Squirrel monkey responses to information from social demonstration and individual exploration using touchscreen and object choice tasks

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Abstract

We aimed to study whether a non-human primate species responded differently to information acquired socially compared with that acquired individually. To do so, we attempted to train squirrel monkeys to perform binary discriminations. These involved exposure to either social information (human or puppet demonstrator performs an initial "information trial") or individual exploration (monkey performs information trial as well as subsequent test trials). In Experiment 1 we presented the task on a touchscreen tablet. Only one monkey appeared to learn the significance of the information trial, and across the group there was no improvement in performance over sessions. The proficient individual showed little evidence of successful transfer to three-way discrimination problems, suggesting limited representation of the task structure. In Experiment 2 we used a logically identical task, presented as a physical object choice (inverted cups concealing a food reward). No monkeys learned to use the information trial cues, and success again did not increase over sessions. We concluded that the monkeys' poor performance in Experiment 1 was not attributable to the mode of presentation (touchscreen), but reflected real difficulties with mastering the task structure. For both experiments, we analysed the monkeys' spontaneous responses to the different trial types (social-win, social-lose, individual-win, and individual-lose). We found that monkeys had a tendency to repeat selections made during the information trial, whether these were made by themselves or by a demonstrator. This tendency to repeat was observed even following lose trials (i.e. when incorrect). Apparent "success" following win trials was probably largely an artefact of behavioural inertia (individual learning conditions) and stimulus enhancement (social learning conditions), rather than sensitivity to the reward cues associated with that stimulus. Although monkeys did respond

39   somewhat differently (more repeats) following win trials, compared with lose trials, this was no

40   more apparent in the object choice task than the touchscreen task, again suggesting that the less

41   ecologically valid presentation medium did not actively disrupt potential for learning the

42   discrimination rule. Both touchscreen and physical object choice tasks appear to be valid

43   methods to study learning in squirrel monkeys, with neither method giving a clear performance

44   advantage over the other. However, this population did not master the contingencies in these

45   tasks.

46 **Introduction**

48 Some explanations of the differences between human culture and the behavioural traditions of

49 other species have suggested that humans are particularly attentive to social information, or even

50 that humans possess specialised cognitive mechanisms for acquiring information from social

51 sources (e.g. Csibra & Gergely, 2011; Dean et al., 2012; Tennie, Call, & Tomasello, 2009;

52 Tomasello, Kruger, & Ratner, 1993). However, it remains difficult to directly compare the

53 effects of exposure to information from a social source with information obtained from one's

54 own experience, since these typically cannot be regarded as equivalent.

56 Whenever information is potentially generalisable, the inference drawn from observation of

57 another's activity is liable to be very different to that drawn from one's own naïve exploration,

58 even when the action itself is identical. For example, consider being faced with a combination

59 lock on a door, for which you do not know the code. Tapping in a random code yourself

60 (unsuccessfully) will likely lead you to conclude that the code is incorrect. However, observing

61 someone else tapping in a code unsuccessfully might lead you to an entirely different conclusion,

62 or at least to entertain a number of alternative possibilities, many of which would likely entail the

63 information contained within the other's actions having some potential value, despite the

64 unsuccessful outcome. For example, you might conclude that the actor knew the code, but

65 entered one or more digits incorrectly. Alternatively, the code could have been entered correctly

66 but the mechanism was broken, or the actor simply failed to use sufficient force in turning the

67 lock.

68

69   The non-equivalence of information acquired from observation of others, compared with

70   personal experience, arises as a consequence of differential knowledge of the prior behavioural

71   history of the actors in question (complete for ourselves, but usually very limited for others). As

72   a result, in many situations learners would be expected to respond differently to information

73   acquired socially compared with that acquired from individual exploration. Such differential

74   responding would be predicted from either reasoning-based or associative learning accounts,

75   even if the fundamental mechanisms underlying that learning were assumed to be the same.

76

77   Theories that propose specialised mechanisms for processing social information in humans

78   would likely predict that humans and non-human primates (NHPs) treat social information

79   somehow differently (Csibra & Gergely, 2011; Dean et al., 2012; Tennie et al., 2009; Tomasello

80   et al., 1993). However, it is unclear how this difference might manifest in terms of relative

81   responsiveness to information obtained from a social source versus information acquired through

82   one's own personal experience. One possibility is that humans would be more likely (compared

83   with NHPs) to repeat behaviours they had seen others perform, even when the behaviours had

84   not appeared to produce any reward, in a manner that would not occur under individual learning

85   conditions (i.e. following their own performance of an unreinforced response). The tendency of

86   humans to "overimitate" others' irrelevant actions in causal sequences has been well documented

87   (Horner & Whiten, 2005; Lyons, Young, & Keil, 2007; Whiten et al., 2016). However, we do not

88   yet know the extent to which humans or NHPs "overimitate" their own unreinforced actions in

89   individual learning conditions; therefore, this first possibility is yet to be empirically assessed.

90   Alternatively, human use of social information might be relatively proficient compared with use

91   of information from direct personal experience, e.g., showing little reduction in learning fidelity,

92   or possibly even equivalent performance, in relation to the likelihood of repetition of reinforced,

93   over unreinforced, responses. This would be expected to be relative to any such pattern observed

94   in the social and individual learning of NHPs, for whom reduced sensitivity would be predicted

95   for vicarious feedback compared with directly experienced reinforcement contingencies.

96

97   Thus, it is problematic to evaluate the claim of specialised mechanisms for processing social

98   information in humans based on existing knowledge of the behaviour of either humans or their

99   closest extant evolutionary relatives. This research aims to contribute to the knowledge base

100   upon which such claims could be evaluated. In the studies reported here we attempted to train

101   squirrel monkeys (*Saimiri sciureus*), a platyrrhine monkey, to learn a discrimination rule using

102   information from either a social demonstration or direct personal experience, with a view to

103   better understanding how these primates respond to information depending on source. In this task

104   the information provided is purely episodic, relating only to that particular problem, and with

105   perfect predictive value. And since the information value of "successful" and "unsuccessful"

106   trials is exactly equivalent across both the social and individual learning conditions, then in

107   principle the performance of any subjects achieving mastery of the task contingencies can be

108   used to evaluate whether source alone affects responses to (otherwise directly comparable)

109   information. We aimed to train monkeys to a pre-set performance criterion which would indicate

110   that they had learned the predictive value of the information available (whether from a social

111   demonstration or their own experience) and could use this to find a rewarded stimulus on

112   subsequent trials involving the same set of stimuli. As well as allowing us to compare the

113   response patterns of those exposed to social information versus personal experience for

114   individuals who reach criterion (i.e. episodic information use), this would also allow us to

115   compare rates of learning between monkeys assigned to a social learning condition and those

116   assigned to an individual learning condition (i.e. achievement of generalisable task competence).

117

118   In this task, information trials could consist of selection of either the rewarded or the unrewarded

119   stimulus. Because the task involves binary discriminations, the information received about a

120   response indicates that it should be either repeated (rewarded stimulus selected, or "win" trial) or

121   avoided (unrewarded stimulus selected, or "lose" trial). Successful performance therefore would

122   encompass both reliable re-selection of rewarded stimuli *and* reliable avoidance of unrewarded

123   stimuli. Within the context of a binary discrimination task, the two information trial types

124   (rewarded and unrewarded) both provide unambiguous information about the location of the

125   reward, and are therefore (in principle) equally informative, assuming the discrimination rule has

126   been learned. We hoped that this format would allow us to examine whether error rates were

127   different following rewarded and unrewarded information trials, and if so, whether this pattern

128   differed between subjects exposed to social information and those learning from their own

129   experience.

130

131   Discrimination learning tasks such as the one we used here have been widely employed in

132   studies of animal learning and developmental psychology. These studies have provided evidence

133   of the formation of "learning sets" in children and NHPs (e.g. Harlow, 1949; Levinson & Reese,

134   1967). However, most have involved learning either only from personal experience, with

135   information trial and test trial both completed by the participant (e.g. Berman, 1971; Berman,

136   Rane, & Bahow, 1970, with children), or only from social information, with vicarious

137   observation of the information trial (e.g. Templeton, 1998, with starlings; n.b., we use

138   "vicarious" throughout to refer to any kind of indirect exposure occurring as a consequence of

139   events that are neither generated, nor directly experienced, by the learner). We know of only one

140   case where similar paradigms have been used to compare performance following exposure to

141   social information with that following individual exploration (Monfardini et al., 2012, with

142   macaques and adult humans). The research questions of Monfardini and colleagues (2012) were

143   rather different from our own, examining how well information was used under significant

144   memory load, with information and test trials separated by several intervening trials.

145   Nonetheless, they found that rewarded and unrewarded trials had differing effects on

146   performance depending on whether they were performed by the subjects themselves or by

147   another monkey. In the individual learning condition, monkeys performed well following a

148   rewarded trial and poorly following an unrewarded trial; but in the social learning condition, the

149   outcome of the information trial did not differentially affect performance.

150

151   We first report our attempt to train squirrel monkeys on a touchscreen version of the task

152   (Experiment 1). Touchscreen tasks have proven useful in making cognition questions feasible to

153   explore in zoo settings (Egelkamp & Ross, 2019), as touching a screen is a fairly straightforward

154   behaviour to train some animals to do. Such tasks have the additional benefit of allowing

155   researchers to escape the "one-off" nature of object-based tasks (Renner, 2015) and expose an

156   individual to multiple trials, which minimises the effects of outlier days or events and enables

157   repeated measurement of a phenomenon. Squirrel monkeys have been shown to master use of a

158   touchscreen in an experimental setting (Kangas & Bergman, 2012), though our specific

159   population of monkeys had limited experience of interaction with touchscreens. In Experiment 1,

160   the squirrel monkeys' success rates were very low, and showed little evidence of improvement

161   over time. To examine whether this was due to the presentation format, we also attempted to

162   train this population using a three-dimensional object-choice version of the task (Experiment 2).

163   The limited success of the squirrel monkeys (on both tasks) meant that we were unable to fully

164   address our original aims of comparing the relative efficacy of social and individual learning and

165   comparing error rates for information trial types. Nevertheless, here we document the monkeys'

166   performance on both tasks. This includes comparisons of the monkeys' performance depending

167   on whether they received information from social demonstrations or their own experience, and of

168   how responses differed following rewarded versus unrewarded information trials. We also

169   compare performance across the two presentation mediums.

170

171   **Experiment 1: Touchscreen**

172

173   **Materials and Methods**

174

175   *Participants*

176   Approval for this project was provided by the Living Links to Human Evolution Research Centre

177   at RZSS Edinburgh Zoo. At the commencement of this research, a total of 30 squirrel monkeys

178   were housed at the Living Links to Human Evolution Research Centre at Edinburgh Zoo, in two

179   social groups, East and West (MacDonald & Whiten, 2011). Monkeys had previously been

180   trained with positive reinforcement to enter the research area and allow themselves to be

181   temporarily separated (for a maximum of 15 minutes) from their social group. Research

182   participation was voluntary. The research area for each group consisted of eight cubicles that

183   could be separated from one another via the use of sliding doors. When separated, monkeys were

184   allowed to rejoin their social group after indicating a desire to do so by making manual contact

185   with the sliding door. Characteristics of monkeys that participated in this study are presented in

186   Table 1. A total of 13 monkeys (8 from the East group and 5 from the West group) passed the

187   touchscreen-training phase of this study (described below). A further 8 monkeys participated in

188   touchscreen training but did not pass the training phase, and 9 monkeys never participated in

189   touchscreen training.

190

191   *Ethics statement*

192   Ethical approval was granted by the University of Stirling Psychology Ethics Committee.

193   Animals were not food or water deprived. The research was conducted in line with the guidance

194   provided by the Association for the Study of Animal Behaviour (2015) in *Guidelines for the*

195   *Treatment of Animals in Behavioural Research and Teaching*, and The British Psychological

196   Society (2012) in *Guidelines for Psychologists Working with Animals*.

197

198   *Apparatus*

199   A Microsoft Surface 4 touch-sensitive capacitive tablet computer was used to present the training

200   and experimental tasks to the monkeys. The tablet was attached to a rolling projector stand via a

201   metal frame and a mobile arm (Ergotron, Minnesota, USA). The custom program for displaying

202   the task was written in PsychoPy (Peirce et al., 2019). A digital video camera was used to record

203   video of experimental sessions.

204

205   *Training procedures*

206   Prior to beginning the experiment, monkeys were trained via shaping (Pryor, 2002) to make

207   manual contact with the tablet or the metal frame bordering the touch-sensitive surface of the

208   tablet. Once they reliably did so, they were trained to touch the active area of the screen; next, to

209   touch a large stimulus (approximately 11 cm in diameter) presented on the screen; and finally, to

210   touch a smaller stimulus (approximately 5.5 cm in diameter) presented on the screen. When

211   monkeys correctly touched the screen or a stimulus at each respective training level, a visual

212   reward cue appeared, an auditory click sound was played by the tablet, and the monkey was

213   rewarded by the experimenter with a raisin. The visual reward cue for correctly touching training

214   stimuli was a "sunburst" image (see Figure 1B).

215

216   At each of the training levels in which monkeys touched stimuli, they were required to make

217   contact with the relevant part of the screen on 8 or more out of the 10 trials presented in a session

218   and within 30 seconds of the beginning of each trial, and to do this for three consecutive research

219   sessions in order to move on to the next level. To progress to the testing phase, monkeys

220   completed a minimum of eight training sessions with the touchscreen. One monkey progressed to

221   the testing phase after eight training sessions; ten progressed to testing after nine training

222   sessions; two progressed to testing after ten training sessions; and all others engaged in

223   touchscreen training fewer than nine times and therefore never completed training.

224

225   *Testing procedures*

226   Once monkeys passed the final touchscreen-training level, they were presented with the

227   experimental task, which consisted of two stages, A and B. Task stimuli consisted of a variety of

228   shapes (circles, triangles, diamonds, pentagons, and hexagons) of various colours (blue, yellow,

229   black, white, and grey), taking into consideration the limited range of colours platyrrhine

230   monkeys are likely to be able to discriminate (Waitt & Buchanan-Smith, 2006). Stimulus fill

231   colour, outline colour, and number of sides, as well as background colour, were randomly

232   generated by the task program. For all trials in Stage A, paired stimuli (one on the left, one on the

233   right) were presented; for all trials in Stage B, three stimuli were presented in a horizontal row on

234   the screen. See Figure 1 for an example.

235

236   Stage A. Experimental sessions consisted of a sequence of four problems. Each problem was

237   presented for five trials: a single initial "information trial" (T1) and four subsequent test trials

238   (T2-T5) (see Supplemental Table S1 for details). Although the first test trial (T2), which

239   immediately followed the information trial, was the critical trial from the perspective of the

240   analysis, additional trials were included for every problem as a means to reinforce the monkeys'

241   learning of the overall task structure. Specifically, this was intended to help the monkeys learn

242   that for any given pair of stimuli, only one was rewarded (and the other unrewarded), and that

243   the identity and location of the rewarded stimulus always remained the same within a problem,

244   such that feedback from a selection made on one trial had perfect predictive value regarding

245   reward status for all subsequent trials involving the same pair of stimuli. Stimuli did not change

246   position between trials within a problem.

247

248   Initial selections were randomly assigned to be either rewarded or unrewarded. That is, we

249   programmed the task to generate a list such as [U R U R], meaning that the stimulus selected on

250   the information trial of the first problem was unrewarded (regardless of which position on the

251   screen the stimulus occupied), and that the alternative stimulus would then be the rewarded

252   stimulus. The stimulus selected on the information trial of the second problem was then the

253   rewarded stimulus (regardless of its position), and so on. We programmed the task to ensure that

254   half of information trials were rewarded and half were unrewarded. This was to help prevent

255   monkeys from developing side biases. For example, if a monkey always selected the stimulus on

256   the left in information trials, the left-side stimulus would be the rewarded stimulus only half of

257   the time.

258

259   When a rewarded stimulus was selected, both stimuli disappeared, a sunburst visual reward cue

260   appeared where the rewarded stimulus had been, and an auditory click was generated by the

261   computer. Additionally, when a monkey selected a rewarded stimulus on any trial, they received

262   a raisin. When an unrewarded stimulus was selected, all stimuli disappeared for a time-out of 3

263   seconds, no auditory cue was emitted, and no raisin was dispensed. The same stimulus, in the

264   same location on the screen, was the rewarded stimulus for an entire problem (i.e. one

265   information trial followed by four test trials using the same pair of stimuli).

266

267   Half of the monkeys were assigned to the individual condition, and the other half were assigned

268   to the social condition. In the individual condition, at the beginning of a session, the tablet was

269   placed within a monkey's reaching distance from the cubicle by use of a mobile trolley. Then

270   monkeys themselves selected one of the stimuli in the information trial, and were rewarded (or

271   not) accordingly. They were then allowed to select one of the stimuli on each of the four

272   subsequent test trials. Between problems, the tablet was moved outside of reaching distance for

273   several seconds before again being placed within reaching distance for the next problem.

274

275 In the social condition, at the beginning of a session, the tablet was placed outside of a monkey's

276 reaching distance from the cubicle. Monkeys saw a social demonstrator select one of the stimuli

277 in the information trial. The tablet was then placed in reaching distance to allow the monkey to

278 perform the next four test trials. After this, the tablet was moved outside of reaching distance to

279 prepare for the start of the next problem.

280

281 In half of the research sessions, the social demonstrator was the human experimenter, and in the

282 other half, this was a puppet (a plush squirrel monkey toy with some of the stuffing removed;

283 Wild Republic, Twinsburg, Ohio) operated by the experimenter (Figure 2). Researchers have

284 successfully used a puppet demonstrator in a study with children (Wood, Kendal, & Flynn,

285 2013), a stuffed conspecific demonstrator in a study with birds (Truskanov & Lotem, 2017), and

286 videos of a human dressed in an ape-like costume in a study with great apes (Krupenye et al.,

287 2016). Because of the previously successful implementation of these methods, we explored

288 whether a puppet demonstrator would induce better performance than a traditional human

289 demonstrator on this task. Previous research also found that a "monkey-like" human

290 demonstrator, who did not solicit monkeys' attention and consumed rewards after rewarded

291 trials, resulted in better subsequent performance than a traditional human demonstrator who

292 solicited monkeys' attention and did not consume rewards (Monfardini, Hadj-Bouziane, &

293 Meunier, 2014). However, due to the potential for distraction, neither the experimenter nor the

294 puppet received a food reward after selecting the rewarded stimulus on T1.

295

296 We were initially interested in whether monkeys would successfully transfer from Stage A (two

297 stimuli) to Stage B (three stimuli). Therefore, we established a performance criterion for

298   advancing from Stage A to Stage B. Criterion was set as correct performance on the second trials

299   (T2s) on three of the four problems (75%) in a session, in addition to correct performance on T3

300   through T5 of 75% or more in a session, for three sessions in a row.

301

302   Stage B. Monkeys that passed criterion (as detailed above) on Stage A commenced Stage B.

303   Testing procedures for Stage B were identical to Stage A with the exception that each problem

304   involved three stimuli, and therefore *two* of these were unrewarded (and only one rewarded, as

305   per Stage A). Otherwise, testing was structured as in Stage A (i.e. four problems per session, five

306   trials per problem, and consistent reward location for all trials of a given problem).

307

308   During the data collection period (May to November 2016), up to two research sessions were

309   conducted per day. All 13 participating monkeys completed at least 10 testing sessions of Stage

310   A (see Table 1), with the minimum number of sessions being 14 and the maximum being 69.

311

312   *Statistical analysis*

313   Statistical analysis was done via logit fit GLMMs using the *lme4* package (Bates et al., 2015) in

314   R (R Core Team, 2017). The following fixed effects were included in at least some of the

315   models: session number (scaled and centred), which was used to determine whether monkeys'

316   performance improved with experience; trial number; the source of information (human, puppet,

317   or individual); and the type of information (whether the information trial was a win or a lose;

318   sum coded). Random effects included in at least some of the models were monkey identity

319   (random intercept effect) and session number and information type by monkey (random slope

320   effects); we used models with "maximal" random effects structures (Barr et al., 2013) in the first

321   instance, removing random slopes followed by random intercepts as necessary to address issues

322   of singular fit or non-convergence. Post hoc analyses were done using the *emmeans* package

323   (Lenth et al., 2019).

324

325   We used three main response variables: (1) trial *success* indicates whether the correct stimulus

326   was selected on a given trial (binary: 1 = yes; 0 = no); (2) *WSLS* (win-stay, lose-shift) indicates

327   which strategy was used on a particular trial in relation to the information trial (binary: 1 = win-

328   stay or lose-shift; 0 = win-shift or lose-stay); and (3) *repeats* indicates whether the same stimulus

329   was selected on a given trial as was selected in the information trial (binary: 1 = repeated; 0 = not

330   repeated). For Stage A (two stimuli), success and WSLS have the same values. However, for

331   Stage B, these variables may hold different values (i.e. it is possible that, after a lose information

332   trial, a subject can shift and select a second unrewarded stimulus, in which case their success

333   score would be 0 and their WSLS score would be 1).

334

335   **Results**

336

337   Although we had hoped to compare the effectiveness of learning from social demonstrations

338   with that of learning from personal experience, in fact only one monkey reached our

339   performance criterion. Aside from the single individual who reached criterion, there was little

340   evidence that the monkeys were learning anything from their increasing experience with the task.

341   Taking correct stimulus choice (success) on T2 as the measure of interest (i.e. re-selection of

342   stimuli that were rewarded in the information trial, and avoidance of stimuli that were

343   unrewarded), overall performance on T2 of the two-stimulus task (Stage A) was slightly greater

344   than chance, with 56% T2 success (Table 2; observed success: 1283/2293 trials; expected:

345   1146.5/2293, $p < 0.001$ in a binomial test). Results of the various models are summarised in

346   Table 3.

347

348   *Effect of experience (session number)*

349   A GLMM with a response variable of T2 success, a fixed effect of session number (scaled and

350   centred), and a random effect of monkey identity showed that performance accuracy did not

351   improve with increasing session number ($b = 0.017$, SE $= 0.024$, Z $= 0.72$, $p = 0.47$). That is,

352   monkeys overall did not improve their task performance with more experience.

353

354   *Information type, information source, and interactions*

355   Although the monkeys had not learned the task, it was nonetheless of interest to know how they

356   performed across the different trial types (i.e. individual-win, individual-lose, social-win, and

357   social-lose, with social demonstrations also broken down into human and puppet

358   demonstrations).

359

360   To explore this, we built a GLMM with T2 success as the response variable; information type,

361   information source, and an interaction of these two variables as fixed effects; a random intercept

362   effect of monkey identity; and session number as a by-monkey random slope effect. We used

363   Helmert contrasts (in the *stats* package in R [R Core Team, 2017]) to examine whether

364   performance differed between the three information sources. In Helmert contrasts, the first two

365   levels of a variable are compared to each other, the third level is compared to the mean of the

366   first two levels, and so on (Fox, 2002; Schad et al., 2018). The key comparisons here are (1)

367   between the two social or vicarious sources of information (human and puppet demonstrations)

368   and (2) between the social and individual sources of information. Therefore, we set the first level

369   as human demonstration, for comparison to the second level, puppet demonstration; and finally,

370   the combined human and puppet levels were compared to the third level, the individual

371   condition. There was a main effect of information type; success after seeing a win trial (68%

372   success) was significantly higher than that after seeing a lose trial (44% success; $b = 0.44$, SE =

373   0.046, $Z = 9.6$, $p < 0.001$). In addition, success after seeing a puppet demonstration (54%) was

374   significantly lower than that after seeing a human demonstration (60%; $b = -0.13$, SE = 0.063, Z

375   $= -2.0$, $p = 0.043$). There was not a significant difference between the combined social

376   conditions (puppet and human) and the individual condition (55% T2 success; $b = -0.020$, SE =

377   0.040, $Z = -0.52$, $p = 0.61$). However, there was an interaction between information type and

378   source, indicating a difference between the third level of the source variable (individual

379   condition) and the other two levels ($b = 0.090$, SE = 0.029, $Z = 3.1$, $p = 0.002$). To clarify this

380   interaction, we performed a post hoc analysis using *emmeans*. This indicated that the

381   disadvantage in performance after lose demonstration trials was greater in the individual

382   condition (after a lose, 40% success; after a win, 70% success) than in the two social conditions

383   (after a lose, 49% success; after a win, 66% success; Supplemental Table S2).

384

385   *Repeating previous selections*

386   While T2 success was the main variable of interest, we noted that the pattern of responses

387   possibly indicated a "stay" bias (that is, a tendency to repeat the selection from the previous trial,

388   regardless of whether this followed a win or lose information trial). This raised the possibility

389   that the monkeys were influenced only minimally, if at all, by the presence or otherwise of the

390   reward cue during the information trial. That is, they may not have been discriminating between

391   win and lose trials at all. In the individual condition the monkeys may have simply had a

392   tendency to repeat their own previous selections, regardless of any feedback obtained. And in the

393   social condition they could have been subject to fairly nonspecific stimulus enhancement effects

394   which drew their attention to previously selected stimuli, again irrespective of whether this had

395   been associated with the reward cue. This would suggest that the monkeys were not using the

396   information trial as "information" at all, if the outcome of the trial did not influence their choice

397   of stimulus.

398

399   Therefore, we analysed another response variable, T2 repeats. This binary variable captured

400   whether, on a given T2, a subject repeated the response (either their own or observed) from the

401   information trial, which was coded as 1, or switched responses, which was coded as 0. We used a

402   GLMM with T2 repeats as the response variable; information type, information source, and an

403   interaction of these two variables as fixed effects; a random intercept effect of monkey identity;

404   and session number as a by-monkey random slope effect. We again used Helmert contrasts to

405   examine the effect of information source. Human demonstration was the first level, puppet

406   demonstration was the second level, and the individual condition was the third level. There was a

407   main effect of information type; tendency to repeat after a win trial (68% repeats) was higher

408   than tendency to repeat after a lose trial (56% repeats; $b = 0.28$, SE $= 0.047$, Z $= 6.0$, $p < 0.001$).

409   (But note that the proportion of repeats following both information trial types is above 50%

410   [Figure 3].) This indicates a degree of sensitivity to the information in T1, even if the difference

411   is modest. There was no main effect of source, indicating that there were not significant

412   differences in the tendency to repeat between puppet and human demonstrations ($b = -0.065$, SE

413    $= 0.063$, $Z = -1.0$, $p = 0.31$) or between vicarious and individual selection of a stimulus ($b =$

414   0.11, $SE = 0.065$, $Z = 1.6$, $p = 0.10$). The interaction between the information type and the

415   individual vs social conditions was not significant ($b = -0.028$, $SE = 0.029$, $Z = -0.95$, $p = 0.34$).

416   The interaction between information type and social demonstration type (puppet and human) was

417   non-significant but near the alpha criterion threshold ($b = -0.12$, $SE = 0.063$, $Z = -1.9$, $p =$

418   0.056). Further analysis of this trend indicates that the tendency to repeat the puppet's selection

419   (after a win, 62% repeats; after a lose, 53% repeats) was less influenced by information type than

420   the tendency to repeat the human's selection (after a win, 70% repeats; after a lose, 50% repeats).

421

422   *Improvement across trials*

423   Because the monkeys appeared not to learn the discrimination rule, and showed a significant

424   tendency to repeat selections from the information trial following both win and lose trials, this

425   raised the question of whether the monkeys were sensitive to task feedback at all. We therefore

426   wished to test whether the additional feedback obtained from the monkeys' selections across all

427   trials for any given problem improved their chance of success (since all information trials were

428   followed by not only the critical test trial T2, but also three further trials using the same

429   problem—T3, T4, and T5—intended to reinforce recognition of the predictive relationship

430   between successive trials using the same pair of stimuli). To determine whether monkeys

431   improved their performance across trials within a problem (as they presumably received

432   confirmatory information about where the rewarded stimulus was or was not), we used a GLMM

433   with success in each trial from T2 to T5 as the response variable; trial number as the fixed effect;

434   a random intercept effect of monkey identity; and session number, information type, and their

435   interaction as by-monkey random slope effects. A non-significant trend towards improvement

436   across trials was demonstrated (Figure 4; $b = 0.036$, SE $= 0.019$, $Z = 1.9$, $p = 0.064$). It is

437   therefore not possible to conclude that monkeys located the reward more accurately in later than

438   in earlier trials.

439

440   *Three-stimulus task (Stage B)*

441   A single monkey (Amarilla) met criterion on the two-stimulus task and was tested on the three-

442   stimulus task (Stage B) for 19 sessions. Amarilla remained in the individual condition throughout

443   the study. Despite having reached criterion on the two-stimulus task, Amarilla failed to reach the

444   same performance criterion (of appropriate stay/shift responses on T2 for 75% of problems in a

445   session, and appropriate stay/shift responses on T3-T5 for 75% or more trials in a session, for

446   three sessions in a row) on the three-stimulus task.

447

448   Our original goal in training the monkeys had been to train them to general competency using

449   this discrimination paradigm, so that we could test the use of social information for more taxing

450   stimulus selection problems. However, this was not possible during the data collection period.

451   Therefore Amarilla's testing sessions were terminated when the planned data collection period

452   ended. Despite this, we did have sufficient data from this subject to perform some analyses on

453   how she transferred her Stage A learning to the novel Stage B context. Her T2 win-stay

454   performance in Stage A was 66% (compared to a chance level of 50%) and in Stage B was 44%

455   (compared to a chance level of 33%). Her T2 lose-shift performance in Stage A was 53%

456   (compared to a chance level of 50%) and in Stage B was 71% (compared to a chance level of

457   67%). The observed values were compared to chance by use of binomial tests: the only category

458   of trial in which Amarilla's performance differed from chance was Stage A win-stay (observed:

459   48 win-stays/73 win trials in Stage A; expected: 36.5/73; $p = 0.0095$).

460

461   This pattern of performance led to Amarilla finding the rewarded stimulus (and therefore

462   experiencing the reward cue and receiving food reinforcement) in 59% of Stage A T2 trials and

463   38% of Stage B T2 trials. A summary of the results (showing performance as measured by T2

464   repeats in order to demonstrate comparisons with chance) is presented graphically in Figure 5.

465

466   To determine whether there was a learning effect (i.e. whether her performance improved with

467   more experience), we used a generalised linear model with T2 WSLS as the dependent variable

468   and session number (scaled and centred) as the fixed effect. This model showed no effect of

469   session number ($b = 0.12$, SE $= 0.45$, Z $= 0.27$, $p = 0.79$), indicating that Amarilla's performance

470   did not improve with experience in Stage B.

471

472   **Conclusion**

473

474   In general, the squirrel monkeys did not appear to have learned to use the information trial as a

475   cue that ensured success on the test trial(s). Although one subject reached the criterion and

476   transferred from Stage A to Stage B, the success with which she ultimately did so was limited.

477   One potential explanation for the monkeys' limited proficiency with the task was the

478   presentation medium. There is evidence that both young children (Barr & Hayne, 1999) and

479   capuchin monkeys (Anderson, Kuroshima, & Fujita, 2017) learn better when using three-

480   dimensional objects than when viewing videos of a demonstration, a phenomenon termed the

481   video deficit effect. If squirrel monkeys' performance on the touchscreen task was hampered by

482   something like the video deficit effect, we reasoned that performance might be improved by

483   arrays consisting of three-dimensional objects. Therefore, we designed Experiment 2 to

484   reproduce the contingencies of Experiment 1 but to utilise three-dimensional objects as stimuli.

485   Although we intended to reproduce our procedures from Experiment 1 as closely as possible, we

486   decided to use human demonstrations only in the social condition, dispensing with the puppet.

487   This was due to the results of Experiment 1 suggesting that the monkeys performed, if anything,

488   less well following puppet demonstrations, compared with human ones.

489

490   Experiment 2: Three-dimensional objects

491

492   Experiment 2 was pre-registered at the Open Science Framework (osf.io/phzf2).

493

494   Materials and Methods

495

496   *Participants*

497   Approval for this project was provided by the Living Links to Human Evolution Research Centre

498   at RZSS Edinburgh Zoo. The same groups of squirrel monkeys participated in Experiment 2 (see

499   Table 1 for biographical details); by the beginning of this study, the number of monkeys had

500   grown via births to 35 individuals. A total of 11 monkeys (7 from the East group and 4 from the

501   West group) participated in 10 or more experimental sessions (the number specified in the pre-

502   registration as the minimum for their data to be included); a further 8 monkeys participated in the

503   experiment but not enough times for their data to be included (<10 sessions each); and 16

504   monkeys never participated in the study. The data from one subject (Toomi) were excluded, as

505   outlined in the pre-registration, because she developed a side bias (>80% of selections on the

506   same side).

507

508   *Ethics statement*

509   Ethical approval was granted by the University of Stirling Animal Welfare and Ethical Review

510   Body under proposal number AWERB (16 17) 117. Animals were not food or water deprived.

511   The research was conducted in line with the guidance provided by the Association for the Study

512   of Animal Behaviour (2015) in *Guidelines for the Treatment of Animals in Behavioural*

513   *Research and Teaching*, and the British Psychological Society (2012) in *Guidelines for*

514   *Psychologists Working with Animals*.

515

516   *Apparatus*

517   Objects were small plastic cups (7 cm tall × 5.5 cm wide × 5.5 cm deep; Sistema, New Zealand)

518   covered with differently coloured and patterned felt sleeves (20 cm long × 7 cm tall) that were

519   attached using strips of Velcro (Figure 6). Objects were presented on top of a mobile trolley. The

520   baiting of the cups was hidden from the monkeys' view with a cardboard occluder. A digital

521   video camera was used to record video of experimental sessions.

522

523   *Training procedures*

524   In the course of their previous experience in the research facility, prior to taking part in the

525   experiments reported here, the monkeys had been familiarised with a training activity. In this

526   activity, a single raisin was visibly placed under one of two cups, in trials involving a range of

527   levels of difficulty, and monkeys were then allowed to choose between the cups. Thus, monkeys

528   were already trained to select one of two objects, one of which contained a treat, using their

529   hands. Therefore, no further task training was undertaken before the commencement of

530   Experiment 2. A brief familiarisation session (to allow the monkeys to become familiar with the

531   materials presented to them) involved giving monkeys rewards while the experimenter

532   manipulated the trolley and occluder.

533

534   *Testing procedures*

535   Testing procedures were similar to those described above for Experiment 1. Each testing session

536   consisted of four problems, and each problem had five trials. For a single problem, two cups,

537   with different sleeves, were placed, open end down, on the rolling trolley. The order of the use of

538   sleeves was random, so that no particular pattern or colour was systematically rewarded or was

539   systematically paired with any other. To begin a problem, the cardboard occluder was placed in

540   front of the cups; a sunflower seed or raisin reward was held above the occluder; and the reward

541   was then lowered behind the occluder and placed under a single cup. During the hiding process,

542   both cups were lifted so that auditory cues would not reveal the location of the reward. Then, the

543   occluder was removed and the information trial was carried out, followed by four test trials.

544   Stimuli remained in the same position for an entire problem. The occluder was brought down in

545   front of the cups between trials, so that re-baiting, if necessary, would not be visible to the

546   monkey.

547

548   Monkeys remained assigned to the same information source condition they experienced in

549   Experiment 1 (so that if they were in the individual condition in Experiment 1, they remained in

550   the individual condition in Experiment 2). In the individual condition, monkeys selected one of

551   the cups in the information trial, and were rewarded (or not) accordingly. The setup was then re-

552   baited, and monkeys were then allowed to select a cup on the subsequent test trials by reaching

553   through the window toward it or touching or lifting it. In the social condition, monkeys saw a

554   social demonstrator select one of the stimuli in the information trial: this was always the human

555   experimenter, who did not consume the food reward if the rewarded cup was selected but did

556   remove the reward as if it had been consumed. The setup was then re-baited, and monkeys were

557   allowed to select a cup on the subsequent test trials. As in Experiment 1, the purpose of the

558   additional test trials using the same pair of stimuli was to provide scaffolding to allow the

559   monkeys to learn that the reward remained in the same single location for any given pair of

560   stimuli, although T2 again was the critical trial for the purpose of analysis. Monkeys received a

561   food reward on each trial where they selected the rewarded stimulus.

562

563   Rewards were randomly allocated to the left or right side for a problem, and patterns of lefts and

564   rights were pseudorandomised so that the reward location would not be predictable and so that

565   rewards would occur equally on each side (to help prevent the development of side biases).

566

567   *Statistical analysis*

568   Statistical analysis was done via logit fit GLMMs using the *lme4* package (Bates et al., 2015) in

569   R (R Core Team, 2017). As in Experiment 1, the main response variables were success, WSLS,

570   and repeats. Fixed effects used in at least some of the models included the session number

571   (centred), trial number, source of information (social or individual; sum coded), and type of

572   information (whether T1 was a win or a lose selection; sum coded). Random effects included

573   monkey identity and side (left or right) of the rewarded stimulus (random intercept effects);

574   similarly to Experiment 1, we removed random effects as necessary to address issues of singular

575   fit or non-convergence.

576

577   **Results**

578

579   As in Experiment 1, overall success on T2 was slightly greater than chance, with 55% T2 success

580   (Table 2; observed success: 305 wins/557 trials; expected: 278.5/557; $p = 0.027$ in a binomial

581   test).

582

583   *Effect of experience (session number)*

584   To evaluate the effect of experience, we used a GLMM with T2 success as the response variable,

585   session number (centred) as the only fixed effect, and monkey identity and side of the rewarded

586   item as random intercept effects[1]. This model showed no significant change in T2 success in

587   relation to session number ($b = 0.025$, SE $= 0.016$, Z $= 1.6$, $p = 0.12$); that is, when stimuli were

588   3D objects, as when they were presented on a touchscreen, monkeys did not improve their task

589   performance with greater experience.

590

591   *Information type and source*

592   The full pre-registered GLMM was built, with T2 WSLS as the response variable; information

593   source (social or individual), information type (win or lose), and their interaction as fixed effects;

---

[1]Due to an oversight, we failed to specify the random effects structure we intended for this model in our the pre-registration. This analysis uses the same random effects structure as pre-registered for our main model (see "Information type and source" below). Alternative random effects structures make no difference to the pattern of results we present here.

594 and monkey identity and side of the rewarded item as random intercept effects. This model

595 revealed a main effect of information type (win trial [64% WSLS] > lose trial [46% WSLS]; $b =$

596 0.54, SE = 0.097, Z = 5.5, $p < 0.001$) and no main effect of source ($b = 0.051$, SE = 0.12, Z =

597 0.44, $p = 0.66$). There was an interaction between information type and source ($b = 0.55$, SE =

598 0.098, Z = 5.7, $p < 0.001$). To clarify this interaction, we used the *emmeans* package to perform a

599 post hoc analysis. This indicated that in the social condition, there was no difference in

600 performance after seeing win (54% WSLS) and lose (55% WSLS) demonstrations; however, in

601 the individual condition, performance was better after experiencing a win (79% WSLS) than a

602 lose (31% WSLS) in the information trial (see Table S3 in the Supplemental Material).

603

604 *Repeating previous selections*

605 We analysed the repeats variable for Experiment 2, following the same logic as for Experiment 1

606 (i.e., to determine whether the monkeys were sensitive to whether they had observed a win or

607 lose trial). Note that analyses using the repeats variable were not pre-registered. We constructed

608 a GLMM with T2 repeats as the response variable; information source, information type, and

609 their interaction as fixed effects; and monkey identity as a random intercept effect. There were

610 main effects of information source and information type, and no interaction between these

611 variables ($b = 0.045$, SE = 0.097, Z = 0.46, $p = 0.64$). The tendency to repeat was stronger in the

612 individual (74% repeats) than the social (49% repeats) condition ($b = 0.52$, SE = 0.14, Z = 3.8, p

613 < 0.001), and the tendency to repeat was stronger after win information trials (64% repeats) than

614 lose information trials (54% repeats; $b = 0.23$, SE = 0.10, Z = 2.3, $p = 0.020$) (although note that

615 the tendency to repeat was greater than 50% even following lose trials). Monkeys' performance

616 using the repeats measure is presented in Figure 7.

617

618 *Improvement across trials*

619 Following the same logic of Experiment 1, we examined whether monkeys improved their

620 performance across trials within a problem, as another means of determining whether monkeys

621 were sensitive to the win/lose feedback they received. We built a GLMM with success in each

622 trial from T2 to T5 as the response variable, trial number as the fixed effect, and side of the

623 rewarded item as a random intercept effect.[2] Trial number did have a significant effect (Figure

624 8), indicating that monkeys more frequently selected the rewarded stimulus as trial number

625 increased ($b = 0.092$, SE $= 0.039$, Z $= 2.3$, $p = 0.020$). The magnitude of the effect was modest,

626 with overall success on T2 of 55% and overall success on T5 of 61%.

627

628 *Comparison of 2D and 3D presentations*

629 To compare the effect of the presentation mediums used in Experiments 1 and 2, we combined

630 the data sets (using only Stage A data from Experiment 1) and built a GLM with T2 WSLS as

631 the response variable; and information type, information source, presentation medium

632 (touchscreen or cups), and interactions between these variables as fixed effects.[3] Similarly to the

633 models of the data from the two experiments run separately, this GLM revealed a main effect of

634 information type (win trial [67% WSLS] > lose trial [45% WSLS]; $b = 0.50$, SE $= 0.053$, Z $=$

635 9.6, $p < 0.001$), while the main effects of the variables information source and presentation

636 medium were non-significant (all ps > 0.67). There was a significant interaction between

---

[2]Due to an oversight, we failed to specify the random effects structure we intended for this model in the pre-registration. In this analysis, we attempted to use the random effects pre-registered for our main model; however, including monkey identity as a random intercept effect caused the model to have a singular fit. Therefore, only side of the rewarded item was included..

[3]Due to an oversight, we failed to specify the random effects structure we intended for this model in our pre-registration. Although we built a model with a random effect of monkey identity, this model had a singular fit, and side of the rewarded item was not an existing variable in the touchscreen data set. This was the reason for use of a GLM.

637 information type and source ($b = 0.33$, SE = 0.053, Z = 6.3, $p < 0.001$), and a three-way

638 interaction between information type, source, and presentation medium ($b = -0.20$, SE = 0.053,

639 Z = -3.8, $p < 0.001$). For post hoc analysis of this interaction, see Table S4 in the Supplemental

640 Material. All other interactions were non-significant.

641

642 *Repeating previous selections: a comparison of 2D and 3D presentations*

643 Additionally, we constructed a non-pre-registered GLMM with T2 repeats as the response

644 variable. This model had fixed effects of information type, information source, presentation

645 medium, and interactions between these variables; and monkey identity as a random intercept

646 effect. This model revealed main effects of information type (more repeats after a win [67%

647 repeats] than a lose [55% repeats] information trial; $b = 0.24$, SE = 0.053, Z = 4.5, $p < 0.001$) and

648 information source (more repeats in the individual condition [66% repeats] than the social

649 condition [56% repeats]; $b = 0.34$, SE = 0.086, Z = 3.9, $p < 0.001$). There was no main effect of

650 presentation medium ($b = -0.017$, SE = 0.057, Z = -0.29, $p = 0.77$). However, there was a

651 significant interaction between information source and presentation medium ($b = -0.22$, SE =

652 0.057, Z = -3.8, $p < 0.001$; see Supplemental Material Table S5). All other interactions in this

653 analysis were non-significant. Results are presented graphically in Figure 9.

654

655 **Discussion**

656

657 In exposing squirrel monkeys to binary discrimination learning problems, we had originally

658 hoped that they would achieve a performance criterion that could be regarded as indicative of

659 having learned the task contingencies, if given experience of multiple sessions each involving

660 several problems. Establishing task competence would have allowed us to answer certain

661 questions about the monkeys' responses to information acquired from social observation

662 compared with that acquired from their own personal experience. Although we had limited

663 success fulfilling this original aim, we were nonetheless able to analyse the squirrel monkeys'

664 spontaneous reactions to the task (presumably relatively uncontaminated by the effects of

665 reinforcement learning within the task itself). In addition, we were able to compare the relative

666 effectiveness of two alternative mediums of task presentation—2D touchscreen interaction and

667 3D object choice—as well as determine whether the monkeys displayed similar patterns of

668 spontaneous responses across these two task types.

669

670 Overall, the performance of the squirrel monkeys in both tasks was only very slightly above

671 chance. This contrasts with the performance of preschool children in a very similar task

672 (Atkinson et al., 2019), who spontaneously adopted a win-stay, lose-shift strategy and thus

673 demonstrated highly proficient performance with little or no previous task experience. The

674 squirrel monkeys' performance suggests that even a very simple choice task, involving

675 straightforwardly predictive task cues, may be difficult for them to master unless they have

676 extensive training with the paradigm and/or elevated motivation to succeed (such as calorie

677 restriction, which has been used in other studies carried out by different research groups (Kangas

678 & Bergman, 2012)).

679

680 In addition, the squirrel monkeys did not show performance improvement across sessions; that

681 is, more experience with the tasks did not lead to better performance. Therefore, inasmuch as

682 they performed marginally above chance, this was not due to learning the task-specific

683   significance of rewarded versus unrewarded information trials, but instead reflected the

684   spontaneous after-effects of having performed an action, or having been exposed to the actions

685   of another, somewhat moderated by whether or not these actions had been associated with

686   rewards and/or reward cues. Although a single monkey did reach our performance criterion on

687   the two-stimulus version of the touchscreen task, her performance upon transfer to the three-

688   stimulus version of the task indicated that, even in this case, there were limits to her

689   understanding of the task contingencies. The monkey's performance suggested that the fidelity

690   of her responses shifted in line with the change in expected response frequencies based on

691   chance dictated by the increase in array size.

692

693   Across trials within a problem, squirrel monkeys either did not improve their performance (with

694   the touchscreen, Experiment 1) or improved their performance modestly (with the 3D objects,

695   Experiment 2, from ~55% correct on T2 to ~61% correct on T5). These results may indicate that

696   squirrel monkeys need more than five trials' worth of experience to reliably locate the reward for

697   any given stimulus array. (Harlow (1949), for example, gave monkeys between 6 and 50 trials

698   for each problem; Darby and Riopelle (1955) gave macaques 6 trials per problem; and Kangas

699   and Bergman (2014) gave squirrel monkeys 200 trials. However, it should be noted that in those

700   paradigms, unlike the ones presented here, the stimuli changed position between trials.) Squirrel

701   monkeys' relatively low problem-level competence in our paradigm would, in turn, make it

702   difficult for them to learn the task-level contingencies.

703

704   The presentation medium (2D touchscreen or 3D object) had no main effect on either the

705   monkeys' success on the task or their tendency to repeat a selection. Thus, we found no evidence

706   to suggest that either task was better suited to the abilities of this population, despite the fact that

707   presentation medium did interact with other variables (information type and source).

708

709   Squirrel monkeys exhibited a strong tendency to repeat their own selections, following both

710   rewarded and unrewarded information trials. This resulted in unrewarded information trials

711   having success rates below chance in the individual conditions. This tendency to repeat one's

712   own previous selections has been documented by other researchers; notably, macaque monkeys,

713   in an individual learning condition, frequently repeated their own selections, regardless of

714   whether they had been rewarded for that selection or not (Monfardini et al., 2012).

715

716   However, even given this tendency, squirrel monkeys repeated their own selection more when

717   that selection had resulted in a win than a lose trial. This result indicates some sensitivity to

718   feedback, in that monkeys were more likely to repeat something that had resulted in either a

719   reward or the appearance of secondary reinforcers (auditory click and sunburst image). A similar

720   differential sensitivity to reward (versus nonreward) feedback has been reported for Japanese

721   macaques (Itoh, Izumi, & Kojima, 2001) as well as baboons and pigeons (Cook & Fagot, 2009).

722

723   The effect of information source on repetition differed between the two presentation mediums. In

724   the touchscreen task (Experiment 1), the tendency to repeat the selection made in the information

725   trial was not different between the individual and social conditions. Monkeys' repeating

726   behaviour did show an interaction that was near the alpha criterion threshold ($p = 0.056$) between

727   information type and social demonstration type (human or puppet). This trend was in the

728   direction of greater sensitivity to the win/lose distinction for the human's demonstration,

729   compared with that of the puppet. This made it logical to use a human demonstrator only in

730   Experiment 2. While the value of puppet or otherwise artificial demonstrators in other contexts is

731   clear (Krupenye et al., 2016; Truskanov & Lotem, 2017; Wood, Kendal, & Flynn, 2013), it was

732   not beneficial for the monkeys' performance in this case.

733

734   In contrast, in the 3D object task (Experiment 2), there was a main effect of information source:

735   monkeys tended to repeat their own selections more than those of the social demonstrator. In this

736   Experiment, there was also a main effect of information type on the tendency to repeat, but no

737   interaction between source and information type. This result indicates a sensitivity to source, and

738   to whether a selection was rewarded, but no differential sensitivity to reward information based

739   on the source.

740

741   Across both tasks (see combined analyses) the monkeys' tendency to repeat selections was

742   greater in the individual condition than the social condition. In contrast, when children were

743   given a similar task on a touchscreen with information acquired from either a social

744   demonstration or individual exploration, they were largely unaffected by the information source

745   (Atkinson et al., 2019). This is likely attributable to the fact that the children apparently

746   understood the predictive value of the information trial (in both conditions), as evidenced by

747   their higher success rates (~73%, c.f. ~55% for the monkeys). Children's performance appeared

748   to reflect the task-specific relevance of win and lose information trials, whereas (as previously

749   noted) the monkeys' performance presumably reflects pre-existing biases in their behaviour (e.g.

750   stimulus enhancement effects in the social condition, and possibly simple behavioural inertia in

751   the individual condition).

752

753 Because the squirrel monkeys did not reach high proficiency levels in our tasks, the results of

754 these experiments cannot be directly compared to results from human children, who

755 demonstrated high levels of task success (Atkinson et al., 2019). Such a comparison would have

756 the goal of illuminating the effects of information source across populations, with a view to

757 better understanding the uniqueness of human culture. Drawing comparisons with human

758 performance will require further study with NHP populations that learn to perform the task

759 proficiently. In our ongoing research, we have also tested capuchin monkeys with the

760 touchscreen task, with several individuals so far achieving above-criterion performance (Kean et

761 al., 2018).

762

763 What our results can reveal, however, is the biases that squirrel monkeys may have when

764 approaching a task. The tendency of squirrel monkeys to repeat selections was not a trained

765 response, and was similar for both mediums of presentation. We speculate that such biases in

766 nonhuman behaviour could, in certain studies, generate patterns of behaviour that would be

767 consistent with certain interpretations of social learning and/or cultural transmission (i.e.

768 apparent "copying" of others' behaviour), in spite of the fact that this could be the outcome of

769 mechanisms very different from those driving human social learning and cultural transmission.

770 For example, following observation of an experienced individual, a previously naïve animal may

771 perform the same foraging behaviour. This might occur in the absence of any understanding of

772 either the goal of the demonstrator or even the effect of the behaviour (i.e. the connection with

773 food), although the individual's behaviour would also be consistent with these higher-order

774 cognitive explanations.

775

776 In the current studies, our research designs have allowed us to directly compare responses to

777 social demonstrations with those following individual exploration, under equivalent conditions.

778 Furthermore, we were able to evaluate the extent to which the subjects were influenced by the

779 outcome of the response observed or experienced. These comparisons illuminate the fact that the

780 monkeys' slight bias to repeat the behaviour of others was both (a) less strong, if anything, than

781 their tendency to repeat their own behaviour, and (b) not motivated by a recognition of the

782 connection between the repeated response and its outcome (since this also occurred—even if to a

783 slightly more limited extent—following unrewarded information trials). Despite our limited

784 success in training the squirrel monkeys on this task, we believe that it is important for

785 researchers interested in animal social learning to pursue designs such as ours, which allow

786 direct comparisons between responses to information acquired from social demonstrations and

787 (equivalent) information acquired from personal experience. Such research may shed valuable

788 light on the mechanisms underlying effects of social influence.

789

790

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792

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795 research. We are also grateful to Lindsay Young for her assistance with experimental materials

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797

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909

910   Figure Legends

911

912   Figure 1. Touchscreen example problem and apparatus setup. (A) A sample two-stimulus (Stage

913   A) problem. (B) Appearance of the screen (example) after the rewarded stimulus was selected,

914   with the reward cue (sunburst) appearing at the location of the rewarded stimulus. (C) A squirrel

915   monkey interacting with the touchscreen task.

916

917   Figure 2. The squirrel monkey puppet used as a demonstrator in Experiment 1.

918

919   Figure 3. The effects of source and information type on whether (in T2) squirrel monkeys

920   repeated the selection from the information trial. Results are from the touchscreen task of

921   Experiment 1. Each point represents the aggregate performance of an individual monkey in the

922   given condition, and the size of each point indicates the number of trials aggregated within that

923   mean. Boxes and whiskers indicate medians and interquartile ranges of performance aggregated

924   by monkey.

925

926   Figure 4. Success across experimental trials in the touchscreen task of Experiment 1. Plotted are

927   the means of by-subject means for illustration purposes; statistical tests did not average subject

928   means. The error bars indicate 95% confidence intervals on the means of means. Statistical tests

929   revealed a non-significant trend towards improvement across trials.

930

931   Figure 5. Probability of repeating in T2 the selection made on the information trial, according to

932   information type, for Stage A and Stage B, for the monkey who passed criterion (Amarilla).

933   Amarilla was in the individual condition. Expected rates of repetition according to chance are

934   indicated by the horizontal lines (separately for each of the stages).

935

936   Figure 6. Two of the cups and felt sleeves in front of the occluder used in Experiment 2.

937

938   Figure 7. The effects of source and information type on whether (in T2) squirrel monkeys

939   repeated the selection from the information trial. Results are from the 3D object task of

940   Experiment 2. Each point represents the aggregate performance of an individual monkey in the

941   given condition, and the size of each point indicates the number of trials aggregated within that

942   mean. Boxes and whiskers indicate medians and interquartile ranges of performance aggregated

943   by monkey.

944

945   Figure 8. Success across experimental trials in the 3D object task of Experiment 2. Plotted are

946   the means of by-subject means for illustration purposes; statistical tests did not average subject

947   means. The error bars indicate 95% confidence intervals on the means of means. Statistical tests

948   revealed a significant effect of trial number.

949

950   Figure 9. The effects of presentation medium, source, and information type on whether squirrel

951   monkeys repeated the selection from the information trial on T2. Each point represents the

952   aggregate performance of an individual monkey, and the size of each point indicates the number

953   of trials aggregated within that mean. Boxes and whiskers indicate medians and interquartile

954   ranges of performance aggregated by monkey.

Participant characteristics

1   Table 1. Participant characteristics

Name	Sex	Group	Age (as of Feb. 2016)	Condition	Participation in Expt 1	No. sessions, Expt 1	Participation in Expt 2	No. sessions, Expt 2
Amarilla	F	East	4	Individual	Training, testing	A: 44 B: 19	Testing (insufficient sessions)	9
Boa	M	East	10	N/A	Training	0	N/A	0
Cali	F	East	10	Social	Training, testing	42	Testing	20
Ciara	F	East	4	Social	Training, testing	55	Testing	19
Dora	F	East	5	Individual	Training, testing	69	Testing	20
Elie	F	East	10	Individual	Training	0	Testing	15
Flora	F	East	7	Individual	Training, testing	34	Testing (insufficient sessions)	3
Gabriela	F	East	4	Social	Training, testing	61	Testing	20
Gisele	F	West	3	Social	Training, testing	27	Testing (insufficient sessions)	0
Jasmin	F	West	13	Individual	Training, testing	14	Testing	14
Lexi	F	East	5	Social	Training	0	Testing (insufficient sessions)	4
Loki	F	West	1	Social	N/A	0	Testing	15
Maya	F	East	12	N/A	Training	0	N/A	0
Orla	F	West	4	Individual	Training, testing	52	Testing (insufficient sessions)	0
Pelusa	F	East	4	Individual	Training, testing	60	Testing	20
Roca	F	East	13	Individual	Training	0	Testing (insufficient sessions)	9
Sancha	F	West	6	Social	Training, testing	67	Testing	20
Sipi	F	East	6	Social	Training	0	Testing (insufficient sessions)	3
Tatu	F	East	14	Social	Training	0	Testing	1

								(insufficient sessions)	
Toomi	F	West	9	Individual	Training, testing		64	Testing (side bias)	12
Valencia	F	East	4	Social	Training, testing		59	Testing	16
Yendi	F	East	7	N/A	Training		0	N/A	0

2 Expt, Experiment; F, female; M, male. For Experiment 1, completion of at least one T2 was

3 required for the data from a session to be used. For Experiment 2, completion of at least one full

4 problem (T1-T5) was required for the data from a session to be used. For Experiment 2, the data

5 from monkeys who completed fewer than 10 sessions, indicated by "(insufficient sessions)",

6 were not included in the analysis.

Performance summary (all trials, un-averaged) for Experiments 1 and 2

1   Table 2. Performance summary (all trials, un-averaged) for Experiments 1 and 2

Study and Condition	T2 success after win trials (%)	T2 success after lose trials (%)
Tablet (Stage A)		
Social: human	70*	50
Social: puppet	62*	47
Individual	70*	40†
Overall	68*	44†
3D		
Social: human	54	55
Individual	79*	31†
Overall	64*	46

2   *, performance significantly above chance; †, performance significantly below chance. Statistical

3   tests were two-tailed binomial tests against 50% (chance) performance.

Model results summary for Experiments 1 and 2

Only models that assessed performance as measured by T2 success in Stage A are included in this Table. GLMMs included random effects not shown here as well as the fixed effects detailed in the Table; please see text for details. N.S., non-significant; ndf, not different from.

1 Table 3. Model results summary for Experiments 1 and 2

Analysis	Experiment	Variable(s) included in the model	p value and direction of effect
Effect of session number	Experiment 1 (tablet)	Session number	N.S., $p = 0.47$
	Experiment 2 (3D)	Session number	N.S., $p = 0.12$
Effect of trial number	Experiment 1 (tablet)	Trial number	N.S., $p = 0.064$
	Experiment 2 (3D)	Trial number	$p = 0.020$ (later > earlier)
Effect of source and information type	Experiment 1 (tablet)	Source	$p = 0.043$ (human > puppet) N.S., $p = 0.61$ (social ndf individual)
		Information type	$p < 0.001$ (win > lose)
		Source * information type	$p = 0.002$ (see Supplemental Table S2)
	Experiment 2 (3D)	Source	N.S., $p = 0.66$ (social ndf individual)
		Information type	$p < 0.001$ (win > lose)
		Source * information type	$p < 0.001$ (see Supplemental Table S3)

2 Only models that assessed performance as measured by T2 success in Stage A are included in
3 this Table. GLMMs included random effects not shown here as well as the fixed effects detailed
4 in the Table; please see text for details. N.S., non-significant; ndf, not different from.

Figure 1

Touchscreen example problem and apparatus setup.

(A) A sample two-stimulus (Stage A) problem. (B) Appearance of the screen (example) after the rewarded stimulus was selected, with the reward cue (sunburst) appearing at the location of the rewarded stimulus. (C) A squirrel monkey interacting with the touchscreen task.
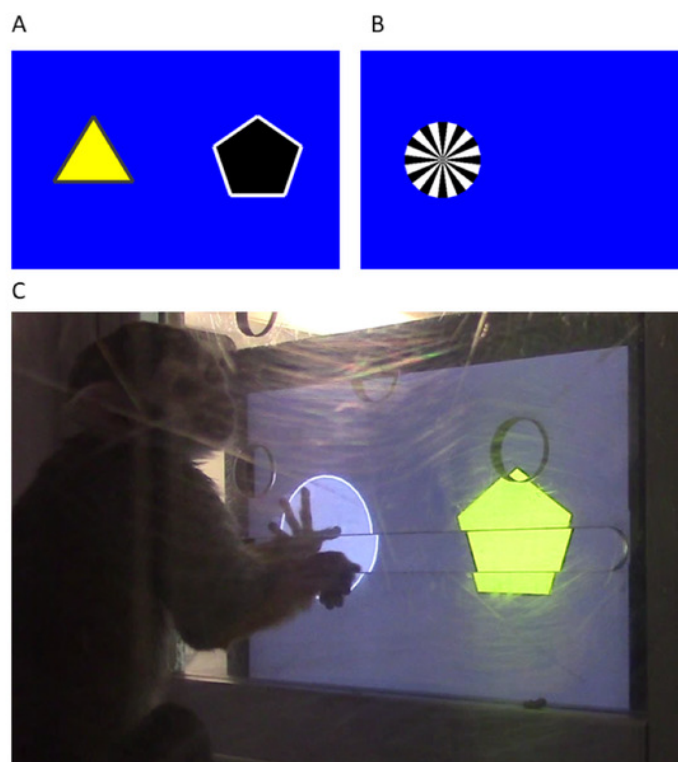
Figure 2

The squirrel monkey puppet used as a demonstrator in Experiment 1.

Figure 3

The effects of source and information type on whether (in T2) squirrel monkeys repeated the selection from the information trial.

Results are from the touchscreen task of Experiment 1. Each point represents the aggregate performance of an individual monkey in the given condition, and the size of each point indicates the number of trials aggregated within that mean. Boxes and whiskers indicate medians and interquartile ranges of performance aggregated by monkey.
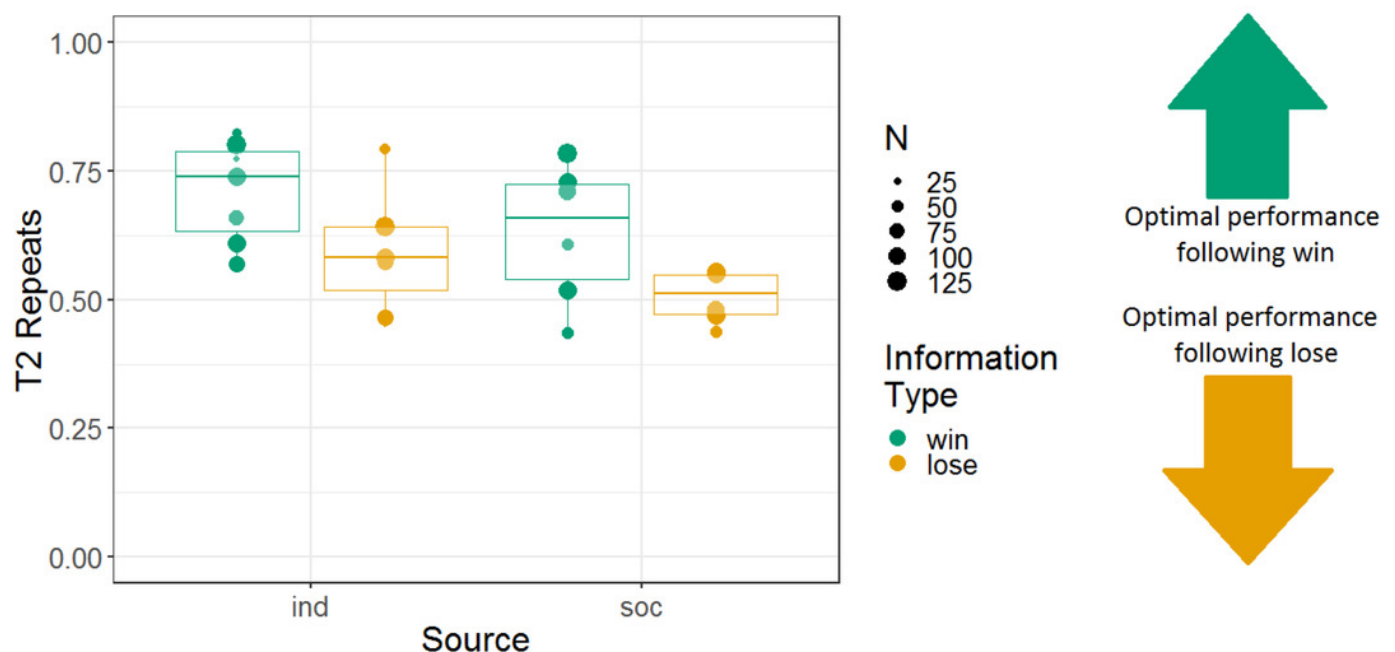
Figure 4

Success across experimental trials in the touchscreen task of Experiment 1.

Plotted are the means of by-subject means for illustration purposes; statistical tests did not average subject means. The error bars indicate 95% confidence intervals on the means of means. Statistical tests revealed a non-significant trend towards improvement across trials.
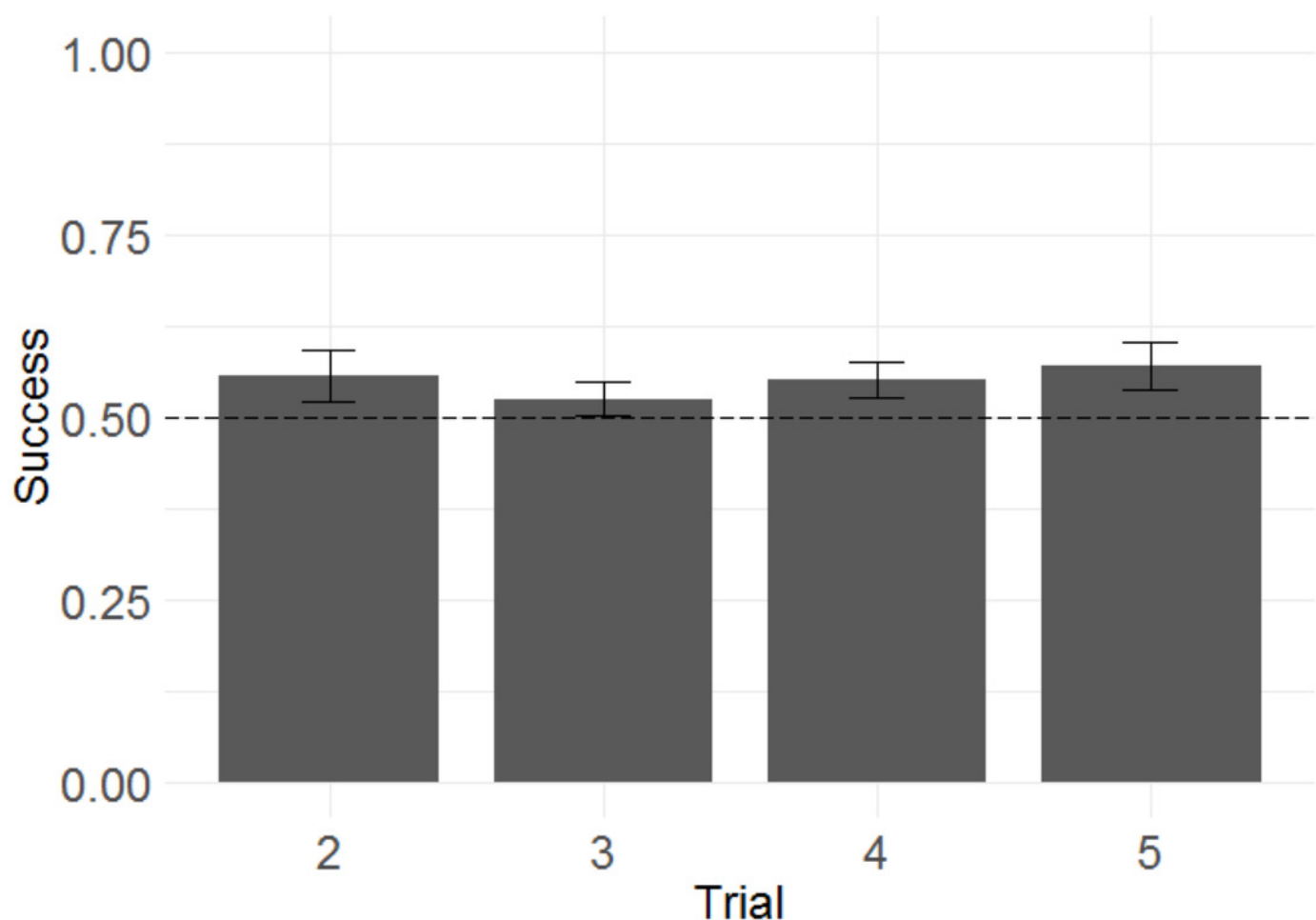
Figure 5

Probability of repeating in T2 the selection made on the information trial, according to information type, for Stage A and Stage B, for the monkey who passed criterion (Amarilla).

Amarilla was in the individual condition. Expected rates of repetition according to chance are indicated by the horizontal lines (separately for each of the stages).
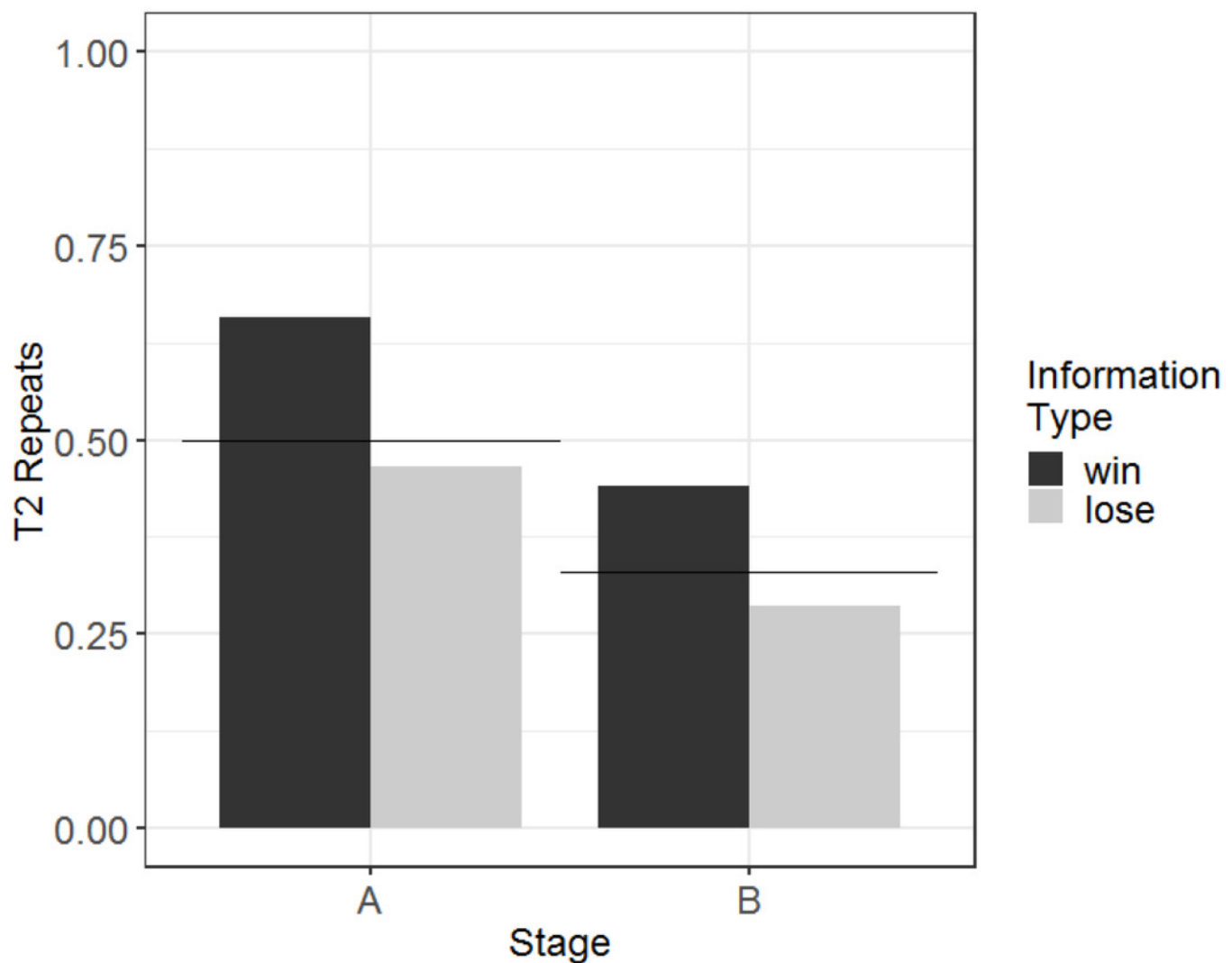
Figure 6

Two of the cups and felt sleeves in front of the occluder used in Experiment 2.

Figure 7

The effects of source and information type on whether (in T2) squirrel monkeys repeated the selection from the information trial.

Results are from the 3D object task of Experiment 2. Each point represents the aggregate performance of an individual monkey in the given condition, and the size of each point indicates the number of trials aggregated within that mean. Boxes and whiskers indicate medians and interquartile ranges of performance aggregated by monkey.
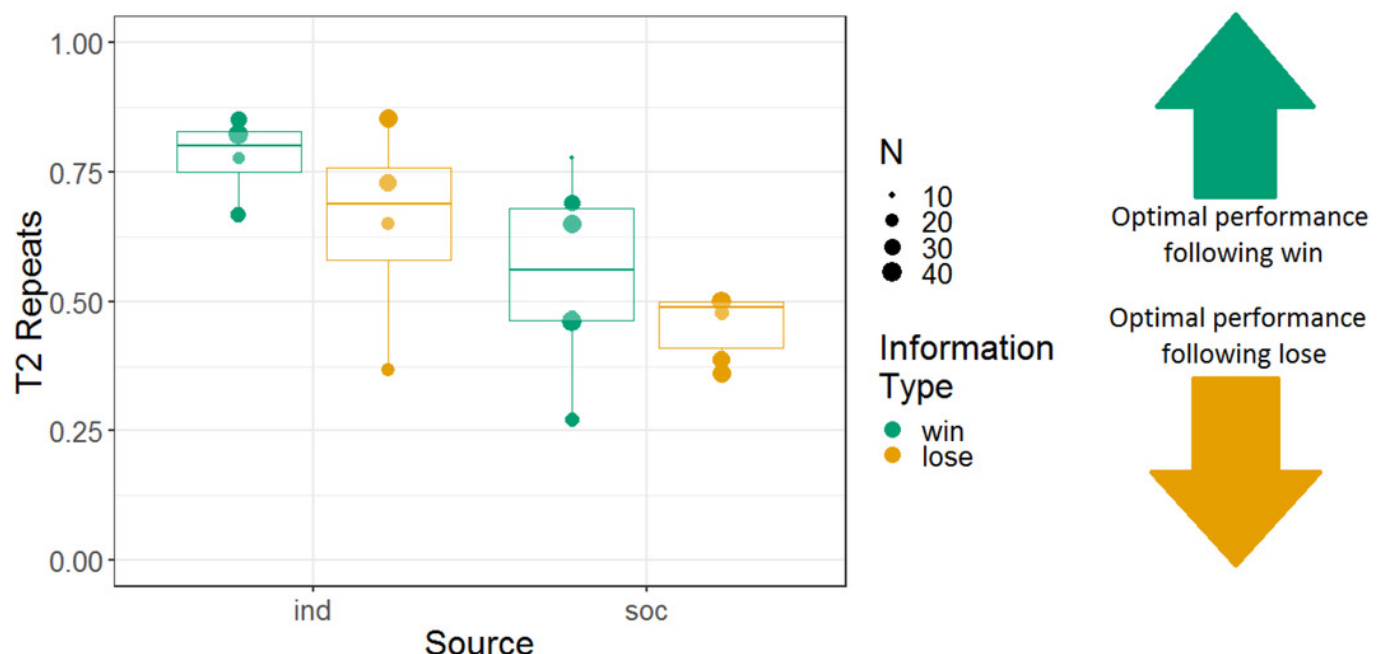
Figure 8

Success across experimental trials in the 3D object task of Experiment 2.

Plotted are the means of by-subject means for illustration purposes; statistical tests did not average subject means. The error bars indicate 95% confidence intervals on the means of means. Statistical tests revealed a significant effect of trial number.
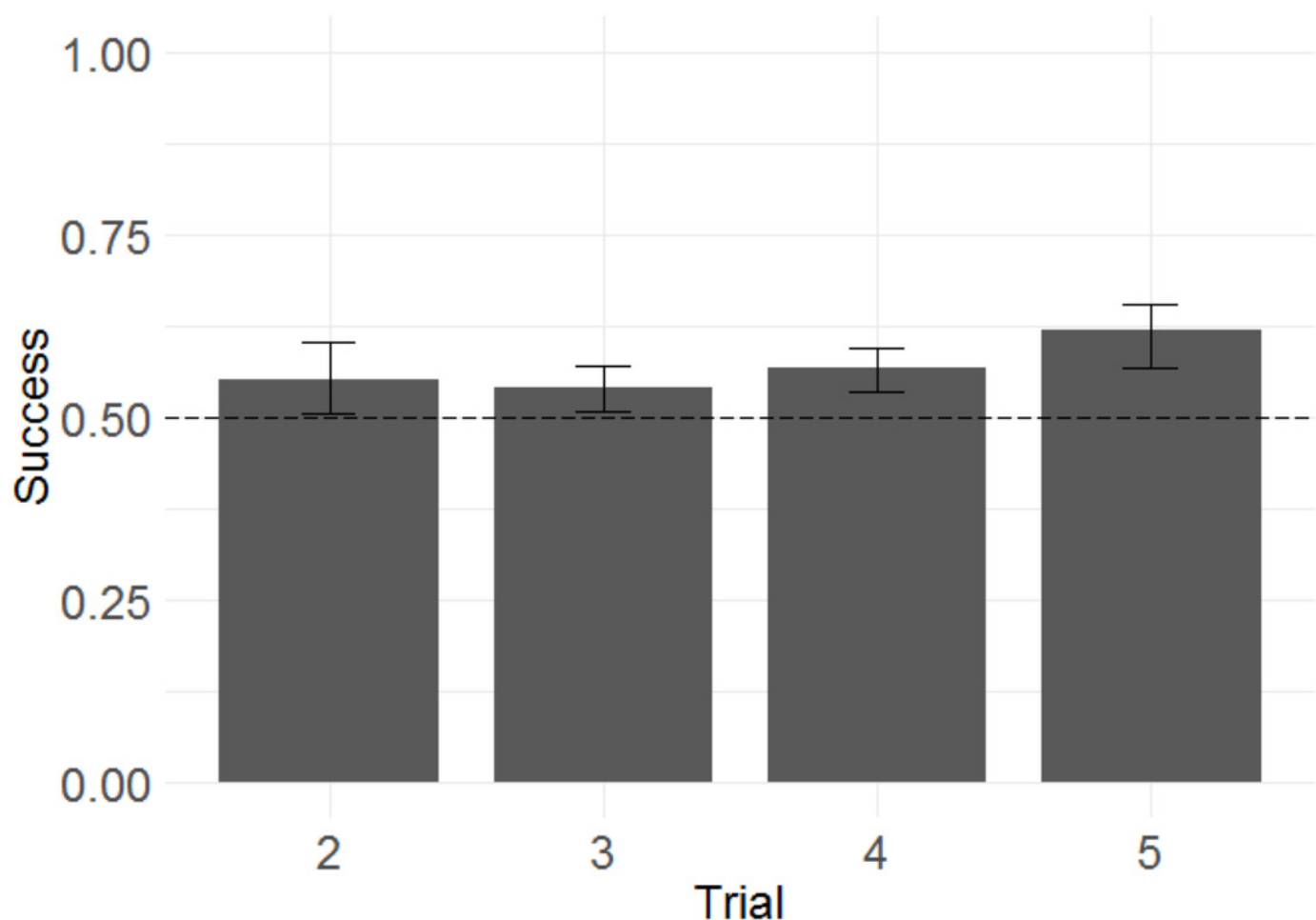
Figure 9

The effects of presentation medium, source, and information type on whether squirrel monkeys repeated the selection from the information trial on T2.

Each point represents the aggregate performance of an individual monkey, and the size of each point indicates the number of trials aggregated within that mean. Boxes and whiskers indicate medians and interquartile ranges of performance aggregated by monkey.