1   **Serial reversal learning and cognitive flexibility in two species of Neotropical parrots**

2   **(*Diopsittaca nobilis* and *Pionites melanocephala*)**

3

4   Jayden O. van Horik[1,2]*, Nathan J. Emery[1]

5

6   [1] School of Biological and Chemical Sciences, Queen Mary University of London, London E1

7   4NS, UK

8   [2] Centre for Research in Animal Behaviour, College of Life and Environmental Sciences,

9   University of Exeter, Exeter EX4 4QG, UK

10

11   * Corresponding author: jayden.van.horik@gmail.com

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

27

28

29

30

31 **ABSTRACT** Serial reversal learning of colour discriminations was assessed as an index of

32 behavioural flexibility in two captive species of Neotropical parrots. Both species showed

33 similar performances across serial reversals and no between species differences were

34 observed. In a second task subjects' performances were assessed after they experienced

35 either a low or high pre-reversal learning criterion. If reversal performances improve through

36 processes of associative learning, a high pre-reversal criterion is expected to strengthen

37 previously learned associations and hence impede post-reversal performances. Conversely,

38 highly reinforced associations may facilitate the use of conditional rules that can be

39 generalised across reversals and improve post-reversal performances. We found that high

40 criterion subjects made fewer post-reversal errors and required fewer trials to reach criterion,

41 than low criterion subjects. Red-shouldered macaws and black-headed caiques may

42 therefore demonstrate capacities for solving serial reversal problems by applying conditional

43 rules, rather than learning solely by associative processes. Such performances coincide with

44 findings in great apes, but contrast with findings in monkeys and prosimians, which generally

45 show impaired reversal performances when trained to a highly rigorous pre-reversal criterion.

46 Overall, these findings suggest an evolutionary convergence of behavioural flexibility between

47 parrots and non-human great apes.

48

49 **Keywords:** comparative cognition, parrots, serial reversal learning, behavioural flexibility

50

51

52

53

54

55

56

57

58

59

INTRODUCTION

The behaviours of some animals appear to be restricted by inflexible stimulus-response action patterns, whereas other animals can respond flexibly to environmental stimuli by generalising learned information across novel situations. For example, some corvids, such as blue jays (*Cynaocitta cristata*), Eurasian jays (*Garrulus glandarius*), crows (*Corvus corone*), rooks (*C. frugilegus*) and jackdaws (*C. monedula*), can extract general rules to rapidly solve a series of novel, but functionally equivalent, discrimination problems; whereas comparable studies on pigeons (*Columba livia*) reveal that they slowly learn each novel discrimination problem anew, suggesting an inability to transfer previously learned information across similar problems (Hunter & Kamil, 1971; Mackintosh, 1988; Wilson, Mackintosh, & Boakes, 1985). Pigeons fail to understand that exemplars can vary with respect to some attributes and not others, such as *same vs different* discriminations, yet they are capable of generalising *identity vs non-identity* discriminations across novel images (Blaisdell & Cook, 2005) and sounds (Cook & Brooks, 2009), and hence may show some understanding of abstract concept learning (Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). However, unlike capuchin (*Cebus apella*) or rhesus (*Macaca mulatta*) monkeys, pigeons generally require much more experience to do so (Katz & Wright, 2006). Primates, parrots and corvids typically outperform other animals in their capacities for analogical reasoning or solving abstract cognitive concepts. For instance, African grey parrots (*Psittacus erithacus*) can understand concepts of category and of *same-different* that are comparable to those of non-human primates (Pepperberg, 1983; 1987; 1988). Amazon parrots (*Amazona amazonica*) and hooded crows (*Corvus corone*) also spontaneously understand particular relationships between novel object pairs, demonstrating capacities for relational matching-to-sample that are on par with apes and crows (Obozova, Smirnova, Zorina, & Wasserman, 2015; Smirnova, Zorina, Obozova, & Wasserman, 2015)*.* Capacities to generalise information across discrimination problems may therefore differ between certain species, possibly because generalising information is cognitively demanding.

Among the methods used to compare behavioural flexibility across species is serial reversal learning. Success on such tasks requires an ability to flexibly respond to a fixed set of stimuli with an alternating reward regimen (Bond, Kamil, & Balda, 2007). Serial reversal

90   learning typically requires subjects to make a binary choice discrimination between one

91   stimulus (i.e., a colour cue) which is repeatedly rewarded and another stimulus which is not.

92   Subjects eventually learn to discriminate between the rewarded and non-rewarded stimuli,

93   after which the reward contingencies are reversed (i.e. A+B– becomes A–B+). Reversed

94   contingencies therefore require subjects to extinguish responses to previously learned

95   associations and then re-learn each new association. Subjects initially require many trials to

96   successfully respond to reversals, but may improve their performances with experience.

97   However, as there are no cues to predict when the contingencies will be reversed, subjects

98   will initially make at least one error after each reversal. Hence, an optimal performance may

99   eventually be achieved on the second post-reversal trial. To do this, subjects must inhibit

100   previously learned associations and adopt a *win stay–lose shift* rule: always try the response

101   that was last rewarded, and if that is no longer rewarded, shift to the other response,

102   otherwise stay (Levine, 1959; 1965). Animals may therefore use their previous experience to

103   develop conditional rules that enable them to rapidly switch between contingencies;

104   demonstrating an ability to generalise information across reversal problems (Bond et al.,

105   2007; Day, Crews, & Wilczynski, 1999; Strang & Sherry, 2014).

106   Performances on reversal learning tasks have previously been used to quantify

107   differences in learning across a wide variety of species (Bitterman, 1965). Yet distantly

108   related species also possess dramatically different perceptual, motivational and

109   morphological traits, which can make direct comparisons of cognitive traits difficult to interpret

110   (Bitterman, 1960, 1965, 1975; Breland & Breland, 1961; Macphail, 1982; Pepperberg &

111   Hartsfield, 2014; Salwiczek et al., 2012; Tomasello, Call, & Hare, 1998; Warren, 1965). One

112   approach that attempts to alleviate such concerns is the comparative method (Harvey &

113   Pagel, 1991). Closely related species may be expected to share similar physiological and

114   cognitive traits as a result of common descent. Hence, by comparing closely related species

115   that differ in certain socio-ecological aspects, any cognitive divergences can be attributed to

116   contrasts in a species ecology or life history (Balda, Kamil, & Bednekoff, 1996; Bond, Kamil, &

117   Balda, 2003; Bond et al., 2007; Day et al., 1999). Bond and colleagues (2003; 2007), for

118   example, used the comparative method to reveal that increased sociality among corvids

119   predicts aptitude on a number of cognitive tests; including serial reversal learning. An

approach that has been applied specifically to serial reversal learning paradigms to reduce the confounds of interspecific differences in perception, manual dexterity and motivation, among primates, is to standardise each species' pre-reversal acquisition performances (Rumbaugh & Pate, 1984a). That is, initially training subjects to a certain level of correct choices, irrespective of the number of trials that it takes to do so, and then comparing subjects' immediate performances after the contingencies have been reversed. Thus, the structural relationships of subjects' performances are assessed, rather than making direct comparisons based on the absolute number of trials that each species requires to solve a certain problem (Bitterman, 1960, 1975; Mackintosh, 1988). The extent of pre-reversal training, however, also appears to have contrasting influences on post-reversal performances across different species. Prosimians and monkeys, for example, tend to show impaired post-reversal performances when trained to a rigorous pre-reversal criterion of 84% correct choices, but enhanced post-reversal performances when trained to a low pre-reversal criterion of 67% correct choices (Rumbaugh & Pate, 1984b). Conversely, non-human apes show enhanced performances when trained to a high pre-reversal criterion of 84% correct choices and impaired post-reversal performances when trained to a low criterion of 67% correct choices (Rumbaugh & Pate, 1984b). Hence, as the strength of the learning criterion increases, prosimians and monkeys have difficulty inhibiting their responses to previously learned associations (De Lillo & Visalberghi, 1994; Rumbaugh & Pate, 1984a, 1984b). Consequently, prosimians and monkeys are considered to solve serial reversal problems through associative processes of repeated conditioning and extinction (De Lillo & Visalberghi, 1994; Rumbaugh, 1970; Rumbaugh & Pate, 1984b). Mixed results have however been reported for rhesus macaques (*Macaca mulatta*) (Essock-Vitale, 1978; Washburn & Rumbaugh, 1991) and capuchin monkeys (*Cebus apella*) (Rumbaugh, 1970) subjected to different testing procedures; although recent studies place capuchin performances among those of other monkeys rather than apes (Beran et al., 2008; De Lillo & Visalberghi, 1994). By contrast, the improved post-reversal performances of apes at high training criterions (Essock-Vitale, 1978; Rumbaugh & Pate, 1984a, 1984b) suggest that they may understand the underlying principles of serial reversals (Shettleworth, 2010) and have been considered to reveal greater flexibility in their learning performances (Rumbaugh & Pate, 1984a, 1984b).

150 Such qualitative differences in learning processes among primates suggest that the ability to

151 generalise conditional rules across reversal tasks may be cognitively demanding as it

152 appears restricted to larger-brained species, such as apes (Rumbaugh, 1971).

153 Parrots and corvids possess a large cortical-like area relatively to their overall brain

154 size (Iwaniuk, Dean, & Nelson, 2005) and high neuronal densities (Olkowicz et al., 2016),

155 which may reflect their ability to flexibly transfer rules to novel situations (Güntürkün,

156 Ströckens, Scarf, & Colombo, 2017). We are however unaware of any studies that have

157 directly compared the serial reversal learning performances of species of these families at

158 high and low pre-reversal criteria. Yet there is precedence to suggest that both families

159 demonstrate flexibility on similar paradigms. Red-billed blue magpies (*Urocissa*

160 *erythrorhyncha*) and Yellow-crowned Amazon parrots (*Amazona ochrocephala*), for instance,

161 outperformed White Leghorn chickens (*Gallus gallus domesticus*) and Bobwhite quails

162 (*Colinus virginianus*) on serial reversals of a spatial discrimination problem (Gossette,

163 Gossette, & Riddell, 1966). Corvids, in particular, show rule learning across a number of

164 different paradigms. For example, Eurasian jays (*G. glandarius*), jackdaws (*C. monedula*),

165 rooks (*C. frugilegus*) and crows (*C. corone*), but not pigeons (*C. Zivza*), demonstrate abilities

166 to solve problems that require the abstraction of a general rule across a change of stimuli,

167 such as matching or oddity discriminations (Wilson et al., 1985) and learning-set problems (N.

168 J. Mackintosh, 1988). Other corvids, such as pinion jays (*Gymnorhinus cyanocephalus*),

169 Clark's nutcrackers (*Nucifraga columbiana*) and western scrub jays (*Aphelocoma californica*)

170 also demonstrate capacities to positively transfer learned rules between colour and spatial

171 serial reversal problems (Bond et al., 2007). Finally, blue jays (*Cyanocitta cristata*) transfer

172 learned information from successive reversals to better solve learning set problems by

173 applying a *win stay–lose shift* strategy (Kamil, Jones, Pietrewicz, & Mauldin, 1977). Although

174 the above studies suggest that many species of corvids are capable of flexible learning, there

175 are few studies that use comparable paradigms to investigate such flexibility in parrots. Yet

176 there is convincing evidence to suggest flexible learning in parrots, such as an ability to

177 understand abstract concepts of category and of *same-different* discriminations (Pepperberg,

178 1983; 1987; 1988), transfer physical concepts of object relations across novel problems (van

179 Horik & Emery, 2016), and their performances on an array of complex problems show

similarities to those of non-human primates and human children (Pepperberg, 2013). Together these findings suggest that parrots and corvids, along with apes, demonstrate capacities for generalised learning and flexible behaviour.

Parrots are a suitable family for investigating behavioural and cognitive flexibility as they are K-selected (Pepperberg, Gray, Lesser, & Hartsfield, 2017), and share with apes and corvids many of the socio-ecological traits that have been considered prerequisites for the evolution of cognition, such as a relatively large brain size, manual dexterity, extractive foraging, longevity and a large multi-layered social organisation (van Horik & Emery, 2011; van Horik, Clayton, & Emery, 2012). Two experiments are reported in the current study. In the first experiment, red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephala*) were presented with a serial reversal learning task involving colour discriminations. The performances of each species were compared as a suggested index of their behavioural flexibility (Bond et al., 2007). To validate claims of behavioural flexibility, we first compared the reversal learning performances of two species of social parrots, black-headed caiques and red-shouldered macaws, on a serial reversal learning task. Previous findings suggest that socio-ecological differences can influence serial reversal learning performances in corvids (Bond et al., 2003, 2007). As both red-shouldered macaws and black-headed caiques possess a similar relative brain size (Iwaniuk et al., 2005) and live in complex social groups (Juniper & Parr, 2003), we may therefore expect both species to demonstrate similar responses to the alternating contingencies. However, given that red-shouldered macaws and black-headed caiques naturally inhabit contrasting environments (Juniper & Parr, 2003), any difference in their ability to respond flexibly to a serial reversal paradigm may also result from cognitive adaptations that are driven by the respective selection pressures of a given environment.

To further investigate behavioural flexibility in parrots, we also presented subjects with a second experiment. Here two alternative hypotheses are addressed: (1) that parrots' reversal learning performances improve solely through processes of associative learning, conditioning and extinction; or (2) that parrots are capable of alternative modes of learning, by generalising conditional rules across serial reversal discrimination problems. To do this, all subjects were pooled and randomly assigned to one of two conditions that required either a

210   high or low learning criterion of successful discriminations prior to each reversal. High

211   Criterion subjects were therefore exposed to a stricter pairing of the colour associations and

212   hence may be confronted with greater interference during their post-reversal trials, potentially

213   requiring a greater number of trials to extinguish and then re-learn each new contingency. By

214   contrast, subjects exposed to a Low Criterion of learning may experience less interference

215   during post-reversal trials. Hence, if parrots use only associative learning to solve each

216   reversal problem, then we predict subjects in the High Criterion group to make more errors

217   than Low Criterion subjects. Conversely, if subjects in the High Criterion group solve post-

218   reversals with fewer errors than Low Criterion subjects, then there must be some additional

219   generalisation of information across reversals; suggesting that their performances may be

220   facilitated by the use of conditional rules.

221

222

223   **GENERAL METHODS**

224

225   *Subjects and Housing*

226   Four red-shouldered macaws: No.2, No.4, No.5, and No.8, and four black-headed caiques:

227   Green, Gold, Purple, and Red, participated in this study (hereafter macaws and caiques). All

228   subjects were male, with the exception of one female macaw (No.4). All subjects were hand-

229   reared, approximately two years old when tested. Each species was housed in a separate

230   indoor aviary ($2m^3$). None of the subjects had experience with serial reversal learning tasks,

231   but they were experienced with a number of tasks employing object manipulation, including

232   removing food hidden under lids or cups. Both species were raised under identical conditions

233   and provided with equal experiences. Food and water were provided *ad libitum* and subjects'

234   participation was voluntary.

235

236   *Apparatus and Training*

237   Two 6 cm diameter plastic lids, of different colours (depending on the experiment; see details

238   below), were attached to a symmetrical wooden base (28 cm x 7 cm), and separated by 12

239   cm. Both lids were fixed to hinges and each concealed a food-well that could be baited with a

240   reward of crushed Lafeber Nutri-Berries. More specific details of the experimental procedures

241   are provided below. During training trials, the apparatus was presented to subjects without

242   lids and with one food-well containing a reward. After subjects fed from the apparatus without

243   hesitation, an orange lid was fixed to each of the baited food wells, again with only one well

244   baited. The location of the baited well was pseudorandomised across training trials so that it

245   did not occur on the same side over more than two consecutive trials. This procedure

246   attempted to control for the formation of side biases and facilitate subjects' searching

247   behaviours. To proceed to test, subjects were required to retrieve the concealed food by

248   opening the lids at least ten times in one 10min session. Training trials were conducted *ad*

249   *hoc* and no data were recorded for these sessions, as performances between birds were not

250   comparable as some individuals required greater encouragement to interact with the

251   apparatus through social facilitation from the experimenter.

252

253   *Procedure*

254   Subjects were not food deprived, although testing was conducted in the morning prior to their

255   regular feeding schedule. Each subject was provided with one session of 10 trials per day.

256   The presentation of rewarded and un-rewarded coloured lids was counterbalanced across

257   subjects. To prevent the development of side biases, the position of the lids (i.e. left or right

258   hand side presentation) was pseudorandomised within sessions so that the lids did not occur

259   on the same side for more than two consecutive trials. Each subject was tested individually in

260   a familiar enclosure ($2m^3$) where they were visually isolated from all other subjects. During

261   testing days, all subjects participated in the experiment in a randomised order. Subjects were

262   familiar with being handled by the experimenter and were transferred to the experimental

263   cage by hand. Daily trials typically began at 08:30 and ceased around 13:00 although

264   duration of each testing session, and the corresponding inter-trial intervals, varied depending

265   on the subject's motivation to interact with the apparatus. The duration of a typical testing

266   session was between 15-20 minutes per bird. During testing trials, the experimenter

267   attempted to avoid providing subjects with any inadvertent cues to the location of the

268   concealed reward by holding and presenting the apparatus in a symmetrical fashion and then

269   placing his hands behind his back and looking only at the centre of the apparatus. Moreover,

270   we consider it unlikely that experimenter cues influenced performances as similar studies

271   have shown that African grey parrots do not readily attend to an experimenters eye-gaze

272   direction (Giret, Miklósi, Kreutzer, & Bovet, 2009). Subjects were only allowed to upturn one

273   lid per trial and were considered to have made a correct choice if they chose the baited lid.

274   Hence, if subjects upturned the correct lid, they were allowed to retrieve the food reward.

275   However, if subjects upturned the un-baited lid, then the apparatus was immediately

276   removed. If subjects failed to upturn the baited lid on one trial, the succeeding trials followed

277   the predetermined pseudorandomised order. The apparatus was re-baited out of view of the

278   subject. Subjects that chose the same side over six consecutive trials in one block were

279   considered to have developed a side bias. To correct for side biases, we presented the baited

280   lid on the non-preferred side until the subject chose the baited side for two consecutive trials.

281   Trials then reverted to the original pseudorandomised configuration. All trials, including side-

282   bias-corrected and non-corrected trials were included in the subsequent analyses. We

283   recorded all trials with a digital camcorder (JVC Everio, Model No. GZ-MG645BEK, Malaysia)

284   and scored the number of number of trials and the number of errors to reach criterion for the

285   initial colour association and for each subsequent reversal.

286

287   *Data Analysis*

288   Details of the number of correct trials to reach the reversal criterion, for each experiment, are

289   described in the corresponding sections below. As any effects of extinction were expected to

290   be most prominent in the initial post-reversal trials (Bond et al., 2007), reversal learning

291   performances were assessed by comparing differences in errors in the first 10 post-reversal

292   trials across subsequent reversals. We ran separate Generalised Linear Mixed-Effect Models

293   (GLMM) with a poisson error structure for our two dependent variables (trials to criterion, and

294   number of errors made in the first 10 post reversal trials), in R version 1.1.383 (R

295   Development Core Team, 2014) using the lme4 package (Bates, Maechler, Bolker, & Walker,

296   2015). In each model (depending on the experiment) we included either species, or criterion

297   (high or low) as fixed effects and bird identify as a random effect to control for

298   pseudoreplication. Observational Level Random Effect (i.e. row number) were also included

299   in each model to control for overdispersion (Harrison, 2014). In Experiment 1, we used GLMM

300   to compare performances between species, by assessing the number of trials each species

301   took to reach criterion in the initial colour association and first reversal discriminations. We

302   also used GLMM to compare the number of trials each species took before reaching criterion

303   and the number of errors they made in the first 10 post reversal trials across reversals. In

304   Experiment 2, we used GLMM to assess performances between the High and Low Criterion

305   groups by comparing the number of trials to reach each criteria and number of errors made in

306   the first 10 post reversal trials for each reversal. A random subset of 46 sessions (724 trials)

307   were coded by three naïve observers (KW and LH) for inter-observer reliability. Observers

308   coded whether the subject made a correct or incorrect choice on a given trial. Observer

309   congruence was 98%.

310

311   **EXPERIMENT 1: Serial reversal learning performances**

312

313   **Methods**

314

315   *Apparatus*

316   The same apparatus as in the training sessions was used but with novel coloured lids, one

317   green and one blue.

318

319   *Procedure*

320   Subjects were presented with at least one block of 10 trials per day. If subjects reached a

321   predetermined criterion of seven consecutive correct trials in one block of 10 trials (significant

322   according to a binomial test with a probability of choosing either side set at 0.5), they were

323   immediately presented with one block of 10 trials with reversed contingencies (i.e. S+

324   becomes S– and vice versa). To avoid satiation and encourage motivation to interact with the

325   apparatus, subjects were presented with only one post-reversal block per day. Hence,

326   subjects could receive a maximum of only two consecutive blocks of 10 trials per day. There

327   were no occurrences where subjects reached criterion again during their first post-reversal

328 block. Each subject was presented with as many blocks as required to reach eight serial

329 reversals.

330

331 **Results**

332 Both species required fewer trials to reach criterion on the colour association discrimination

333 than in the first reversal (GLMM: $Z = 4.89 \pm 0.14$ SEM; $P < 0.001$, Figure 1). However,

334 macaws required fewer trials than caiques to reach criterion on the initial colour association

335 discrimination and the first reversal (GLMM: $Z = -2.10 \pm 0.14$ SEM; $P = 0.04$, Figure 1). Yet,

336 there were no overall differences in performances between caiques and macaws across the

337 serial reversals (Figure 2a). The two species did not differ in the number of trials to reach

338 criterion (macaws summed trials mean = 493.25 ± 67.55 SEM; caiques summed trials mean

339 = 539.50 ± 44.23 SEM; GLMM: $Z = -0.72 \pm 0.10$ SEM; $P = 0.47$) or errors made in their first

340 10 post reversal trials (macaws summed errors mean = 57.25 ± 2.18 SEM; caiques errors

341 mean = 61.75 ± 1.37 SEM; GLMM: $Z = -0.73 \pm 0.12$ SEM; $P = 0.46$) across the serial reversal

342 discriminations (Figure 2). We found no difference in errors, or trials across serial reversals

343 (Table 1).

344   The number of initial post-reversal blocks (i.e. the first ten trials after each reversal of

345 the colour contingencies) where subjects developed a side bias were as follows (R1

346 represents the first reversal; R8 represents the last reversal): Macaws; No.2 (R1), No.4 (R7,

347 R8), No.5 (R5), No.8 (R2, R6, R7), Caiques; Green (R2, R4, R6), Gold (R5), Purple (R5, R6,

348 R8), Red (R3, R6).

349

350 -----------INSERT Figure 1--------------

351 -----------INSERT Figure 2--------------

352 -----------INSERT Table 1--------------

353

354

355 **EXPERIMENT 2: High Criterion and Low Criterion Learning**

356

Methods

Subjects, Apparatus and Training

The same subjects and general procedures as in Experiment 1 were used, however, in this experiment novel coloured lids, either pink with a green circle sticker or yellow with an orange circle sticker, were introduced. The presentation order of the rewarded colour lids was counterbalanced across subjects.

Procedure

As no between species differences were observed in Experiment 1, subjects were pooled and individuals from each species were randomly assigned into either High or Low Criterion conditions. Subjects were presented with an initial discrimination problem requiring them to learn the Colour Associations, as in Experiment 1, and then subsequent serial reversal trials. However, in this experiment, each block consisted of up to 20 trials (rather than the 10 trial blocks presented in the previous experiment).

The High Criterion group (No.4, No.5, Green & Red) were presented with reversals once they scored at least 19/20 correct choices in one 20 trial session. Conversely, the Low Criterion group (No.2, No.8, Gold & Purple) were presented with reversals once they achieved either: 15 correct choices in one 20 trial session, 7 consecutive correct choices in the first 10 trials of one session, 9/10 correct choices in either the first or last 10 trials of a 20 trial session, or 10 consecutive correct choices within one 20 trial session. The Low Criterion group included multiple pre-reversal criteria to ensure that the number of trials subjects required to reach each learned association was minimised and hence subjects were not over-trained. All criteria were significant according to a binomial test, with a probability of choosing either side set at 0.5, and alpha set at 0.05. Subjects were presented with as many trials as required to reach 11 reversals.

If subjects reached criterion within one 20 trial session, they were immediately presented with one reversal session. On two occasions, subjects (No.8 and Gold) reached criterion within

13

387   their first post-reversal session (on the same day). On these occasions, we did not provide a

388   further post-reversal session and resumed testing on the following day. Subjects therefore

389   experienced a maximum of up to 40 trials per day. These procedures were used to maintain

390   motivation by prohibiting subjects from becoming satiated on rewards. Side biases were

391   corrected for, and all corrected and non-corrected trials were included in the analysis as in

392   Experiment 1. We ceased testing individual subjects once they had participated in 11

393   reversals. All trials were coded live but digitally recorded for subsequent analysis if required.

394

395   **Results**

396   Low Criterion (mean = 72.75 ± 23.86 SEM) and High Criterion (mean = 75 ± 9.57 SEM)

397   groups did not differ in the number of trials to reach criterion during the initial Colour

398   Association discriminations (GLMM: Z = 0.92 ± 0.16 SEM; P = 0.36). There were also no

399   differences in the number of trials to reach criterion between the Colour Association and first

400   Reversal (GLMM: Z = 1.45 ± 0.16 SEM; P = 0.15). There were no differences in the number

401   of trials to complete 11 serial reversals between the High and Low Criterion groups (Low

402   summed mean = 744.75 ± 24.87 SEM; High summed mean = 695 ± 28.72 SEM; GLMM: Z =

403   0.85 ± 0.11 SEM; P = 0.39). However, subjects in the High Criterion group made fewer errors

404   during the first 10 post reversal trials across successive reversals (R1-R11) than subjects in

405   the Low Criterion group (GLMM: Z = -3.58 ± 0.09 SEM; P < 0.001; Figure 3). The number of

406   errors, and trials to reach criterion differed across reversals (Table 3; Table 4). Subjects in the

407   High Criterion condition showed a consistent reduction in post reversal errors from their

408   seventh reversal onwards (Table 3), and a reduction in the number of trials to reach criterion

409   from their third reversal (Table 4). Conversely, subjects in the Low Criterion condition showed

410   no reduction in errors across serial reversals (Table 3), and an inconsistent reduction in trials

411   to reach criterion on their fourth, seventh and ninth reversals (Table 4).

412   The number of initial blocks where subjects developed a side bias were as follows:

413   High Criterion; No.4 (R4, R10), No.5 (R4, R5), Green (R6), Red (R1), Low Criterion; No.2

414   (R3), No.8 (R1, R2, R7, R10, R11), Gold (R4, R5, R9, R10, R11), Purple (R2, R3, R7, R10,

415   R11).

416

417 -----------INSERT Figure 3-------------

418 -----------INSERT Table 2-------------

419 -----------INSERT Table 3-------------

420

421 **DISCUSSION**

422 In Experiment 1, the serial reversal learning performances of two species of parrots were

423 investigated, as a suggested index of their behavioural flexibility (Bond et al., 2007). Macaws

424 took fewer trials to reach criterion during the initial Colour Acquisition and first reversal. It is

425 unlikely that these findings were due to differences in experiences, as both species had been

426 reared, from birth, in a standardised environment with identical enrichment. It is possible that

427 the superior performance of macaws was due to subtle differences in their overall brain-size;

428 macaws 4.29% vs caiques 3.80% of body mass (Iwaniuk et al., 2005), yet sample sizes are

429 low for such comparisons (macaws n = 3; caiques n = 8) and hence such interpretations

430 remain speculative. Both species, however, showed comparable performances across

431 subsequent serial reversals. Both species required more trials to reach criterion during the

432 first reversal than compared to the Colour Association problem, suggesting that the previously

433 learned contingencies initially impaired subjects' reversal performance. Hence, both species

434 required trial and error experience of the reversed contingencies to first extinguish previously

435 learned associations and then re-learn each following association anew. However, when

436 trained to a pre-reversal criterion of seven consecutive correct choices in one block of 10

437 trials per day, we found no improvement in performances across serial reversals. Although a

438 variety of taxa demonstrate improvements in performance across serial reversals (Bond et al.,

439 2007; Day et al., 1999; Strang & Sherry, 2014), it remains possible that either the learning

440 criteria in the current study was not stringent enough to facilitate improvement across

441 reversals for caiques and macaws, or that these birds required a greater number of serial

442 reversals before any improvement could be observed.

443 To determine whether the serial reversal learning performance of red-shouldered

444 macaws and black-headed caiques were mediated solely by associatively learned processes

445 or whether they were capable of using conditional rules to improve their performance, we

446 randomly assigned two individuals from each species to either a High or a Low Criterion pre-

447 reversal learning condition (Experiment 2). Although there were no differences in the number

448 of trials to learn the Colour Association between the Low and High Criterion groups, subjects

449 in the High Criterion group made fewer post-reversal errors than subjects in the Low Criterion

450 group across 11 serial reversals. These findings suggest that subjects in the High Criterion

451 group may therefore use the enhanced strength of previously learned contingencies to

452 improve their reversal performances; in contrast to subjects in the Low Criterion group, which

453 showed no improvement across reversals.

454 When presented with reversed contingencies, each previously learned association

455 requires a number of trials before it is lost through extinction. Each new association then

456 requires further trials to re-learn through conditioning. In the current study, the relatively poor

457 performances of Low Criterion subjects suggests that their response to the reversals was

458 limited to associative learning processes. Conversely, when presented with a high pre-

459 reversal criterion, subjects made fewer post-reversal errors across successive reversals.

460 Rather than being impaired by the enhanced strength of the conditioned associations,

461 subjects appear to use this information to better understand the conditional principles

462 underlying serial reversals. Such findings are consistent with the reversal performances of

463 other large-brained species, such as non-human great apes, but contrast with those of

464 monkeys and prosimians (Essock-Vitale, 1978; Rumbaugh & Pate, 1984a, 1984b). Although

465 the enhanced associative strength of the contingencies may have allowed subjects to better

466 respond to the reversed contingencies by generating a conditional rule, these findings show

467 no evidence of a *win stay-lose shift* rule within 11 serial reversals. Support for a *win stay-lose*

468 *shift* rule would only be revealed if subjects made one error after they experienced an

469 unpredicted reversal of the previously learned contingencies. High Criterion subjects,

470 however, made approximately three errors in their first 10 post reversal trials; although their

471 performances may have improved with further experience. Nonetheless, results from the

472 current study support our second hypothesis that parrots' reversal performances are not

473 solely restricted by associative learning mechanisms, but that parrots may be capable of

474 other cognitive modes of learning that involve an ability to generalise conditional rules across

475 discrimination problems.

16

476   It is possible, albeit unlikely, that the High Criterion group produced fewer post

477   reversal errors due to an Overtraining Reversal Effect (ORE). First observed by Reid (1953),

478   the ORE is a phenomenon where overtraining on discrimination problems enhances post-

479   reversal performances. Reid (1953) presented rats with a black-white discrimination problem

480   in a Y maze. All of the rats were initially trained to a specific criterion, and then separated into

481   three conditions depending on the amount of their post-criterion training. Rats exposed to

482   increasingly rigorous training regimes made fewer post-reversal errors. Such findings are

483   considered paradoxical as overtraining, according to classical learning theory, is predicted to

484   increase the excitatory strength of S+ and inhibitory strength of S– and thus impede extinction

485   when contingencies are reversed (Hull, 1943; Spence, 1956). Although ORE is commonly

486   observed in rat studies, it is rarely reported in monkeys (Essock-Vitale, 1978; Sutherland &

487   Mackintosh, 1971), with the exception of one account from stump-tailed macaques (Schrier,

488   1974). Typically, when presented with increasing numbers of acquisition trials, monkeys show

489   impaired post reversal performances and do not improve with subsequent experience. Like

490   monkeys, overtraining has also been reported to impair reversal performances in birds, such

491   as myna (Gossette, 1969), chicks (Mackintosh, 1965; Warren, Brookshire, Ball, & Reynolds,

492   1960), pigeons and Japanese quail (Gonzalez, Berger, & Bitterman, 1966), suggesting that in

493   these species, the ability to learn each new contingency is governed by processes of

494   association and extinction. However, it has been suggested that post-reversal performances

495   typical of an ORE should not only improve following overtraining, but that performances on

496   early post-reversal trials should also be initially impaired following overtraining (Sutherland &

497   Mackintosh, 1971; pp. 258-261). In the current study, subjects in the High Criterion condition

498   showed a significant reduction in errors across subsequent reversals, although subjects in the

499   Low Criterion condition did not improve their performances. If these findings were due to an

500   ORE, we might also expect subjects in the High Criterion condition to perform significantly

501   worse than Low Criterion subjects during initial reversals. However, performances on the first

502   10 post-reversal trials across the first three reversals were comparable for both Low and High

503   Criterion subjects (see R1-R3; Figure 3), revealing that subjects were not initially impaired by

504   differences in reversal criteria. These findings therefore suggest that subjects' performances

505   in the High Criterion condition were unlikely to be a result of an ORE.

506   Parrots in the current study, like corvids (Bond et al., 2007; Hunter & Kamil, 1971;

507   Mackintosh, 1988; Wilson et al., 1985) and non-human great apes (Essock-Vitale, 1978;

508   Rumbaugh & Pate, 1984a, 1984b), show capacities for generalised rule learning of reversal

509   learning discrimination problems. Rumbaugh (1995) argues that great apes, because of their

510   ability to transfer abstract information across reversal tasks, are capable of mediating their

511   behaviours through more cognitively demanding modes of learning than monkeys and

512   prosimians. Such findings also correspond with species' encephalisation coefficients (Jerison,

513   1973; Rumbaugh & Pate, 1984b), suggesting there may be a link between relative brain size

514   and behavioural flexibility (Emery & Clayton, 2004). Further evidence of generalised learning

515   strategies, demonstrated by the positive transfer of information across serial reversal or

516   learning set tasks involving disparate stimulus dimensions (i.e. space and colour), also

517   support our findings. For example, chimpanzees and a number of species of macaques

518   (reviewed in Macphail, 1982) and corvids (Bond et al., 2007; Gossette et al., 1966; Kamil et

519   al., 1977; Mackintosh, 1988; Wilson et al., 1985) rapidly develop generalised learning

520   strategies, whereas rats, cats, and pigeons do not (Durlach & Mackintosh, 1986; Mackintosh

521   & Holgate, 1969; Mackintosh, McGonigle, Holgate, & Vanderver, 1968; Warren, 1966). More

522   recently however, pigeons have been shown to adopt a *win stay–lose shift* rule when

523   presented with a mid-session reversal task involving short inter-trial intervals (Rayburn-

524   Reeves, Laude, & Zentall, 2013).

525   There are growing accounts of flexible behaviours in parrots and corvids (Auersperg,

526   Szabo, Von Bayern, & Kacelnik, 2012; Auersperg, von Bayern, Gajdon, Huber, & Kacelnik,

527   2011; Pepperberg & Carey, 2012). The relationship between brain size and behavioural

528   flexibility suggests that relatively large brains may afford a selective advantage when

529   responding to unusual, novel or complex socio-ecological challenges. For instance, large

530   brains may provide a foundation for novel or altered behaviours, which may be applied to

531   solve an array of problems through domain general cognitive processes (Sol, 2009).

532   Moreover, as relatively large brains are found across phylogenetically distinct species, certain

533   cognitive traits may have also evolved independently among several vertebrate groups that

534   share similar socio-ecological selection pressures (van Horik et al., 2012). Indeed, brain size

535   appears to be a good proxy for the ability of species to flexibly respond to environmental

536 change and hence fluctuations in resource abundance. As such, relative brain size correlates

537 positively with the ability of species to accommodate habitat change (Shultz, Bradbury,

538 Evans, Gregory, & Blackburn, 2005), climatic change (Schuck-Paim, Alonso, & Ottoni, 2008),

539 invade novel environments (Sol, Bacher, Reader, & Lefebvre, 2008; Sol, Duncan, Blackburn,

540 Cassey, & Lefebvre, 2005; Sol, Székely, Liker, & Lefebvre, 2007; Sol, Timmermans, &

541 Lefebvre, 2002; Sol & Lefebvre, 2000) and generate innovative foraging behaviours

542 (Lefebvre, Reader, & Sol, 2004; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Reader &

543 Laland, 2002). Hence, large brains may be particularly advantageous in complex

544 environments or habitats that are novel or likely to change.

545   Given that red-shouldered macaws and black-headed caiques naturally inhabit

546 contrasting environments (Juniper & Parr, 2003), such differences do not appear to have

547 resulted in any obvious divergences in their abilities to respond flexibly to a serial reversal

548 paradigm. Both macaws and caiques, however, possess a similar relative brain size (Iwaniuk

549 et al., 2005), and share a complex social organisation characterised by long-term pair bonded

550 relationships and fission-fusion foraging groups (Juniper & Parr, 2003). Similarities in the

551 complexity of their social relationships, rather than habitat or foraging niche, may therefore

552 promote behavioural flexibility in these species. Social complexity has long been considered

553 to play an important role in the evolution of a flexible and intelligent mind (Social Intelligence

554 Hypothesis: Humphrey 1976; Jolly, 1966), with social group size and neocortex size

555 corresponding positively in primates (Dunbar, 1998), ungulates (Shultz & Dunbar, 2006) and

556 cetaceans (Marino, 1996). Brain size also correlates positively in birds and mammals that

557 form stable or pair-bonded relationships (Dunbar & Shultz, 2007; Emery, Seed, von Bayern, &

558 Clayton, 2007; Shultz & Dunbar, 2006). Species that live in social groups, in contrast to more

559 solitary or asocial species, may therefore develop particular cognitive adaptations to

560 accommodate for the additional complexities that arise from maintaining relationships and

561 flexibly interpreting others' behaviours. Hence, primates that live in groups characterised by

562 fission-fusion social dynamics also show enhanced inhibitory control (another proposed index

563 of behavioural flexibility), in contrast to species that live in more cohesive groups. Fission-

564 fusion societies may therefore promote cognitive adaptations that result in greater

565 behavioural flexibility; independent of phylogenetic relatedness or feeding ecology (Amici,

Aureli, & Call, 2008). Capacities for inhibitory control have previously been demonstrated in parrots (Auersperg, Laumer, & Bugnyar, 2013; Koepke, Gray, & Pepperberg, 2015; Vick, Bovet, & Anderson, 2010) and corvids (Dufour, Wascher, Braun, Miller, & Bugnyar, 2012; Hillemann, Bugnyar, Kotrschal, & Wascher, 2014) on delayed gratification tasks. Serial reversal learning also involves inhibitory control, as it requires an ability to restrain responses to previously reinforced stimuli, and instead flexibly direct behaviours towards potentially unrewarded alternatives. Hence, it has been proposed that serial reversal learning bears resemblance to the demands of a complex social system (Bond et al., 2007). Comparative research on corvids provides support for such claims by revealing that variation in performances on serial reversal and transitive inference tasks are best explained by social complexity, rather than ecological or spatial complexity (Bond et al., 2003, 2007). The reversal learning performances in the two species of social parrots reported here may further support such claims. As such, social living may facilitate cognitive adaptations that favour an individual's ability to interpret, predict and respond flexibly to change. Behavioural flexibility may be shared among species that possess a relatively large brain size. As such, flexibility has been suggested as one of the fundamental cognitive tools that arose as a result of the evolution of complex cognition in corvids and apes (Emery & Clayton, 2004). Overall, findings from the current study provide further empirical support of an evolutionary convergence of behavioural flexibility between distantly related species that possess a relatively large brain size.

ETHICAL STANDARDS

All research undertaken was non-invasive and therefore fell outside of the Animal (Scientific Procedures) Act, and hence did not require Home Office UK approval. Subjects were however housed in accordance with these regulations and the local ethical committee were consulted and agreed to all aspects of this research. Home Office Inspectors and veterinarians regularly visited the lab to ensure these procedures were maintained.

596

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

599

REFERENCES

Amici, F., Aureli, F., & Call, J. (2008). Fission-Fusion Dynamics, Behavioral Flexibility, and
Inhibitory Control in Primates. *Current Biology*, *18*(18), 1415–1419.
https://doi.org/10.1016/j.cub.2008.08.020

Auersperg, A. M. I., Laumer, I. B., & Bugnyar, T. (2013). Goffin cockatoos wait for qualitative
and quantitative gains but prefer "better" to "more". *Biology Letters*, *9*(3), 20121092.
https://doi.org/10.1098/rsbl.2012.1092

Auersperg, A. M. I., Szabo, B., Von Bayern, A. M. P., & Kacelnik, A. (2012). Spontaneous
innovation in tool manufacture and use in a Goffin's cockatoo. *Current Biology*, *22*(21),
1–2. https://doi.org/10.1016/j.cub.2012.09.002

Auersperg, A. M. I., von Bayern, A. M. P., Gajdon, G. K., Huber, L., & Kacelnik, A. (2011).
Flexibility in problem solving and tool use of kea and new caledonian crows in a multi
access box paradigm. *PLoS ONE*, *6*(6). https://doi.org/10.1371/journal.pone.0020231

Balda, R. P., Kamil, A. C., & Bednekoff, P. a. (1996). Predicting cognitive capacity from
natural history: Examples from four species of Corvids. *Current Ornithology*, *13*, 33–66.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models
Using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Beran, M. J., Klein, E. D., Evans, T. A., Chan, B., Flemming, T. M., Harris, E. H., …
Rumbaugh, D. M. (2008). Discrimination reversal learning in capuchin monkeys (Cebus
apella). *The Psychological Record*, 3–14.

Bitterman, M. E. (1960). Toward a comparative psychology of learning. *American
Psychologist*, *15*, 704–712. https://doi.org/10.1037/h0048359

Bitterman, M. E. (1965). Phyletic Differences in Learning. *The American Psychologist*, *20*,
396–410. https://doi.org/10.1037/h0022328

Bitterman, M. E. (1975). The Comparative Analysis of Learning Are the laws of learning the
same in all animals ? *Science*, *188*(4189), 699–709.

626 Blaisdell, A. P., & Cook, R. G. (2005). Two-item same-different concept learning in pigeons.

627   *Learning & Behavior*, *33*(1), 67–77. https://doi.org/10.1007/3-540-35375-5

628 Bond, A. B., Kamil, A. C., & Balda, R. P. (2003). Social complexity and transitive inference in

629   corvids. *Animal Behaviour*, *65*(3), 479–487.

630   https://doi.org/http://dx.doi.org/10.1006/anbe.2003.2101

631 Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of

632   behavioral flexibility in three species of North American corvids (Gymnorhinus

633   cyanocephalus, Nucifraga columbiana, Aphelocoma californica). *Journal of Comparative*

634   *Psychology (Washington, D.C. : 1983)*, *121*(4), 372–9. https://doi.org/10.1037/0735-

635   7036.121.4.372

636 Breland, K., & Breland, M. (1961). The misbehavior of organisms. *American Psychologist*,

637   *16*(11), 681–684. https://doi.org/10.1037/h0040090

638 Cook, R. G., & Brooks, D. I. (2009). Generalized auditory same-different discrimination by

639   pigeons. *Journal of Experimental Psychology. Animal Behavior Processes*, *35*(1), 108–

640   115. https://doi.org/10.1037/a0012621

641 Day, L., Crews, D., & Wilczynski, W. (1999). Spatial and reversal learning in congeneric

642   lizards with different foraging strategies. *Animal Behaviour*, *57*(2), 393–407.

643   https://doi.org/10.1006/anbe.1998.1007

644 De Lillo, C., & Visalberghi, E. (1994). Transfer index and mediational learning in Cebus

645   apella. *Ethology Ecology & Evolution*, *5*(2), 390–391.

646   https://doi.org/10.1080/08927014.1993.9523044

647 Dufour, V., Wascher, C. a F., Braun, A., Miller, R., & Bugnyar, T. (2012). Corvids can decide if

648   a future exchange is worth waiting for. *Biology Letters*, *8*(2), 201–4.

649   https://doi.org/10.1098/rsbl.2011.0726

650 Dunbar, R. I. M. (1998). The Social Brain Hypothesis. *Evolutionary Anthropology*, 178–190.

651   https://doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.3.CO;2-P

652 Dunbar, R. I. M., & Shultz, S. (2007). Understanding primate brain evolution. *Philosophical*

653   *Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 649.

654   https://doi.org/10.1098/rstb.2006.2001

655 Durlach, P. J., & Mackintosh, N. (1986). Transfer of serial reversal learning in the pigeon. *The*

656   *Quarterly Journal of Experimental Psychology. B, Comparative and Physiological*

657   *Psychology*, *38*(1), 81–95.

658   Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of

659   intelligence in corvids and apes. *Science (New York, N.Y.)*, *306*(5703), 1903–1907.

660   https://doi.org/10.1126/science.1098410

661   Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive

662   adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society*

663   *of London. Series B, Biological Sciences*, *362*(1480), 489–505.

664   https://doi.org/10.1098/rstb.2006.1991

665   Essock-Vitale, S. M. (1978). Comparison of ape and monkey modes of problem solution.

666   *Journal of Comparative and Physiological Psychology*, *92*(5), 942–957.

667   https://doi.org/10.1037/h0077530

668   Giret, N., Miklósi, Á., Kreutzer, M., & Bovet, D. (2009). Use of experimenter-given cues by

669   African gray parrots (Psittacus erithacus). *Animal Cognition*, *12*(1), 1–10.

670   https://doi.org/10.1007/s10071-008-0163-2

671   Gonzalez, R., Berger, B., & Bitterman, M. (1966). Improvement in habit-reversal as a function

672   of the amount of training per reversal and other variables. *American Journal of*

673   *Pycholgy*, (79), 517–524. https://doi.org/10.1007/sl0869-007-9037-x

674   Gossette, R. L. (1969). Magnitude of negative transfer, 621–622.

675   Gossette, R. L., Gossette, M. F., & Riddell, W. (1966). Comparisons of successive

676   discrimination reversal performances among closely and remotely related avian species.

677   *Animal Behaviour*, *14*, 560–564. https://doi.org/10.1016/S0003-3472(66)80060-X

678   Güntürkün, O., Ströckens, F., Scarf, D., & Colombo, M. (2017). Apes, feathered apes, and

679   pigeons: differences and similarities. *Current Opinion in Behavioral Sciences*, *16*, 35–

680   40. https://doi.org/10.1016/j.cobeha.2017.03.003

681   Harrison, X. A. (2014). Using observation-level random e ff ects to model overdispersion in

682   count data in ecology and evolution. https://doi.org/10.7717/peerj.616

683   Harvey, P., & Pagel, M. (1991). *he comparative method in evolutionary biology*. Oxford:

684   Oxford University Press.

685   Hillemann, F., Bugnyar, T., Kotrschal, K., & Wascher, C. A. F. (2014). Waiting for better, not

686   for more: corvids respond to quality in two delay maintenance tasks. *Animal Behaviour*,

687   (90), 1–10. Retrieved from http://doi.org/10.1016/j.anbehav.2014.01.007

688 Hull, C. (1943). *Principles of behavior*. New York: Appleton- Century-Crofts.

689 Hunter, M. W., & Kamil, A. C. (1971). Object-discrimination learning set and hypothesis

690   behavior in the northern bluejay (Cynaocitta cristata). *Psychonomic Science*, *22*(5),

691   271–273. https://doi.org/10.3758/BF03335950

692 Iwaniuk, A. N., Dean, K. M., & Nelson, J. E. (2005). Interspecific allometry of the brain and

693   brain regions in parrots (Psittaciformes): Comparisons with other birds and primates.

694   *Brain, Behavior and Evolution*, *65*(1), 40–59. https://doi.org/10.1159/000081110

695 Jerison, H. (1973). *Evolution of the Brain and Intelligence*. New York: Academic Press.

696 Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science (New York, N.Y.)*,

697   *153*(3735), 501–506.

698 Juniper, T., & Parr, M. (2003). *Parrots: a guide to the parrots of the world*. London:

699   Christopher Helm.

700 Kamil, A. C., Jones, T. B., Pietrewicz, A., & Mauldin, J. E. (1977). Positive transfer from

701   successive reversal training to learning set in blue jays (Cyanocitta cristata). *Journal of*

702   *Comparative & Physiological Psychology*, *91*(1), 79–86.

703   https://doi.org/10.1037/h0077295

704 Katz, J. S., & Wright, A. A. (2006). Same/different abstract-concept learning by pigeons.

705   *Journal of Experimental Psychology: Animal Behavior Processes*, *32*(1), 80–86.

706   https://doi.org/10.1037/0097-7403.32.1.80

707 Koepke, A. E., Gray, S. L., & Pepperberg, I. M. (2015). Delayed gratification: A grey parrot

708   (Psittacus erithacus) will wait for a better reward. *Journal of Comparative Psychology*,

709   *129*(4), 339–346.

710 Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and

711   primates. *Brain, Behavior and Evolution*, *63*(4), 233–246.

712   https://doi.org/10.1159/000076784

713 Lefebvre, L., Whittle, P., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and

714   forebrain size in birds. *Animal Behaviour*, *53*(3), 549–560.

715   https://doi.org/10.1006/anbe.1996.0330

716   Levine, M. (1959). A Model of Hypothesis Behavior in Discrimination Learning Set.

717   *Psychological Review*, *66*(6), 353–366. https://doi.org/10.1037/h0044050

718   Levine, M. (1965). Hypothesis behavior. In A. Schrier, H. Harlow, & F. Stollnitz (Eds.),

719   *Behavior in Non-human Primates* (1st ed., pp. 97–127). NY: Academic Press.

720   Mackintosh, N. J. (1965). Overtraining, Reversal, and Extinction in Rats and Chicks. *Journal

721   of Comparative & Physiological Psychology*, *59*(1), 31–36.

722   https://doi.org/10.1037/h0021620

723   Mackintosh, N. J. (1988). Approaches to the study of animal intelligence. *British Journal of

724   Psychology*, (79), 509–525. https://doi.org/10.1111/j.2044-8295.1988.tb02749.x

725   Mackintosh, N. J., & Holgate, V. (1969). Serial reversal training and nonreversal shift learning.

726   *J Comp Physiol Psychol*, *67*(1), 89–93. https://doi.org/10.1037/h0026661

727   Mackintosh, N., McGonigle, B., Holgate, V., & Vanderver, V. (1968). Factors underlying

728   improvement in serial reversal learning. *Canadian Journal of Experimental Psychology*,

729   *22*(2), 85–95.

730   Macphail, E. (1982). *Brain and intelligence in vertebrates*. Oxford, England: Clarendon Press.

731   Marino, L. (1996). What can dolphins tell us about human evolution? *Evolutionary

732   Anthropology*, *5*, 81–86.

733   Obozova, T., Smirnova, A., Zorina, Z., & Wasserman, E. (2015). Analogical reasoning in

734   amazons. *Animal Cognition*, *18*(6), 1363–1371. https://doi.org/10.1007/s10071-015-

735   0882-0

736   Olkowicz, S., Kocourek, M., Lučan, R. K., Porteš, M., Fitch, W. T., Herculano-Houzel, S., &

737   Němec, P. (2016). Birds have primate-like numbers of neurons in the forebrain.

738   *Proceedings of the National Academy of Sciences*, *113*(26), 7255–7260.

739   https://doi.org/10.1073/pnas.1517131113

740   Pepperberg, I. M. (1983). Cognition in the African Grey parrot: Preliminary evidence for

741   auditory/vocal comprehension of the class concept. *Animal Learning & Behavior*, *11*(2),

742   179–185. https://doi.org/10.3758/BF03199646

743   Pepperberg, I. M. (1987). Acquisition of the same/different concept by an African Grey parrot

744   (Psittacus erithacus): Learning with respect to categories of color, shape, and material.

745   *Animal Learning & Behavior*, *15*(4), 423–432. https://doi.org/10.3758/BF03205051

746 Pepperberg, I. M. (1988). Comprehension of "absence" by an African Grey parrot: Learning

747   with respect to questions of same/different. *Journal of the Experimental Analysis of*

748   *Behavior*, *50*(3), 553–564. https://doi.org/10.1901/jeab.1988.50-553

749 Pepperberg, I. M. (2013). Abstract concepts: Data from a Grey parrot. *Behavioural*

750   *Processes*, *93*, 82–90. https://doi.org/10.1016/j.beproc.2012.09.016

751 Pepperberg, I. M., & Carey, S. (2012). Grey Parrot Number Acquisition: the Inference of

752   Cardinal Value from Ordinal Position on the Numeral List. *Cognition*, *125*(2), 219–232.

753   https://doi.org/http://doi.org/10.1016/j.cognition.2012.07.003

754 Pepperberg, I. M., Gray, S. L., Lesser, J. S., & Hartsfield, L. A. (2017). Piagetian liquid

755   conservation in grey parrots (Psittacus erithacus). ,. *Journal of Comparative Psychology*,

756   *131*(4), 370–383. https://doi.org/http://dx.doi.org/10.1037/com0000085

757 Pepperberg, I. M., & Hartsfield, L. A. (2014). Can Grey parrots (Psittacus erithacus) succeed

758   on a "complex" foraging task failed by nonhuman primates (Pan troglodytes, Pongo

759   abelii, Sapajus apella) but solved by wrasse fish (Labroides dimidiatus)? J. *Ournal of*

760   *Comparative Psychology*, *128*(3), 298–306.

761   https://doi.org/http://dx.doi.org/10.1037/a0036205

762 R Development Core Team. (2014). R: a language and environment for stastical computing.

763   Vienna Austria: R Foundation for Statistical Computing.

764 Rayburn-Reeves, R. M., Laude, J. R., & Zentall, T. R. (2013). Pigeons show near-optimal

765   win-stay/lose-shift performance on a simultaneous-discrimination, midsession reversal

766   task with short intertrial intervals. *Behavioural Processes*, *92*, 65–70.

767   https://doi.org/10.1016/j.beproc.2012.10.011

768 Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain

769   size in primates. *Proceedings of the National Academy of Sciences of the United States*

770   *of America*, *99*(7), 4436–4441. https://doi.org/10.1073/pnas.062041299

771 Reid, L. S. (1953). The development of noncontinuity behavior through continuity learning.

772   *Journal of Experimental Psychology*, *46*(2), 107–112. https://doi.org/10.1037/h0062488

773 Rumbaugh, D. (1995). Primate Language and Cognition: Common Ground. *Social Research*,

774   *62*(3), 711–730. https://doi.org/10.1111/psyp.12437.How

775 Rumbaugh, D. M. (1970). Learning skills of anthropoids. In L. Rosemblum (Ed.), *Primate*

776   *Behaviour: Developments in Field and Laboratory Research* (1st ed., pp. 1–70). New

777   York: Academic Press.

778 Rumbaugh, D. M. (1971). Evidence of qualitative differences in learning processes among

779   primates. *Journal of Comparative and Physiological Psychology*, *76*(2), 250–255.

780   https://doi.org/10.1037/h0031401

781 Rumbaugh, D. M., & Pate, J. L. (1984a). Primates' learning by levels. In G. Greenberg & E.

782   Tobach (Eds.), *Behavioural evolution and integrative levels* (pp. 221–240). Hillsdale, NJ:

783   Lawrence Erlbaum Associates.

784 Rumbaugh, D. M., & Pate, J. L. (1984b). The evolution of cognition in primates: a

785   comparative perspective. In N. Roitblat, T. Bever, & H. Terrace (Eds.), *Animal Cognition*

786   (pp. 569–587). Hillsdale, NJ: Lawrence Erlbaum Associates.

787 Salwiczek, L. H., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., … Bshary, R.

788   (2012). Adult Cleaner Wrasse Outperform Capuchin Monkeys, Chimpanzees and

789   Orang-utans in a Complex Foraging Task Derived from Cleaner - Client Reef Fish

790   Cooperation. *PLoS ONE*, *7*(11). https://doi.org/10.1371/journal.pone.0049068

791 Schrier, A. M. (1974). Transfer Between the Repeated Reversal and Learning Set Tasks :,

792   *87*(5), 1004–1010.

793 Schuck-Paim, C., Alonso, W. J., & Ottoni, E. B. (2008). Cognition in an ever-changing world:

794   Climatic variability is associated with brain size in neotropical parrots. *Brain, Behavior*

795   *and Evolution*, *71*(3), 200–215. https://doi.org/10.1159/000119710

796 Shettleworth, S. J. (2010). *Cognition, evolution, and behavior, 2nd ed.* New York, NY, US:

797   Oxford University Press.

798 Shultz, S., Bradbury, R. B., L Evans, K., Gregory, R. D., & Blackburn, T. M. (2005). Brain size

799   and resource specialization predict long-term population trends in British birds.

800   *Proceedings. Biological Sciences / The Royal Society*, *272*(1578), 2305–11.

801   https://doi.org/10.1098/rspb.2005.3250

802 Shultz, S., & Dunbar, R. I. M. (2006). Both social and ecological factors predict ungulate brain

803   size. *Proceedings of the Royal Society B-Biological Sciences*, *273*(1583), 207–215.

804   https://doi.org/10.1098/rspb.2005.3283

805 Smirnova, A., Zorina, Z., Obozova, T., & Wasserman, E. (2015). Crows spontaneously exhibit

806   analogical reasoning. *Current Biology*, *25*(2), 256–260.

807   https://doi.org/10.1016/j.cub.2014.11.063

808   Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains.

809   *Biology Letters*, *5*(1), 130–3. https://doi.org/10.1098/rsbl.2008.0621

810   Sol, D., Bacher, S., Reader, S. M., & Lefebvre, L. (2008). Brain size predicts the success of

811   mammal species introduced into novel environments. *The American Naturalist*, *172*

812   *Suppl*(july), S63-71. https://doi.org/10.1086/588304

813   Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains,

814   enhanced cognition, and response of birds to novel environments. *Proceedings of the*

815   *National Academy of Sciences of the United States of America*, *102*(15), 5460–5465.

816   https://doi.org/10.1073/pnas.0408145102

817   Sol, D., & Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds

818   introduced to New Zealand. *Oikos*, *90*(3), 599–605. https://doi.org/10.1034/j.1600-

819   0706.2000.900317.x

820   Sol, D., Székely, T., Liker, A., & Lefebvre, L. (2007). Big-brained birds survive better in

821   nature. *Proceedings of the Royal Society of London, Series B*, *274*(1611), 763–9.

822   https://doi.org/10.1098/rspb.2006.3765

823   Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success

824   in birds. *Animal Behaviour*, *63*(3), 495–502. https://doi.org/10.1006/anbe.2001.1953

825   Spence, K. (1956). *Behavior theory and conditioning*. New Haven, CT: Yale University Press.

826   Strang, C. G., & Sherry, D. F. (2014). Serial reversal learning in bumblebees (Bombus

827   impatiens). *Animal Cognition*, *17*(3), 723–734. https://doi.org/10.1007/s10071-013-0704-

828   1

829   Sutherland, N., & Mackintosh, N. (1971). *Mechanisms of animal discrimination learning*. New

830   York: Academic Press.

831   Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of

832   conspecifics. *Animal Behaviour*, *55*, 1063–1069. https://doi.org/10.1006/anbe.1997.0636

833   van Horik, J., & Emery, N. J. (2011). Evolution of cognition. *Wiley Interdisciplinary Reviews:*

834   *Cognitive Science*, *2*(6), 621–633. https://doi.org/10.1002/wcs.144

835   van Horik, J. O., Clayton, N. S., & Emery, N. J. (2012). Convergent Evolution of Cognition in

836   Corvids, Apes and Other Animals. *The Oxford Handbook of Comparative Evolutionary*

837   *Psychology*, 80–101. https://doi.org/10.1093/oxfordhb/9780199738182.013.0005

838   van Horik, J. O., & Emery, N. J. (2016). Transfer of physical understanding in a non-tool-using

839   parrot. *Animal Cognition*, *19*(6), 1195–1203. https://doi.org/10.1007/s10071-016-1031-0

840   Vick, S. J., Bovet, D., & Anderson, J. R. (2010). How do African grey parrots (Psittacus

841   erithacus) perform on a delay of gratification task? *Animal Cognition*, *13*(2), 351–358.

842   https://doi.org/10.1007/s10071-009-0284-2

843   Warren, J. M. (1965). The Comparative Psychology of Learning. *Annual Review of*

844   *Psychology*, *16*(1), 95–118. https://doi.org/10.1146/annurev.ps.16.020165.000523

845   Warren, J. M. (1966). Reversal learning and the formation of learning sets by cats and rhesus

846   monkeys. *Journal of Comparative and Physiological Psychology*, *61*(3), 421–428.

847   Warren, J. M., Brookshire, K. H., Ball, G. G., & Reynolds, D. V. (1960). Reversal learning by

848   White Leghorn chicks. *Journal of Comparative and Physiological Psychology*, *53*(4),

849   371–375. https://doi.org/10.1037/h0048127

850   Washburn, D. a, & Rumbaugh, D. M. (1991). Rhesus monkey (Macaca mulatta) complex

851   learning skills reassessed. *International Journal of Primatology*, *12*(4), 377–388*.*

852   Wilson, B., Mackintosh, N. J., & Boakes, R. A. (1985). Transfer of relational rules in matching

853   and oddity learning by pigeons and corvids. *The Quarterly Journal of Experimental*

854   *Psychology Section B*, *37*(789998259), 313–332.

855   https://doi.org/10.1080/14640748508401173

856   Zentall, T. R., Wasserman, E. A., Lazareva, O. F., Thompson, R. K., & Rattermann, M. J.

857   (2008). Concept Learning in Animals. *Comparative Cognition & Behavior Reviews*, *3*,

858   13–45. https://doi.org/10.3819/ccbr.2008.30002

859

860

Figure Legends:

Figure 1 Experiment 1. Mean number of trials (± SEM) to reach reversal criterion for the

colour association (CA) and first reversal (R1) conditions, for macaws and caiques

Figure 2 Experiment 1. Mean number of errors (± SEM) for the first 10 post reversal trials

across eight successive colour reversals (R1-R8) for macaws and caiques.

Figure 3 Experiment 2. Mean number of errors (± SEM) for the first 10 post reversal trials

across eleven successive colour reversals (R1-R11), for Low and High Criterion conditions

Table 1 Results of GLMM of number of trials to reach criterion and errors made in the first 10

post reversal trials across serial reversals for caiques and macaws.

Table 2 Results of GLMM of number of trials to reach criterion and errors made in the first 10

post reversal trials across serial reversals for subjects trained to either a High or Low pre-

reversal criterion.

Table 3 Results of GLMM of number of errors made in the first 10 post reversal trials across

serial reversals for subjects trained to either a High or Low pre-reversal criterion.
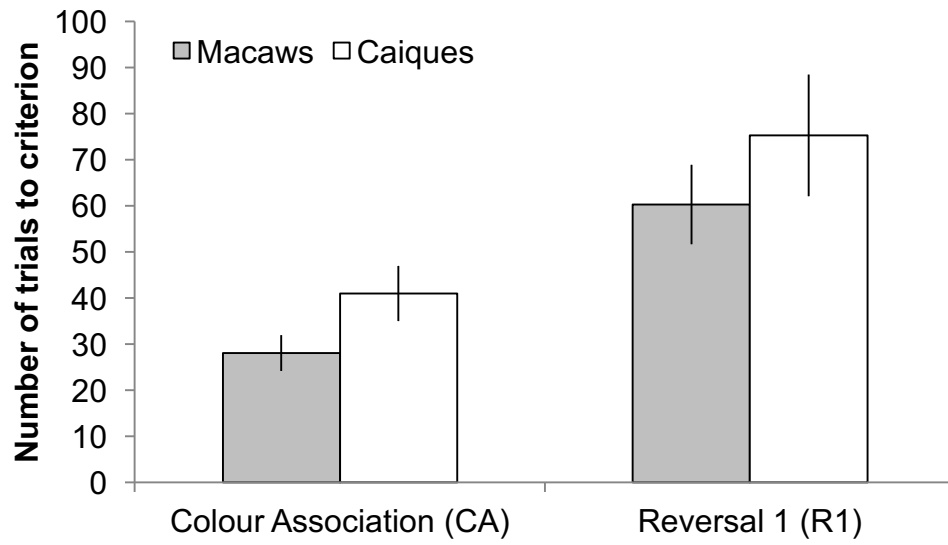
Table 4 Results of GLMM of number of trials to reach criterion across serial reversals for

subjects trained to either a High or Low pre-reversal criterion.

886

Figure 1

888

889

890

891

892

893
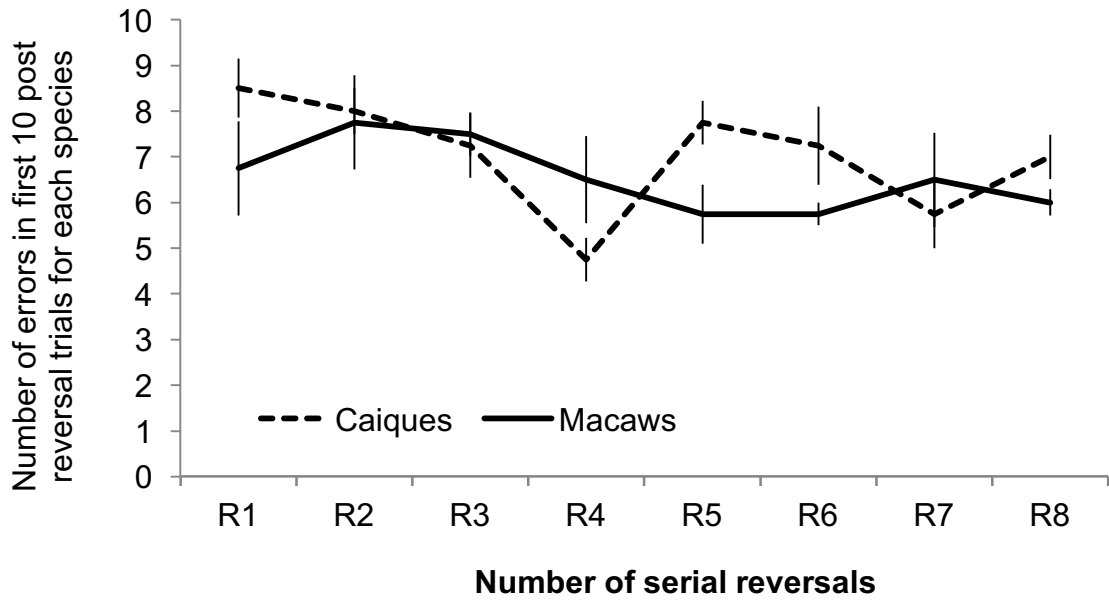
894

895

896

897

898

899

900

901

902

903

904

905

906

Figure 2

909
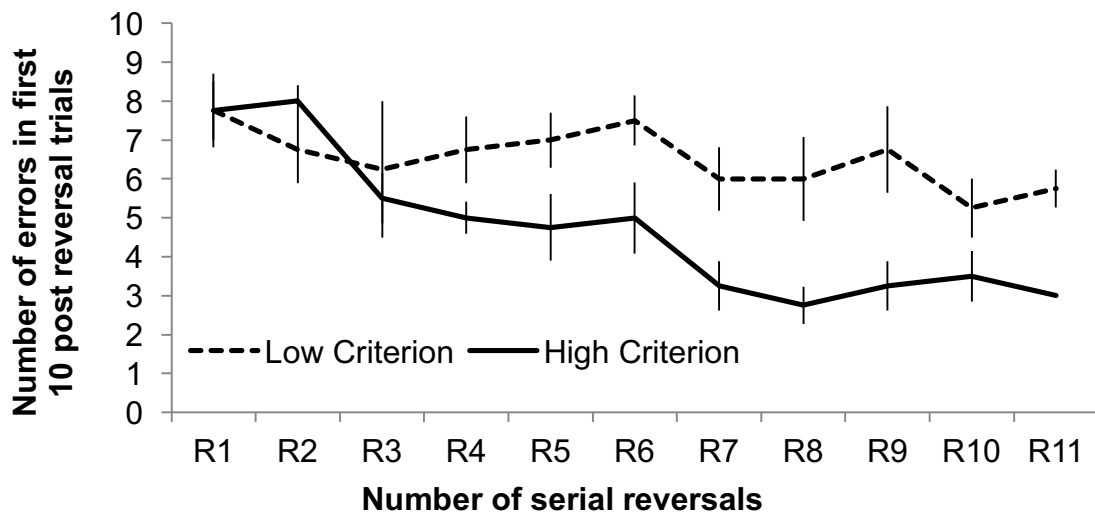910
911
912
913
914
915
916
917
918
919
920
921
922
923
924
925
926
927

928

929

930 **Figure 3**

931

932

933

934

935

936

937

938

939

940

941

942

943

944

945

946

947

948

949

950 **Table 1**

	Errors	Trials
Reversal 2	Z = 0.18; 0.18 ± SEM; P = 0.86	Z = 0.59; 0.21 ± SEM; P = 0.55
Reversal 3	Z = -0.18; 0.18 ± SEM; P = 0.86	Z = -1.13; 0.21 ± SEM; P = 0.26
Reversal 4	Z = -1.55; 0.20 ± SEM; P = 0.12	Z = 0.37; 0.21 ± SEM; P = 0.71
Reversal 5	Z = -0.65; 0.19 ± SEM; P = 0.51	Z = -0.16; 0.21 ± SEM; P = 0.88
Reversal 6	Z = -0.85; 0.19 ± SEM; P = 0.40	Z = 0.60; 0.21 ± SEM; P = 0.55
Reversal 7	Z = -1.14; 0.19 ± SEM; P = 0.25	Z = -1.21; 0.21 ± SEM; P = 0.23
Reversal 8	Z = -0.85; 0.19 ± SEM; P = 0.40	n/a

951

952

953

954

955

956

957

958

959

960

961

962

963

964

965

966

967

968

969

970

971

972

973

974

975

Table 2

	Errors	Trials
Reversal 2	Z = -0.27; 0.18 ± SEM; P = 0.79	Z = -0.26; 0.15 ± SEM; P = 0.79
Reversal 3	Z = -1.43; 0.19 ± SEM; P = 0.15	Z = -2.73; 0.15 ± SEM; P < 0.01
Reversal 4	Z = -1.43; 0.19 ± SEM; P = 0.15	Z = -2.72; 0.15 ± SEM; P < 0.01
Reversal 5	Z = -1.43; 0.19 ± SEM; P = 0.15	Z = -2.91; 0.15 ± SEM; P < 0.01
Reversal 6	Z = -1.13; 0.19 ± SEM; P = 0.26	Z = -3.05; 0.15 ± SEM; P < 0.01
Reversal 7	Z = -2.49; 0.21 ± SEM; P = 0.01	Z = -3.56; 0.15 ± SEM; P < 0.01
Reversal 8	Z = -2.70; 0.21 ± SEM; P < 0.01	Z = -3.18; 0.15 ± SEM; P < 0.01
Reversal 9	Z = -2.16; 0.20 ± SEM; P = 0.03	Z = -3.96; 0.15 ± SEM; P < 0.01
Reversal 10	Z = -2.70; 0.21 ± SEM; P < 0.01	Z = -2.74; 0.15 ± SEM; P < 0.01
Reversal 11	Z = -2.70; 0.21 ± SEM; P < 0.01	n/a

977

978

979

980

981

982

983

984

985

986

987

988

989

990

991

992

993

994

995

996

997

998

999

1000 **Table 3**

	High Criterion Errors	**Low Criterion Errors**
Reversal 2	Z = 0.13; 0.25 ± SEM; P = 0.90	Z = -0.53; 0.26 ± SEM; P = 0.60
Reversal 3	Z = -1.23; 0.28 ± SEM; P = 0.22	Z = -0.80; 0.27 ± SEM; P = 0.42
Reversal 4	Z = -1.53; 0.29 ± SEM; P = 0.13	Z = -0.53; 0.26 ± SEM; P = 0.60
Reversal 5	Z = -1.68; 0.29 ± SEM; P = 0.09	Z = -0.39; 0.26 ± SEM; P = 0.70
Reversal 6	Z = -1.53; 0.29 ± SEM; P = 0.13	Z = -0.13; 0.26 ± SEM; P = 0.90
Reversal 7	Z = -2.63; 0.33 ± SEM; P < 0.01	Z = -0.94; 0.27 ± SEM; P = 0.35
Reversal 8	Z = -2.95; 0.35 ± SEM; P < 0.01	Z = -0.94; 0.27 ± SEM; P = 0.35
Reversal 9	Z = -2.63; 0.33 ± SEM; P < 0.01	Z = -0.53; 0.26 ± SEM; P = 0.60
Reversal 10	Z = -2.47; 0.32 ± SEM; P = 0.01	Z = -1.38; 0.28 ± SEM; P = 0.17
Reversal 11	Z = -2.79; 0.34 ± SEM; P < 0.01	Z = -1.09; 0.15 ± SEM; P = 0.27

1001

1002

1003

1004

1005

1006

1007

1008

1009

1010

1011

1012

1013

1014

1015

1016

1017

1018

1019

1020

1021

1022

1023

1024 **Table 4**

	High Criterion Trials	Low Criterion Trials
Reversal 2	Z = -0.49; 0.11 ± SEM; P = 0.62	Z = -0.09; 0.22 ± SEM; P = 0.93
Reversal 3	Z = -5.47; 0.12 ± SEM; P < 0.01	Z = -0.78; 0.22 ± SEM; P = 0.44
Reversal 4	Z = -2.73; 0.11 ± SEM; P < 0.01	Z = -2.38; 0.23 ± SEM; P = 0.02
Reversal 5	Z = -6.24; 0.12 ± SEM; P < 0.01	Z = -0.60; 0.22 ± SEM; P = 0.55
Reversal 6	Z = -7.05; 0.12 ± SEM; P < 0.01	Z = -0.36; 0.22 ± SEM; P = 0.72
Reversal 7	Z = -4.05; 0.11 ± SEM; P < 0.01	Z = -2.74; 0.23 ± SEM; P < 0.01
Reversal 8	Z = -6.25; 0.12 ± SEM; P < 0.01	Z = -0.96; 0.22 ± SEM; P = 0.34
Reversal 9	Z = -5.47; 0.12 ± SEM; P < 0.01	Z = -2.49; 0.23 ± SEM; P = 0.01
Reversal 10	Z = -4.72; 0.11 ± SEM; P = 0.01	Z = -1.23; 0.22 ± SEM; P = 0.22

1025

1026

1027