly into the tube, as opposed to being

267   knocked in accidentally by removing the baited insect, or first pushing it around on the platform

268   or dropping it onto the table from the platform.

269   Subjects moved from stage one to stage two when they had accidentally knocked the object

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

271   gradually moved down the tube during stage two until the subject inserted the object from the

272   platform when it was placed at the bottom of the tube on 10 consecutive insertions (Figure 1b). If

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

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

275   a reward for inserting the object). A bird was considered to have solved the task when they had

276   inserted the object from the table into the final stage apparatus and obtained the reward in 10

277   consecutive insertions (Figure 1c).

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

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

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

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

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

283   attempts.

284

285   **Observer group**

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

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

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

289   successful solves per observer bird. Observers were given four demonstration sessions of 10

290   solves per session per stage. The stages were the same as those used for the trained group (Table

291   1; Figure 1). As these stages facilitated the training of the trained group to solve the task, we

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

293   demonstrations of each stage. Each demonstration session lasted approx. three min, with a

294   maximum of two sessions run per day. The demonstrations took place on a table in one

295   compartment, with the observers located in an adjacent, but separate compartment with free

296   visual access between compartments via mesh panels. There were three to four observer birds

297   per adjacent compartment and there were sufficient perches for all observers to view the

298   demonstrations at the same time. The observer group was split into two smaller sub-groups of

299   three birds per group for observations to ensure each bird had sufficient visual access of the

300   demonstrator and to reduce crowding within the test compartments. Each observer subject had

301   the opportunity to watch 16 demonstration sessions, with one or two sessions per day, ensuring

302   that each observer had ample opportunities to observe demonstrations.

303   Immediately after an observer saw 40 demonstrated solutions at a particular stage, observer

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

305   removable platform and with the object on the table). They were then given one five-min test

306   trial to determine whether they had learnt to solve the task. Observer subjects received five five-

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

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

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

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

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

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

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

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

315

316   **Control group**

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

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

319   that the observer group received the apparatus (i.e., five test trials). Test trials were run on the

320   same test days as the observer group to avoid any potential differences between the groups due to

321   age or other environmental factors.

322

323   **Data analysis**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

344   or object per test trial per bird.

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

346   compared with all model combinations and their Akaike weights, which sum to one across the

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

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

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

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

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

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

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

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

355   object insertions required to complete stage three (insert the object from the table into the tube in

356   10 consecutive insertions; response variable) was compared across conditions (trained, observer,

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

358

359   **Results**

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

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

362   drop objects over a period of eight to 21 training sessions (4-11 days). In the observer group,

363   zero of six jays learned to drop objects by observing the demonstrator. In the control group, zero

364   of three jays learned to drop objects without training or demonstrations. Only one bird ('Gizmo'

365   – observer bird), on her final test trial, lifted the object high up while standing near the tube, but

366   she did not insert it into the tube.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

389 while the control group's latencies increased.

390   Following this experiment, all nine jays in the observer and control groups underwent

391 training to drop objects over a period of 8-12 training sessions (five to seven days). Therefore,

392 the number of object insertions required to reach proficiency was compared between the trained,

393 observer, and control groups. Birds in the trained group required more insertions to solve the task

394 (i.e., to insert objects from the table into the tube of the final stage apparatus; mean insertions to

395 solve=167, GLM estimate=0.39, SE=0.06, z=6.26, p<0.001), than observer and control birds.

396 Birds in the observer (mean insertions to solve=114, GLM estimate=0.01, SE=0.07, z=0.20,

397 p=0.84) and control (mean insertions to solve=113, GLM [intercept] estimate=4.72, SE=0.05,

398 z=86.86, p<0.001) groups did not differ in the number of insertions (Figure 4; ESM1 Table S1).

399

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

401 **Materials**

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

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

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

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

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

407

408   **Procedure**

409   **Demonstrator training**

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

411   visual isolation from the observer group, Homer received four sessions (5-10 mins per session)

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

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

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

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

416   on to the demonstrations for observers. Homer touched both cups in session one and two, but

417   passed criterion in session three. He was given four training sessions in total to ensure

418   comparability with the number of demonstrator training sessions used for the carrion crows and

419   ravens in Miller, Schwab & Bugnyar (2016). Homer chose the white cup 100% of the time

420   during demonstrators for observers; therefore observers did not see any incorrect choices.

421

422   **Demonstrations for observers**

423   The observer group consisted of seven birds in order to be comparable with the sample size

424   in Miller and colleagues (2016): four females and three males. These individuals also

425   participated in Experiment 1: three from the trained group, three from the observer group, and

426   one from the control group. In an adjacent compartment with visual access to the observers, the

427   demonstrator lifted the demonstrated cup (white) and obtained the reward in four sessions, with

428   10 trials per session. Both cups were baited and could potentially be lifted, though the

429   demonstrator only lifted the demonstrated cup. The demonstrated cup location (left or right) was

430   counterbalanced across trials. Each observer watched one session per day.

431

432   **Testing observers**

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

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

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

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

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

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

439   this to be using social information from the demonstrator.

440

441   **Data analysis**

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

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

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

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

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

447

448   **Results**

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

450   Two of seven jays (one male, one female) chose the same coloured cup (white) as the

451   demonstrator (i.e., copied the demonstrator), while the other five jays (three females, two males)

452   chose the non-demonstrated coloured cup (black; Table 3). In comparison, Miller, Schwab &

453   Bugnyar (2016) found that eight of eight crows (five females, three males) and eight of eight

454   ravens (three females, five males) copied the conspecific demonstrator, which was significant

455   (Binomial test: p=0.008 for each species). We additionally examined whether there was a

456   difference in the latency to make the first choice between the birds that chose the demonstrated

457   colour versus those that did not. The jays that chose the demonstrated colour did not have shorter

458   latencies to their first choice (Welch two-sample t-test: t=0.88, p=0.47, n=7, 95% confidence

459   interval=-36-57; data in ESM1 Table S1). We also explored whether relatedness influenced

460   likelihood to copy the demonstrator. Zero of two jays that selected the demonstrated coloured

461   cup (Binomial test: p=0.5, n=2) and two of five jays that did not select the demonstrated

462   coloured cup were siblings of the demonstrator bird (Binomial test: p=1.00, n=5). The birds did

463   not appear to show a group side bias because they did not select the cup on the same side

464   regardless of colour (Table 3: Binomial test: p=1.00, n=7).

465

466   **Discussion**

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

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

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

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

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

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

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

474   result in colour choice copying in Experiment 2.

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

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

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

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

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

480   experiment, solving this task required the observer birds to copy several actions of the

481   demonstrator: lifting the object from the table to insert into the tube to drop the collapsible

482   platform and obtain the reward, rather than just knocking an object into the tube from the tube

483   ledge, which is typically stage one of training. In further support of the suggestion that this task

484   is difficult for birds to learn is that only one bird has spontaneously solved the object-dropping

485   task in a previous study (one New Caledonian crow; Mioduszewska, Auersperg & von Bayern,

486   2015), without any demonstrations or training. Additionally, birds, including corvids, typically

487   require a relatively large number of training trials to learn to solve this task, indicating that it is

488   fairly difficult to learn even with explicit training (e.g., 90-275 trials in the present experiment;

489   135-362 trials in great-tailed grackles: Logan, 2016; 76-255 trials in California scrub-jays: Logan

490   et al., 2016 – though note that definitions for reaching proficiency differ between these studies

491   and the current experiment).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

517   movements and reward outcomes.

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

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

520   1994; Range, Bugnyar & Kotrschal, 2008). For example, there is evidence that juvenile Eurasian

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

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

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

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

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

526   Further, the same task used in Experiment 2 was used previously in eight ravens and eight

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

528   While the methods have some limitations (e.g., no counterbalancing of rewarded cup color, using

529   only one demonstrator whose characteristics might have made him less likely for observers to

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

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

532   experiments, including the use of one male, same-age conspecific demonstrator to an observer

533   group and one test trial. Additionally, all birds were hand-reared in species groups in a similar

534   manner, tested by the same experimenter (RM) and similar sample sizes were used (eight ravens,

535   eight crows, seven jays). We also similarly controlled for the influence of spatial location by

536   randomizing the location of the demonstrated cup across subjects, and we found no group-level

537   bias for one location (right/left) over the other (Table 3).

538   There were two notable differences between these experiments. Firstly, the colour

539   discrimination task used different colours: blue and yellow cups in Miller, Schwab & Bugnyar

540   (2016) compared with white and black cups in the present experiment. The justification for this

541 difference was the need to avoid a possible overlap between this experiment and the prior

542 experience of the jays with several different colours in differing reward scenarios during

543 previous studies (e.g., Davidson et al., Under Review). Furthermore, Shaw and colleagues (2015)

544 suggest that colour discrimination tasks should aim to use gray scale cues (e.g., light vs. dark

545 gray) to avoid innate species-level colour preferences. We cannot entirely rule out innate colour

546 preferences, because we did not transfer birds to novel colour combinations. However, innate

547 preferences would likely have been expressed at the species level, which did not occur here

548 because jays randomly chose white and black cups in their first trials.

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

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

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

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

553 2014). To our knowledge, no corvid studies have compared juvenile and adult social information

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

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

556 California scrub-jays: Salwiczek et al., 2009). Specifically, jays reach a full (i.e., stage six

557 Piagetian) understanding of object permanence within their first few months of life (Zucca,

558 Milos & Vallortigara, 2007). As the jays we tested were more than a few months of age, we do

559 not expect their behaviour to differ from adult behaviour with regard to social learning. The

560 finding that the jays behaved differently from the more social carrion crows and ravens in the use

561 of social information in this task is important. It raises the question of whether these more social

562 species - as with the more social rook (Bird & Emery, 2009b) and New Caledonian crow

563 (Mioduszewska, Auersperg & von Bayern, 2015) - might be able to learn to copy the

564 demonstrator in the object-dropping task (Experiment 1).

565 Previous experiments have indicated that Eurasian jays do attend to social context in caching

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

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

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

569 previous experiments required the birds to copy a demonstrator. Jays may also be more likely to

570 pay attention to and copy different demonstrators, such as an older, more affiliated or related

571 individuals, as model identity has been found to influence social learning in other corvids

572 (ravens, jackdaws: Schwab, Bugnyar & Kotrschal 2008a; Schwab et al., 2008b). For example,

573 presence of siblings enhances social learning in ravens (Schwab et al., 2008b). Our demonstrator

574 was a sibling of some of the observers, which suggests that there was no influence of relatedness

575 to demonstrator on likelihood of copying in Experiment 2. However, our experiment was not

576 designed to test the relationship between relatedness and social learning and we do not have the

577 statistical power to make a firm conclusion on this point.

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

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

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

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

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

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

584 <5% of occasions, and information use was dependent on phenotypic constraints such as network

585 position and dominance status (Carter, Tico & Cowlishaw, 2016). The results of Experiments 1

586 and 2 demonstrated that Eurasian jays did not appear to apply or exploit the social information

587 available even though they had the opportunity to acquire it. Although we reiterate that social

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

589 Experiment 1.

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

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

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

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

594 previous studies with social corvids, the birds had been explicitly tested for influences of social

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

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

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

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

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

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

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

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

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

604 experiment may indicate that Eurasian jays secondarily lost the ability to copy social information

605 provided by a conspecific, at least in some contexts, while maintaining the ability to attend to the

606 general movements of others, due to lack of selection pressure from an asocial environment.

607 However, more comparisons between social and relatively asocial corvids are needed to confirm

608 this hypothesis.

609

Data Availability

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

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

613

Acknowledgements

615   We thank Elsa Loissel and Natalie Williams for their help in the early stages of preparing for

616   Experiment 1 and discussion. Thank you to Maggie Dinsdale, Sam Melvin, Sarah Manley, Ivan

617   Vakrilov for animal care, to Ian Millar for help in apparatus construction, and to Mark Ghobain

618   for assistance in hand-rearing the Eurasian jays.

619

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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.
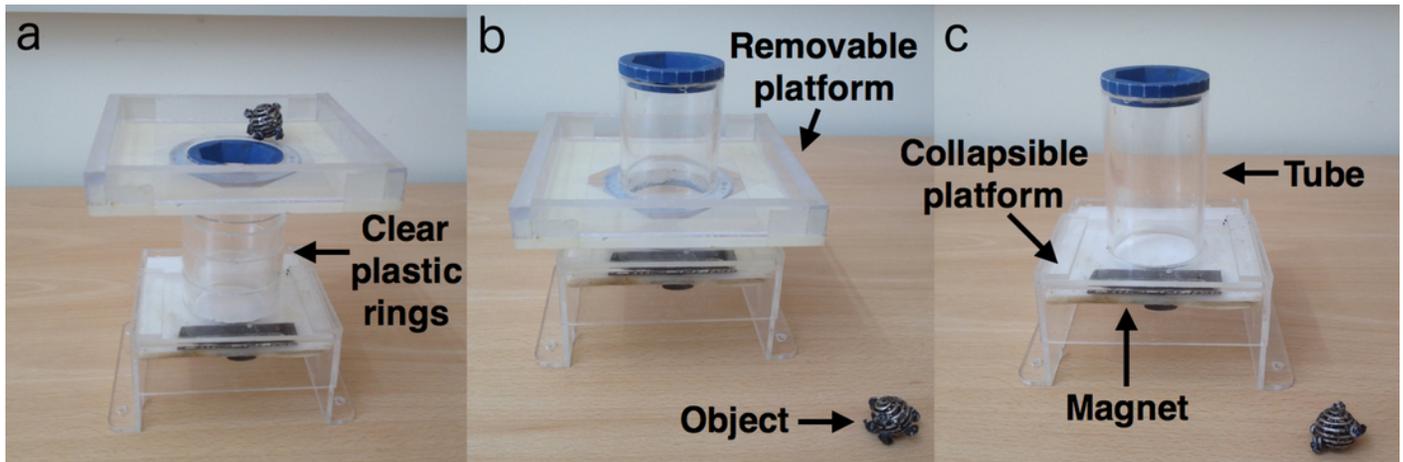
Figure 2

Experiment 2 set up.

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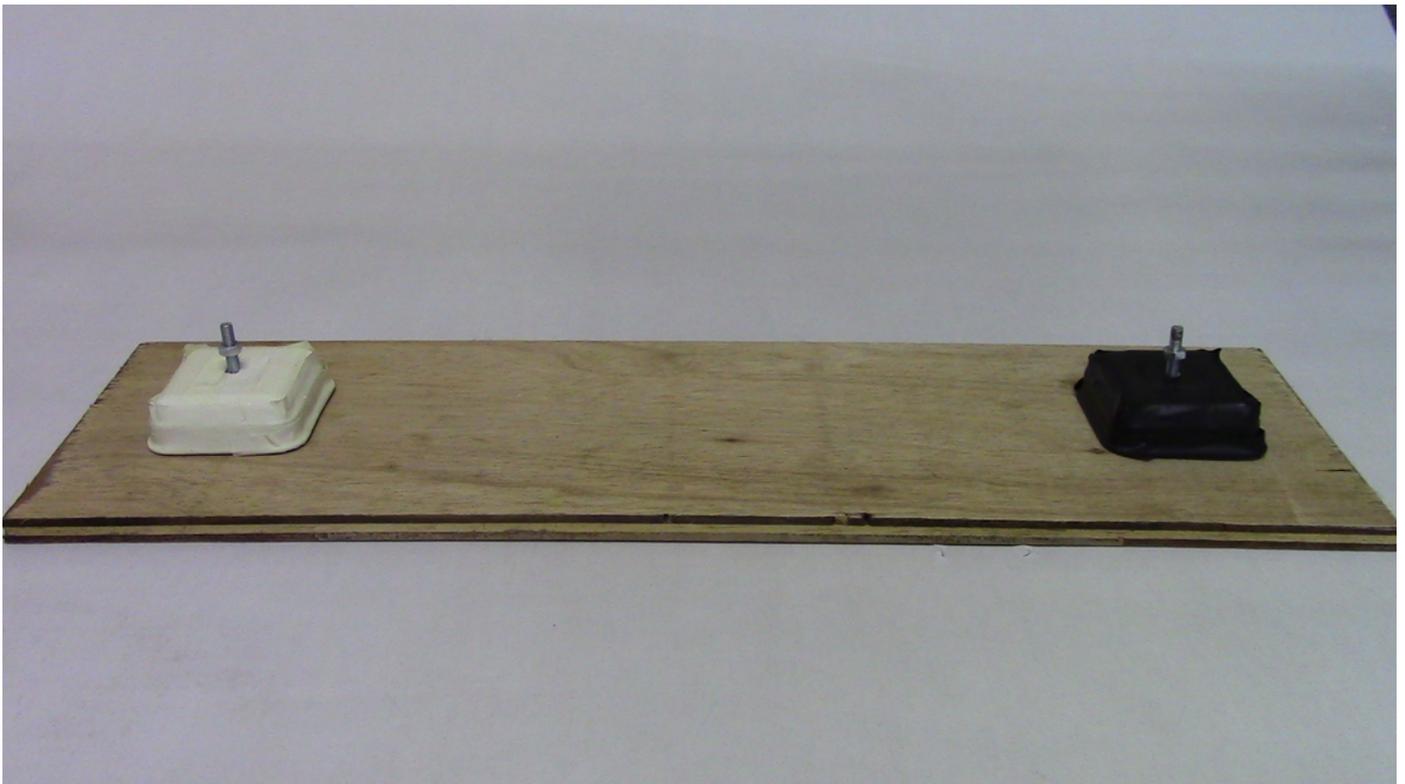
Figure 3

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.
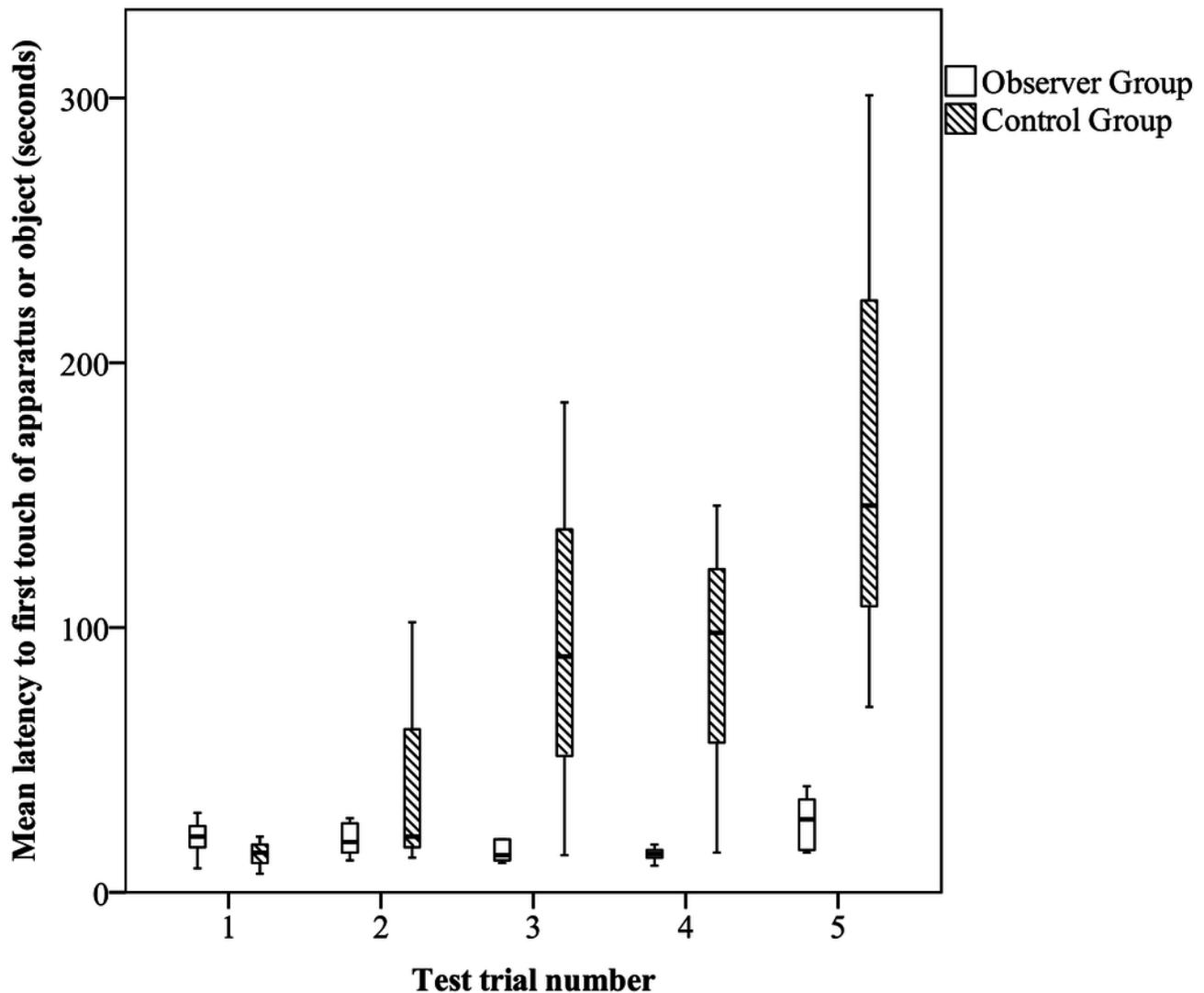
Figure 4

Experiment 1: number of object insertions to solve

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