

1 **Sub-problem learning and reversal of a multidimensional visual cue**
2 **in a lizard: Evidence for behavioural flexibility?**

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26 ABSTRACT

27 Behavioural flexibility, the ability to adjust behaviour to environmental change by adapting
28 existing skills to novel situations, is key to coping with, for example, complex social
29 interactions, seasonal changes in food availability or detecting predators. We tested the tree
30 skink (*Egernia striolata*), a family-living skink from eastern Australia, in a set-shifting
31 paradigm of eight colour/shape discriminations including reversals, an intra-dimensional
32 acquisition of a new colour/shape and extra-dimensional shift from colour to shape (and *vice*
33 *versa*). Skinks could learn to discriminate between colour/shape pairs and reverse this initial
34 stimulus-reward association; however, they showed no significant decrease in the probability
35 of making a correct choice in the extra-dimensional shift suggesting that they did not form an
36 attentional set. Subjects appear to have learnt each stage as a new problem instead of
37 generalizing stimuli into specific dimensions (set-formation). In conclusion, tree skinks
38 solved a discrimination reversal by focusing their attention towards visual stimuli and flexibly
39 adjusting their choice behaviour accordingly. These lizards learned to use multidimensional
40 visual stimuli to find a food reward, but did not generalise stimuli into dimensions.
41 Furthermore, this study is the first to test for set-shifting in a lizard species and thereby
42 allows us to extend set-shifting theory to a new taxon for comparison with primates, rodents,
43 a bird and a turtle.

44

45 *Keywords:* cognition, discrimination learning, ID/ED task, reptile, set-shifting

46

47 INTRODUCTION

48 Social living has many benefits, but can also be a demanding environment in which
49 interactions between individuals shape their social structure (Hinde, 1987). The resulting
50 selective pressure is thought to have led to the evolution of extensive abilities in attention,
51 memory and learning (Byrne, 1998; Byrne, 1994; Byrne & Whiten 1988), forming the
52 foundation of the 'social intelligence hypothesis' (Humphrey, 1976). Complex cognition has
53 been frequently investigated through behavioural flexibility—the ability to adjust behaviour to
54 changes in the environment (Brown & Tait, 2015) by directing attention to essential stimuli
55 (Dias, Robbins, & Roberts, 1996; Welsh & Pennington, 1988) and adjusting existing skills to
56 a new problem (Manrique & Call, 2015). Behavioural flexibility can be a valuable tool in the
57 social domain. To react flexibly to a change in the social environment (addition or removal of
58 group members) and to selectively pay attention to interactions between individuals can be
59 useful for tracking relationships within a social group (social monitoring; McNelis & Boatright-
60 Horowitz, 1998). The insights gained can then be used to adjust behaviour directed towards
61 conspecifics according to the current state of their inter-individual relationships (Byrne, 1998;
62 McNelis & Boatright-Horowitz, 1998).

63 A common test for behavioural flexibility involves a test of attentional set-shifting
64 which investigates the ability to apply an acquired attentional bias (by forming an attentional
65 set) to novel situations (ID - intra-dimensional; Brown & Tait, 2015; Mukhopadhyay et al.,
66 2008) and then to shift attention away from this established bias when relevance changes to
67 a previously irrelevant stimulus aspect or dimension (ED - extra-dimensional; Brown & Tait,
68 2015). It is possible to examine set-formation in a series of discriminations by quantifying
69 acquisition speed and errors during each stage (Brown & Tait, 2015; Garner, Thogerson,
70 Wurbel, Murray, & Mench, 2006). Perseverative errors to the former relevant dimension and
71 a performance drop during a shift indicate a subject's level of behavioural flexibility (Brown &
72 Tait, 2015; Garner et al., 2006).

73 A touch-screen test for ID/ED attentional set-shifting was first developed to compare

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74 human and non-human primates' attentional set-shifting ability (Dias, et al., 1996; Roberts,
75 Robbins, & Everitt 1988). The task consists of multiple sequential visual discriminations
76 (using shapes and lines as stimulus dimensions), designed to encourage an attentional set
77 (through repeated exposure to consistently relevant and irrelevant information; Sutherland &
78 Mackintosh, 1971) and then test the ability to shift away from that set. First, subjects learn a
79 simple discrimination (SD) between stimuli of only one dimension. After reaching a
80 predetermined learning criterion the stimulus-reward association is reversed and the other
81 stimulus in the pair is reinforced. Next, stimuli of the irrelevant dimension are superimposed
82 onto the SD stimuli, producing compound cues (CD), with the SD stimuli still associated with
83 reward. After reaching criterion the reward associations are again reversed. Next, during the
84 intra-dimensional acquisition (ID), new examples of shapes and lines are introduced. With
85 dimensional relevance staying the same, subjects must maintain their attentional set and
86 apply it to unfamiliar stimuli. After reaching criterion, the reward contingencies are again
87 reversed. Finally, during the extra-dimensional shift (ED), again, unfamiliar shapes and lines
88 are introduced. Contrary to the intra-dimensional acquisition, the reinforcement is now
89 associated with the formerly irrelevant dimension. If set-formation occurred during earlier
90 stages, performance in the extra-dimensional shift is expected to be worse compared to the
91 intra-dimensional acquisition, since the previously established attentional set does not apply
92 any more (Garner et al., 2006; Roberts et al., 1988). The extra-dimensional shift is again
93 followed by a reversal.

94 The assumption that the number of trials to reach criterion during extra-dimensional
95 shifting is higher than during the intra-dimensional acquisition (as a measure of attentional
96 set-shifting) does not rely on absolute values. It is therefore possible to compare shift
97 performance in different species (Table 1). For example, marmosets (*Callithrix jacchus*) can
98 form an attentional set and shift to a previously irrelevant second dimension (Dias et
99 al., 1996; Roberts et al., 1988); and similar results have been obtained in rhesus monkeys
100 (*Macaca mulatta*; Weed, Bryant, & Perry, 2008; Baxter & Gaffan, 2007). Rodents, such as
101 rats (e.g. Kim, Choi, Jeon, & Han, 2016; Hecht, Will, Schachtman, Welby, & Beversdorf,

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102 2014; McGaughy et al., 2014; McAlonan & Brown, 2003; Birrell & Brown, 2000) and mice
103 (e.g. Janitzky et al., 2015; Bissonette, Lande, Martins, & Powell, 2012; Garner et al., 2006;
104 Colacicco, Welzl, Lipp, & Wuerbel, 2002) also show the ability to form and shift attentional
105 sets. Comparable findings in other taxa such as birds, fishes and reptiles are scarce (Table
106 1). One study in great tits (*Parus major*) showed their ability to form an attentional set and
107 shift to a new dimension (Titulaer, van Oers, & Naguib, 2012). Painted turtles (*Chrysemys*
108 *picta*) show an improved performance during successive compound discrimination reversals,
109 perhaps indicative of set-formation. However, without comparison between intra-dimensional
110 and extra-dimensional stages, this improvement could equally be evidence of learning set-
111 formation (training effect) instead of attentional set-formation (Cranney & Powers, 1983).

112 Most studies in lizards lack the details needed for a comprehensive comparison of
113 attentional set-shifting because most focus on reversal performance only. For example,
114 *Anolis evermanni* (Leal & Powell, 2012) were presented with two food wells covered by lids
115 which animals had to dislodge to access a reward. Lizards learnt to open the food dishes
116 using multiple methods and to discriminate between the two wells based on colour (blue and
117 yellow); furthermore, two out of four individuals could reverse this learnt association showing
118 flexibility in their use of visual information. A similar study investigated discrimination
119 learning and reversal in hatchling three-lined skinks (*Bassiana duperreyi*). Almost all lizards
120 (13/14) that learnt to displace lids could associate lid colour with reinforcement and eight
121 showed flexibility by reversing this learnt association (Clark, Amiel, Shine, Noble, & Whiting,
122 2014).

123 We tested tree skinks (*Egernia striolata*), which are viviparous, diurnal, family-living
124 lizards found in arboreal as well as rocky habitats throughout eastern Australia (Wilson &
125 Swan, 2008). Tree skinks show complex sociality in which lizards frequently live in family
126 groups consisting of a socially monogamous parental unit and at least one generation of
127 offspring (Whiting & While, 2017; Duckett, Morgan, & Stow, 2012; Chapple, 2003). They are
128 visual foragers that eat plant material (including fruits) as well as insects such as
129 cockroaches and grasshoppers (Chapple, 2003). As a diurnal, visual forager, *E. striolata* is a

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130 good model to investigate learning in a visual discrimination task. Furthermore, flexibly
131 adjusting behaviour to changing conditions is beneficial for survival (Manrique & Call, 2015).
132 Finally, complex sociality can select for enhanced cognitive abilities including flexibility in
133 learning, attention, and memory (Byrne, 1998; Byrne, 1994; Byrne & Whiten 1988) which
134 can be important tools within a social context as well as outside a social context (Byrne &
135 Bates, 2007).

136 Our aim was to investigate behavioural flexibility in *E. striolata* by using a species-
137 appropriate modified version of the widely-used set-shifting paradigm designed by Roberts
138 et al. (1988). We presented individuals with visual compound cues consisting of two
139 dimensions (colour and shape) across a series of stages including acquisitions and
140 reversals and a final stage (extra-dimensional shift) in which the reward contingencies were
141 shifted to the formerly irrelevant dimension. Based on this species' ecology and social
142 structure, we predicted animals would learn the visual discriminations and show learning
143 patterns indicative of set-formation and successful shift of attention.

144

145 **METHODS**146 *Study Animals and Husbandry*

147 We hand-captured 24 adult (snout-vent-length [SVL] ≥ 100 mm; Chapple, 2003) *E. striolata*
148 (12 males and 12 females, mean SVL \pm standard deviation all: 106.08 ± 3.69 mm; male:
149 105.58 ± 4.14 mm; female: 106.58 ± 3.29 mm) near Albury, New South Wales (-35.980 S,
150 146.970 E), Australia, during April 2016. SVL, total length (TL), mass and sex (presence of
151 hemipenes) were determined on site (Appendix Table A1). Additionally, each lizard was
152 subcutaneously injected with a PIT-tag (Passive Integrated Transponder, Biomark, HPT8,
153 8.4 mm; this method was chosen because animals do not show distinctive markings and it is
154 preferable over toe-clipping) laterally 1.5 cm behind the front leg (no anaesthetic was
155 applied), for individual identification. Skinks were transported to Macquarie University within
156 two days of capture and transferred into individual plastic tubs (487 L x 350 W x 260 H mm)

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157 immediately after arrival. Lizards were housed indoors, with room temperature set at $22.7 \pm$
158 $1.9 \text{ }^\circ\text{C}$ (mean \pm standard deviation, depending on season), relative humidity of 30-65% and
159 a 12:12 h light:dark cycle. We installed heat cord underneath the enclosure to create a
160 thermal gradient between $16\text{-}30^\circ\text{C}$ ($\pm 4^\circ\text{C}$). For the duration of the experiment, room
161 temperature was monitored within enclosures using iButtons (Thermochron iButton model
162 DS1921) which recorded temperature hourly. We used newspaper as a substrate and each
163 enclosure had a hide, a small water bowl, and a wooden ramp. We fed lizards three times a
164 week (Monday, Wednesday and Friday); twice with crickets powdered with vitamins
165 (aristopet Repti-vite) and calcium (URS Ultimate Calcium) and once with baby food (2 ± 0.1
166 g, Heinz™). During experiments, skinks were fed small amounts (0.15 ± 0.01 g) of baby food
167 daily and crickets on Fridays; animals had *ad libitum* access to water. To ensure that
168 animals had acclimated to the conditions of captivity, we kept them undisturbed for two
169 weeks and made sure they were feeding consistently. All subjects were naïve and had never
170 participated in any other cognition experiments.

171

172 *Learning experiment*

173 Habituation

174 To habituate the animals to the experimental setup, we transferred them to bigger tubs (683
175 L x 447 W x 385 H mm) 12 days prior to the start of the experiment. Previous studies have
176 shown that extensive handling and unfamiliar environments induce increased levels of stress
177 which affects learning (Langkilde & Shine, 2006; Burghardt, 1978); therefore, animals were
178 kept and tested in these enclosures for the entire experiment. They were identical to
179 previous enclosures except that a second ramp was introduced (Figure 1). Baby food was
180 presented on top of one ramp in a small white plastic saucer (3 cm in diameter) for two days
181 (counterbalanced for side).

182

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183 Setup

184 During trials the newspaper substrate was taped down to prevent animals from crawling
185 underneath and a small opaque food dish (12 mm high x 55 mm diameter, covered on the
186 outside with black electrical tape) was placed on the top of each ramp. Both dishes
187 contained a small amount of baby food (0.15 ± 0.01 g) and were covered with fine mesh
188 screen; however, the reward was made accessible by a hole cut through the screen.
189 Animals were not able to see into the feeding dishes from the starting position on the other
190 side of the tub. Cue cards containing the stimuli (colour/shape) were fixed directly behind
191 and as close as possible to the dishes. Half of the subjects ($N = 12$) were first tested with
192 colour as the relevant cue dimension, the other half ($N = 12$) with shape (Figure 2). Within
193 these two groups half of the subjects ($N = 6$) started with stimulus 1 (Stages 1&2:
194 triangle/light blue, stages 3&4: X/dark blue, stages 5&6: O/light orange, stages 7&8: H/light
195 pink) and the other half ($N = 6$) with stimulus 2 (second stimulus in the pair, Figure 2);
196 making four stimulus groups and effectively counterbalancing the rewarded stimulus within
197 the groups. All groups were counterbalanced for sex and mean SVL (± 0.1 mm).

198

199 Stimuli

200 Cue cards with the stimuli (S) were made of pressed wooden coaster cards (rectangle
201 coaster, Boyle Industries Pty Ltd, 11.3 L x 9.3 W x 0.3 H mm) and sprayed with differently
202 coloured spray paint (Appendix Table A3). Shapes were drawn onto the sprayed cards by
203 tracing a previously created pattern made of cardboard with a black waterproof marker
204 (Figure 2; for information on area and circumference of the shapes see Appendix Table A5).
205 Colour pairs were chosen to be easily discriminable based on lizards' perception
206 (Fleishman, Loew, & Whiting, 2011) and shapes were made up of lines (e.g. X, O, H) or
207 were solid. During experiments, left/right position was pseudo-randomly predetermined and
208 counterbalanced for side, so that each stimulus was never on the same side more than twice
209 in a row. For compound cues, the left/right position of each stimulus dimension varied

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210 independently of each other.

211

212 Experimental Procedure

213 At the start of a trial, each individual was ushered into its hide if not already in it and placed
214 at the start position opposite the ramps. Next, both cue-cards were simultaneously fixed with
215 putty (Bostik Blu-Tack) to the inner wall of the tub and immediately afterwards feeding
216 dishes were placed on the ramps in the same manner in front of the stimuli. The order in
217 which the subjects were set up was kept constant over the course of the study. After about
218 three minutes of acclimation, the hide was removed and the trial lasted for 1.5 hours. We
219 then returned the hide and removed feeding bowls and cues. Between trials both dishes
220 were cleaned and rebaited, making sure that both bowls were touched. We made sure that
221 cues and feeding dishes were never interchanged between individuals. Trials were
222 conducted from May 2016 to March 2017. We tested subjects twice a day, between 08:00-
223 12:30 h, five days a week (= 10 trials per week) with an inter-trial interval (ITI) of 40 minutes.
224 All trials were videotaped (H.264 Digital Video Recorder, 3-Axis Day & Night Dome
225 Cameras) and scored afterwards. Furthermore, during trials animals were left undisturbed to
226 minimise stress caused by the inability to hide.

227 Choice (correct/incorrect) was scored as the first food dish an animal's snout passed
228 over the edge of. Latency was scored as the time from first movement (directed,
229 uninterrupted forward movement of the whole body ending in the examination of a food
230 bowl; an interruption is defined as no movement for 10 s or more) to the first food dish
231 examined. Animals were not actively corrected when making a wrong choice (non-correction
232 method) and had ample opportunity to visit both stimuli and feeding dishes during trials. We
233 used a learning criterion of 6/6 or 7/8 correct choices in consecutive trials. These criteria
234 were chosen because they have shown to be good indicators of successful learning (Leal &
235 Powell, 2012). To avoid overtraining, an animal was allowed no more than 100 trials for each
236 stage. If a subject showed chance or below chance performance for at least six consecutive

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237 weeks (60 trials) or did not show criterion performance of 6/6 or 7/8 consecutive trials correct
238 within the 100 trials, it was removed from the experiment ('non-learner'); as soon as an
239 individual reached criterion, however, it moved on to the next stage.

240

241 Coding

242 A subset (about 17% = 809) of trials randomly chosen from all subjects and stages was
243 rated by two researchers (ML and PY) unfamiliar with the experiment and blind to the tested
244 questions as well as the first author (BS). Inter-observer reliability was calculated based on
245 Cohens kappa (Falissard, 2012), which estimates the inter-rater agreement between two
246 independent raters; 100% agreement equals a kappa of 1, 0% agreement a kappa of 0. It
247 was estimated at 0.92 and 0.94 between ML and BS and PY and BS, respectively.

248

249 Simple Discrimination and Reversal

250 We conducted a simple associative learning test with one stimulus (e.g. X) being positively
251 reinforced (S^+) and the other (e.g. triangle) being unrewarded (S^-). This stage required
252 subjects to associate one of the stimuli with a reward. After reaching the learning criterion
253 they moved on to a reversal (SDR). Reversals incorporated the same stimulus pairs as the
254 simple discrimination (SD), but with reward contingencies reversed so that the former S^-
255 became S^+ and *vice versa* (e.g. the previously-unrewarded X was now rewarded, and the
256 triangle was no longer rewarded, Figure 2).

257

258 Compound Discrimination and Reversal

259 As soon as subjects reached criterion on the simple discrimination reversal, they were tested
260 on the compound discrimination (CD), introducing a second stimulus dimension. The initially
261 trained stimulus dimension remained relevant (e.g. triangle and X), while the second
262 dimension acted as an irrelevant distractor (e.g. background colour). Stimulus group 1 was
263 presented with two different shapes (triangle and X) superimposed on the dark and light

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264 green background colours and stimulus group 2 with two different colours at the background
265 (light and dark blue, Figure 2). To succeed at this stage, animals had to maintain their
266 attention on the already learnt stimulus-reward association (e.g. X is rewarded regardless of
267 background colour), while ignoring the new stimulus dimension. After the performance
268 criterion was met on the CD, subjects moved on to a reversal (CDR), again changing the
269 former unrewarded S^- to S^+ and *vice versa* (e.g. triangle is rewarded regardless of
270 background colour).

271

272 Intra-dimensional Acquisition and Reversal

273 After reaching the learning criterion on the compound discrimination reversal, we introduced
274 new examples of shapes and colours, however, the relevant dimension (stimulus group 1:
275 shape, stimulus group 2: colour) stayed the same as in previous stages (Figure 2). Test
276 subjects had to apply their attentional set to novel pairs of stimuli (e.g. a square and circle),
277 while still ignoring the second dimension (e.g. background colour). After reaching criterion at
278 the intra-dimensional acquisition (ID), subjects were tested on a reversal (IDR), changing
279 reinforcement to the alternate stimulus in a pair.

280

281 Extra-dimensional Shift and Reversal

282 As with the previous stage, we again introduced unfamiliar colours and shapes to the test
283 subjects, however, S^+ was shifted to one of the two stimuli within the former irrelevant
284 dimension (stimulus group 1 to colours and stimulus group 2 to shapes; Figure 2). We
285 introduced new stimuli to avoid any partial reinforcement effects (Shanab, & McClure, 1983),
286 and to ensure the intra-dimensional (ID) and extra-dimensional (ED) stages were equivalent
287 (save for the effects of the primed attentional set). Therefore, the reward contingencies
288 changed so that the previously irrelevant dimension now contained the positive and negative
289 stimuli (e.g. light and dark pink), whereas the former relevant dimension (shapes) became
290 irrelevant to reinforcement. After reaching criterion at the ED, subjects were presented with a

291 reversal (EDR)—the reward now associated with the formerly unreinforced stimulus in the
292 new relevant dimension (e.g. ED: light pink was reinforced, EDR: dark pink was reinforced).

293

294 *Statistical Analyses*

295 All statistical analyses were performed in R version 3.2.4 (R Development Core Team, 2008)
296 and reported p-values are two tailed (raw data files and R-code are available online through
297 Zenodo, doi: 10.5281/zenodo.1162406). Prior to the start of the experiment, we measured
298 snout-vent length (SVL; proxy for body size) to the nearest 1 mm using a plastic ruler and
299 mass to the nearest 0.1 g using a digital balance. We compared body condition between
300 learners and non-learners using a linear model (LM; Bates, Maechler, Bolker, & Walker,
301 2015) with mass as the response variable and SVL and exclusion (categorical: yes or no) as
302 fixed effects. Furthermore, we determined whether our learning criterion was robust by
303 examining if the number of errors per stage differed between learners and non-learners
304 (exclusion: yes or no) in a generalized linear mixed-effects model (GLMM; Bates et al.,
305 2015). We performed this analysis to test the prediction that ‘non-learners’ make more errors
306 than learners. Learners could have made many errors before reaching criterion and non-
307 learners could have made few errors but never made enough correct choices in a row to
308 reach the learning criterion. If our criterion was robust enough to detect learning, we would
309 expect non-learners to make significantly more errors than learners.

310 To base estimates on as many data points as possible we included data from all
311 animals that reached criterion in any given stage (excluding the stage they were removed) in
312 the analysis. This means that the number of individuals decreases with stage (as they were
313 removed after not reaching criterion) which can compromise statistical power. We applied
314 Bayesian GLMMs (Hadfield, 2010) to test if the probability of choosing correctly increased
315 with the number of trials (indicative of learning) each animal participated in, in each of the
316 eight stages separately. We used the same approach to test if learning performance was
317 influenced by sex or stimulus group as well as interactions between sex and stage, sex and
318 stimulus group, and stimulus group and stage. However, non-significant interactions were

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319 subsequently dropped and the best-fitting model, based on DIC (deviance information
320 criterion), presented (Appendix Table A4). The final global model included only sex and
321 stimulus group as fixed effects. Our analysis did indicate a significant sex difference in one
322 stage (SDR) and sex was therefore included in the analysis of this stage (Table 3). In all
323 models, “trial” was z-transformed (mean centred and scaled by the standard deviation) for
324 better interpretability of probabilities. Models also included individual level random slopes
325 (trial) and intercepts to account for the possible autocorrelation between successive choices.

326 Instead of an attentional set, animals might have formed a learning set (training
327 effect). To test this, we used a Bayesian approach, like the stage-by-stage analysis but
328 including a random intercept for stage in the random effects term. Furthermore, we ran
329 separate GLMMs to find out if performance on the extra-dimensional shift stage differed from
330 the intra-dimensional acquisition stage (shift performance) as well as between acquisition
331 and reversal stages of compound, intra-dimensional and extra-dimensional discrimination
332 (reversal learning) by focusing only on data from stages of interest (either ID and ED, CD
333 and CDR, ID and IDR or ED and EDR) (Table 3). Trial was included in the models as a fixed
334 effect as a scaling variable to make estimates interpretable. Model diagnostics were
335 performed on all models to ensure that no auto-correlation between samples of the posterior
336 distribution occurred (correlation between lags < 0.1 ; Hadfield, 2010) and that sufficient
337 mixing took place (by visually inspecting plots of MCMC chains). We used a Heidelberg and
338 Welch diagnostic tests to ensure that the chain was long enough. Lastly, to find out if
339 animals made perseverative errors after the initial shift (extra-dimensional shift stage),
340 indicative of the formation of an attentional set (Garner et al., 2006), we investigated their
341 choice during the first 10 trials of the extra-dimensional shift stage using the binomial test.

342

343 *Ethical note*

344 Our study involved non-invasive observations of animal behaviour which were approved by
345 the Macquarie University Animal Ethics Committee (ARA # 2013/031). Collection of skinks
346 was approved by the New South Wales National Parks and Wildlife Service, Office of

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347 Environment and Heritage (License # SL101264). Skinks were captured individually by hand
348 and placed in cloth bags until they could be transported by vehicle to Macquarie University
349 from Albury, New South Wales, in an insulated box. If possible both animals in a pair were
350 collected. All animals were euthanized by injecting Lethobarb, diluted 1:1 with saline buffer
351 solution (100mg/kg) intrapleuroperitoneally at the end of the study to extract the brain for a
352 comparative brain study.

353

354 RESULTS

355 Of the 24 animals tested, 15 were excluded because they did not reach the learning criterion
356 in 100 trials: eight (five males and three females) during the simple discrimination; four (two
357 males and two females) during the simple discrimination reversal, two females during the
358 intra-dimensional reversal; and one female during the extra-dimensional shift. Motivation
359 was high during the experiment: in a total of 4854 trials (sum of all 24 individuals) there were
360 only two trials (one each for two subjects) during which the reward was not eaten.

361 Body condition did not differ between learners and non-learners (LM: estimate = -
362 0.49, std. error = 0.95, $t = -0.52$, $P = 0.610$). As predicted, animals that were removed (non-
363 learners) during the experiment made significantly more errors compared to learners
364 (GLMM: estimate = 0.16, std. error = 0.05, $Z = 3.14$, $P = 0.002$) showing that non-learners
365 were actually performing badly. Additionally, the probability of choosing correctly increased
366 with trial number, indicated by a positive value, for learners in each stage confirming the
367 robustness of our learning criteria. Due to the decrease in samples size with each stage,
368 statistical power decreases, and consequently, the width of confidence intervals increases to
369 cross zero leading to non-significant results (Table 2). Neither stimulus group nor sex
370 affected performance within any given stage except simple discrimination reversal, in which
371 males' probability of choosing correctly was significantly higher than females (Table 2).
372 Furthermore, animals did not show a shift cost (increase in number of trial to learn the extra-
373 dimensional shift stage compared to intra-dimensional acquisition, Table 3 & Figure 3) or

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374 reversal cost (increased number of trials to learn between acquisition and reversal stages,
375 Table 3 & Figure 3) and animals did not perseverate (base their choice on the previously
376 reinforced dimension) on the formerly relevant dimension (Binomial test, $N = 10$, $P > 0.05$;
377 Supplementary material Table 2) during the first 10 trials of the extra-dimensional shift stage.
378 The probability of choosing correctly did not increase significantly with trial when controlling
379 for stage as a random effect, showing that no learning set was formed either (GLMM, post.
380 mean = 0.23, lower 95% Ci = -0.21, upper 95% Ci = 0.66, $P = 0.275$).

381

382 **DISCUSSION**

383 Tree shrews learnt to discriminate between three pairs of either two shapes or two colours.
384 Contrary to our predictions, however, animals did not show a significant decrease in the
385 probability of choosing correctly between acquisition and reversal (no reversal cost:
386 compound discrimination and reversal, intra-dimensional acquisition and reversal and extra-
387 dimensional shift and reversal). Furthermore, animals learnt the extra-dimensional shift with
388 the same level of performance as the intra-dimensional acquisition; showing no shift cost
389 either. However, they did learn to use each new set of stimuli to find a reward and to reverse
390 their initial association, indicating behavioural flexibility. Furthermore, the lack of evidence of
391 attentional set-formation and the associated cost to set-shift cannot be based on our failure
392 to reliably detect learning. Non-learners made more errors than learners during the trials
393 they were given and our analyses show a positive effect of trial on choice performance for
394 animals that did learn within a stage. Additionally, we found no effect of body condition or
395 stimulus group on learning ability. Initially males were better at reversing the simple
396 discrimination, but this difference disappeared as stages became more complex.

397 The attentional set-shifting task is designed to show attentional set-formation only if
398 animals experience an increase in trials to criterion during the extra-dimensional shift relative
399 to the intra-dimensional acquisition, after forming a set during the sequential progression
400 from simple (in which an animal first learns what stimuli are relevant to find a reward; Baxter

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401 & Gaffan, 2007), then compound (in which the same stimuli plus a distractor in the form of a
402 second dimension are presented; Birrell & Brown, 2000), to intra-dimensional discrimination
403 (during which animals have to transfer previously acquired knowledge to unfamiliar stimuli;
404 Brown & Tait, 2015; Dias et al., 1996). Subjects need to overcome this previously learnt
405 attentional set, and shift their attention away from one dimension to the second, formerly
406 irrelevant, dimension. Our data do not show evidence that the tested group of lizards formed
407 an attentional set; therefore, we are not able to conclude that their performance at the extra-
408 dimensional stage reflected an attentional shift. This stands in contrast to findings in
409 primates, rodents and a bird which all showed a decrease in learning speed during the shift
410 stage compared to the intra-dimensional acquisition (Table 1), whereas our lizards showed
411 similar levels of learning in those stages.

412 In addition to the extra-dimensional shift stage, the standard set-shifting task includes
413 reversal stages. During the acquisition (learning) of a discrimination, positive (rewarded
414 stimulus) and negative (unrewarded stimulus) values are assigned to each stimulus (Wise,
415 Murray, & Gerfen, 1996, cited by Manrique & Call, 2015) and the proportion of behavioural
416 responses is increasingly directed towards the reinforced stimulus (learning). When a
417 subject is confronted with a reversal it first must inhibit responding to the formerly positive
418 stimulus and then form a new reward association with the formerly negative stimulus (Dias
419 et al., 1996). Most of our lizards that could learn during acquisitions were able to reverse
420 during the following stage, showing the ability to inhibit responding to an established
421 stimulus-reward relationship and showing flexibility in their response behaviour.
422 Furthermore, our lizards performed well during reversals showing no decrease in
423 performance compared to the respective acquisition stages. This result stands in contrast to
424 findings in rhesus monkeys (e.g. Weed et al., 2008), rats (e.g. McAlonan & Brown, 2003)
425 and mice (e.g. Garner et al., 2006) which perform worse in reversals compared to
426 acquisition.

427 During attentional set-formation, a subject first perceives both dimensions as equal
428 and attention is increasingly directed towards the relevant dimension (Wise et al., 1996,

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429 cited by Manrique & Call, 2015). When an attentional set has formed, attention is focused on
430 the relevant information and responses are directed towards the rewarded stimulus (Brown
431 & Tait, 2015) within the relevant dimension. However, a shift to the second dimension
432 requires subjects to inhibit responding to the whole dimension (Dias et al., 1996). Our
433 animals were able to learn the dimensional shift without showing perseverative responses,
434 but as to what strategy they used (e.g. attentional set-shift or learning of each compound
435 cue as a distinct stimulus), and whether an attentional set was overcome, needs to be
436 investigated in future studies. Additionally, based on our analysis, tree skinks also did not
437 form a learning set (training effect), a predisposition to learn based on previous experience.
438 It seems that animals treated each new version of the stimuli as a novel problem and
439 subsequently learnt each acquisition stage individually without experiencing a training effect.
440 The specific learning strategy used by our subjects is also unclear; our dataset is too small
441 to permit any further analysis. Although both concepts, reversal learning and attentional
442 shifts, are similar in the respect that they require some level of behavioural flexibility in
443 responding to the change in stimulus relevance, attentional shifts are generally seen as
444 more complex (Birrell & Brown, 2000; Colacicco et al., 2002).

445 In this study, colour pairs were chosen based on human-perceived brightness and
446 shapes could be categorised into those made up of lines (e.g. X, O, H), and those that were
447 solid (e.g. triangle, square, star). Combinations were chosen to be easily distinguishable
448 based on the lizards' perceptual ability (they are tetrachromatic and have good visual acuity;
449 Fleishman et al., 2011). Furthermore, skinks could have experienced a sensory bias towards
450 one or more stimuli or a dimension. For example, rhesus monkeys perform differently when
451 shifting according to the stimulus dimension they initially encountered. Monkeys had
452 difficulty shifting from colour to shape but not *vice versa* (Baxter & Gaffan, 2007). During the
453 first stage, we started each of four subsets of lizards (stimulus groups) with one of the four
454 stimuli (light blue, dark blue, X or triangle). However, performance did not differ between
455 stimulus groups, indicating that our dimensions were of similar difficulty to our test animals.
456 There is a possibility that lizards used brightness instead of chroma or hue to learn the

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457 discrimination. As the order of presentation from simple discrimination to intra-dimensional
458 reversal was bright-dark-dark-bright-bright-dark this can be seen as a sequence of simple
459 acquisition and reversal stages. Therefore, if animals had used brightness, our data would
460 show a decrease in trials to criterion since a reversal to a previously correct stimulus is
461 easier than a reversal to a previously not-reinforced stimulus, but no such decrease was
462 found. The same is true for shape solidity, area and circumference (line-solid-solid-line-solid-
463 line, small-large-large-small-large-small and long-short-short-long-short-long). However,
464 there is a small chance that animals used some other property of the cue cards (surface
465 texture or minor imperfections due to the painting process) to learn the discrimination that
466 was not visible to a human observer.

467 In conclusion, tree skinks can learn to distinguish between two visual cues made up of either
468 two colours and/or two shapes. Furthermore, they can reverse an initial stimulus reward
469 association and show behavioural flexibility which can be a beneficial trait while coping with
470 environmental and social challenges. The pattern of learning suggests, however, that they
471 neither formed an attentional set (establishment of a rule set on which subsequent choices
472 are based) nor a learning set (animals' performance increases based on extensive training).
473 From our results, it is unclear if the tested species is unable to establish dimensionality in
474 compound visual stimuli, or if our methodology was not suitable to test attentional set-
475 formation and shifting in this reptile species. It is most likely that they viewed each new pair
476 of stimuli as a distinct problem and learnt to discriminate the stimuli as a whole, instead of
477 generalizing to a dimension. Our study revealed new insights into visual discrimination
478 learning in lizards that will help design future studies investigating learning in non-avian
479 reptiles. Furthermore, adding evidence on set-shifting in species with a varying degrees of
480 sociality will help understand the relationship between sociality and behavioural flexibility in
481 lizards.

482

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614 **Table 1.** Literature comparison between studies incorporating the described methodology.

Species	Age	Methodology	Dimensions	ED>ID	Study
Primates					
Common Marmoset	Sub-adult	CANTAB ID/ED	Visual	Yes	Dias et al., 1996
Common Marmoset	Sub-adult	CANTAB ID/ED	Visual	Yes	Roberts et al., 1988
Rhesus Monkeys	Juvenile	CANTAB ID/ED	Visual	Yes	Weed et al., 2008
Rhesus Monkeys	Adult	CANTAB ID/ED	Visual	Yes	
Rhesus Monkeys	Adult	CANTAB ID/ED	Visual	Partly validated	Baxter & Gaffan, 2007
Rodents					
Wistar rats	Adult	ID/ED	Olfactory/touch	Yes	Kim et al., 2016
Sprague Dawley rats	Adult	ID/ED	Olfactory/touch	Yes	Hecht et al., 2014
Long-Evans hooded rats	Adult	ID/ED	Olfactory/touch	Yes	McGaughy et al., 2014
Lister hooded rats	Adult	ID/ED	Olfactory/touch	Yes	McAlonan & Brown, 2003
Lister hooded rats	Adult	ID/ED	Olfactory/touch	Yes	Birrell & Brown, 2000
Mice (B6.Cg-Tg(Th-cre)1Tmd/J)	Adult	ID/ED	Olfactory/touch	No	Janitzky et al., 2015
Mice (C57BL/6)	Adult	ID/ED	Olfactory/touch	Yes	Bissonette et al., 2012
Mice (C57BL/6)	Adult	ID/ED	Olfactory/touch	Yes	Garner et al., 2006
Mice (C57BL/6J)	Adult	ID/ED	Olfactory/touch	Yes	Colacicco et al., 2002
Birds					
Great tits	Adult	Reversals and shift	Visual/spatial	Yes	Titulaer et al., 2012
Reptiles					
Painted turtle	adult	Series of ED and REV	Visual	No direct comparison	Cranney & Powers, 1983

615 Findings in primates, rodents (some examples), birds and reptiles including species tested, age of subjects, methodology and stimuli used are
 616 listed as well as if set-formation impaired performance during the extra-dimensional shift. ID – intra-dimensional acquisition, ED – extra-
 617 dimensional shift, REV – reversal, CANTAB ID/ED - Cambridge Neuropsychological Automated Test Battery ID/ED attentional set-shifting test.

618

619 **Table 2.** Summary of parameter estimates and test statistics calculated for each stage.

Parameter	posterior Mean	Lower 95% Confidence interval	Upper 95% Confidence interval	<i>p</i> MCMC
Simple Discrimination				
Intercept	0.424	0.055	0.813	0.0228
Trial	0.373	0.068	0.704	0.0183
Simple Discrimination Reversal				
Intercept	1.383	-0.562	4.363	0.1225
Trial	1.286	-0.754	4.179	0.1743
Sex	1.704	0.453	3.015	0.0083
Compound Discrimination				
Intercept	1.147	0.069	2.368	0.0151
Trial	1.209	0.091	2.538	0.0149
Compound Discrimination Reversal				
Intercept	1.023	-0.136	2.521	0.0455
Trial	0.781	-0.288	2.094	0.1058
Intra-dimensional Discrimination				
Intercept	0.915	0.083	1.896	0.0200
Trial	0.589	-0.114	1.389	0.0735
Intra-dimensional Discrimination Reversal				
Intercept	1.196	-0.199	2.904	0.0585
Trial	0.996	-0.418	2.733	0.1242
Extra-dimensional Shift				
Intercept	1.241	-0.175	2.971	0.0539
Trial	0.757	-0.625	2.306	0.2251
Extra-dimensional Shift Reversal				
Intercept	1.363	0.023	2.872	0.0320
Trial	1.107	-0.267	2.463	0.0953
Global model				
Intercept	0.170	-0.034	0.380	0.1000
Sex	0.223	-0.082	0.532	0.1440

620 Learning performance (probability of correct choices) was analysed separately for each of
621 the eight stages of the experiment including a global model based on data of all stages to
622 investigate the effect of sex on performance. Sample sizes decreased with stage due to
623 animals being removed as non-learners, they are as follows: $SD_N = 24$, $SDR_N = 16$, $CD_N =$
624 12 , $CDR_N = 12$, $ID_N = 12$, $IDR_N = 12$, $ED_N = 10$, $EDR_N = 9$. Significant parameters are
625 indicated in bold. *p*MCMC – significance of parameter based on Bayesian modelling.

626

627 **Table 3.** Summary of parameter estimates and test statistics to investigate reversal and shift
 628 performance.

Parameter	Posterior Mean	Lower 95% Confidence interval	Upper 95% Confidence interval	<i>p</i> MCMC
Shift performance				
Intercept	0.663	0.116	1.261	0.0181
Stage	0.009	-0.480	0.505	0.9692
Trial	0.391	-0.110	0.885	0.1027
Interaction Stage & Trial	-0.145	-0.640	0.348	0.5633
Reversal learning in Compound stages				
Intercept	0.690	-0.005	1.391	0.0315
Stage	-0.133	-0.579	0.311	0.5667
Trial	0.581	-0.046	1.259	0.0512
Interaction Stage & Trial	-0.144	-0.639	0.353	0.5680
Reversal learning in Intra-dimensional stages				
Intercept	0.886	0.195	1.671	0.0105
Stage	-0.148	-0.575	0.278	0.4952
Trial	0.626	0.014	1.289	0.0285
Interaction Stage & Trial	-0.115	-0.556	0.343	0.6126
Reversal learning in Extra-dimensional stages				
Intercept	0.958	0.125	1.860	0.0226
Stage	-0.108	-0.525	0.317	0.6160
Trial	0.545	-0.221	1.378	0.1452
Interaction Stage & Trial	-0.126	-0.539	0.287	0.5493

629 Shown is the difference of the probability of a correct choice between the intra-dimensional
 630 and extra-dimensional shift stage (shift performance) as well as acquisition and reversal
 631 stages. Significant parameters are indicated in bold. *p*MCMC – significance of parameter
 632 based on Bayesian modelling.

633

634 **Table A1.** Summary of measurements and stimulus group composition.

PIT	Sex	SVL (mm)	TL (mm)	Mass (g)	Learnt	Stimulus group
1469228	F	110	189	24.5	No	Shape 1
1469674	M	108	210	29.8	No	Shape 1
1469711	F	105	210	29.6	Yes	Shape 1
1469738	M	103	221	25.8	No	Shape 1
1469743	F	105	179	24.1	Yes	Shape 1
1469675	M	105	215	27.4	No	Shape 1
1469662	F	106	201	25.6	No	Shape 2
3366149	M	108	214	28.1	No	Shape 2
1469657	F	111	209	26.3	No	Shape 2
1469715	M	108	204	31.4	Yes	Shape 2
1469722	F	103	154	20.5	No	Shape 2
1469708	M	101	219	23.7	Yes	Shape 2
1469735	F	105	170	25.2	No	Colour 1
1469677	M	103	185	27.6	Yes	Colour 1
1468492	F	109	199	24.7	Yes	Colour 1
1469685	M	103	206	26.5	Yes	Colour 1
1469744	F	106	198	24.3	Yes	Colour 1
1469705	M	106	187	27.5	No	Colour 1
1469667	F	110	186	24.9	No	Colour 2
1469719	M	105	165	23.2	No	Colour 2
1469713	F	100	193	23.2	No	Colour 2
1469742	M	101	160	23.2	No	Colour 2
1469655	F	109	203	26.4	No	Colour 2
1469709	M	116	190	28.0	Yes	Colour 2

635 Measurements from time of capture as well as if the lizard finished the eight stages of the

636 task (learnt) and which stimulus group each animal belonged to. PIT – animal ID, SVL –

637 Snout Vent Length, TL – Total length.

638

639 **Table A2.** Perseverative errors.

PIT	Sex	Stimulus group	Perseverative trials (out of 10)	Stimulus	Binomial significance level
1469711	F	Shape 1	6/4	Star/H	0.7539
1469743	F	Shape 1	4/6	Star/H	0.7539
1469715	M	Shape 2	5/5	Star/H	1
1469708	M	Shape 2	4/6	Star/H	0.7539
1469677	M	Colour 1	5/3	DP/LP	0.7266
1469492	F	Colour 1	6/4	DP/LP	0.7539
1469685	M	Colour 1	3/7	DP/LP	0.3438
1469744	F	Colour 1	5/5	DP/LP	1
1469709	M	Colour 2	5/5	DP/LP	1

640 Number of perseverative errors during the first 10 trials (677 received only eight trials) of the
641 extra-dimensional shift stage of the nine individuals reaching criterion during this stage. The
642 table includes PIT (animal identification), sex of subjects, stimulus group subjects were in,
643 number of errors to the previously reinforced dimension, stimulus perseverative errors were
644 focused on and significance based on a two-tailed binomial test. DP – dark pink, LP – light
645 pink.

646

647 **Table A3.** Spray paints used to create the colour dimension on the cue cards.

Stage	Colour	Brand	Colour name
SD/SDR/CD/CDR colour group	Light blue	White Knight, Squirts	Gloss Sky Blue
	Dark blue	White Knight, Squirts	Gloss Bermuda Blue
SD shape group	Beige	Fiddly Bits	Ivory (discontinued)
	Light green	British Paints, Spray Easy	Lime Green
CD/CDR shape group	Dark green	White Knight, Squirts	Gloss Bright Green
	Light orange	White Knight, Squirts	Gloss Golden Yellow
ID/IDR	Dark orange	White Knight, Squirts	Gloss Orange X15
	Light pink	White Knight, Squirts	Gloss Pink
ED/EDR	Dark pink	White Knight, Squirts	Gloss Fuchsia

648 List includes the stage cards were used in, the colour, the name of the paint brand and
649 name of the colour as per manufacturer. SD – simple discrimination, SDR – simple
650 discrimination reversal, CD – compound discrimination, CDR – compound discrimination
651 reversal, ID – intra-dimensional acquisition, IDR – intra-dimensional reversal, ED – extra-
652 dimensional shift, EDR – extra-dimensional reversal.

653

654 **Table A4.** Order of stepwise model simplification.

Order	Model	DIC	Reason for removal of terms
1	Correct ~ Sex + Stimulus group + Sex : Stage + Sex : Stimulus group + Stimulus group : Stage	4750.95	Important interactions Stimulus group:Stage in CD, ID and ED are not significant (interaction dropped)
2	Correct ~ Sex + Stimulus group + Sex : Stage + Sex : Stimulus group	4736.71	Sex:Stimulus group interaction was only partly estimable due to insufficient data (interaction dropped)
3	Correct ~ Sex + Stimulus group + Sex : Stage	4736.92	Only one interaction significant (Sex:Stage – SDR), added to stage analysis (interaction dropped)
4	Correct ~ Sex + Stimulus group	4736.35	Neither Sex nor stimulus group are significant
5	Correct ~ Sex	4735.07	Best fitting model based on DIC
6	Correct ~ Stimulus group	4736.81	Model 5 explains the data better

655 Models were run to explore the effect of sex, stimulus group, stage and interactions between
656 the three effects on the probability of choosing correctly during the whole experiment (all
657 stages). Reasons for removal of terms is given as well as the DIC (deviance information
658 criterion). The final model was selected based on DIC.

659

660 **Table A5.** Shape area and circumference.

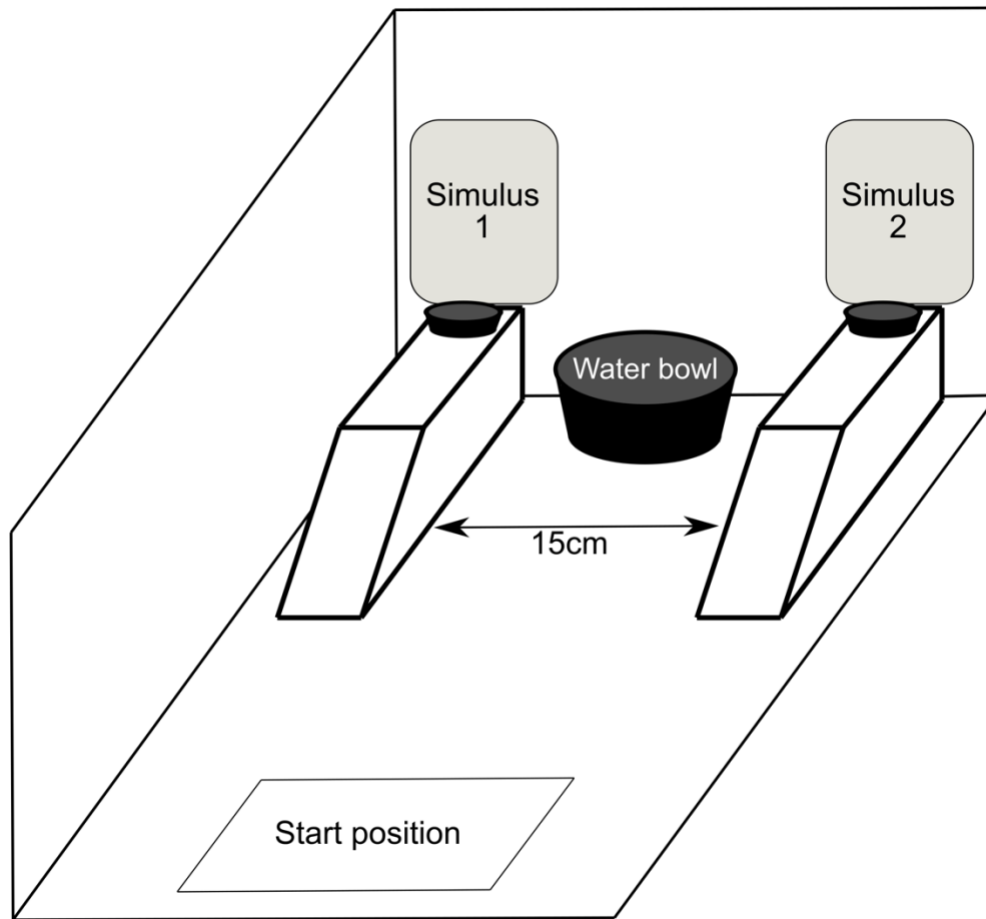
Shape	Stage	Area (cm ²)	Circumference (cm)
X	Simple & compound discrimination and reversal	14.08	36.80
Triangle	Simple discrimination and reversal	22.01	21.30
Circle	Intra-dimensional acquisition and reversal	13.85	30.47
Square	Intra-dimensional acquisition and reversal	26.01	22.00
H	Extra-dimensional shift and reversal	13.28	35.00
Star	Extra-dimensional shift and reversal	17.43	28.00

661 Amount of black area and circumference of the different shapes used during the set-shifting

662 experiment. Shapes are given in writing and as symbols, as well as what stages they were

663 used in and their area and circumference.

664



665

666 **Figure 1.** Schematic representation of the setup used during the set-shifting experiment.

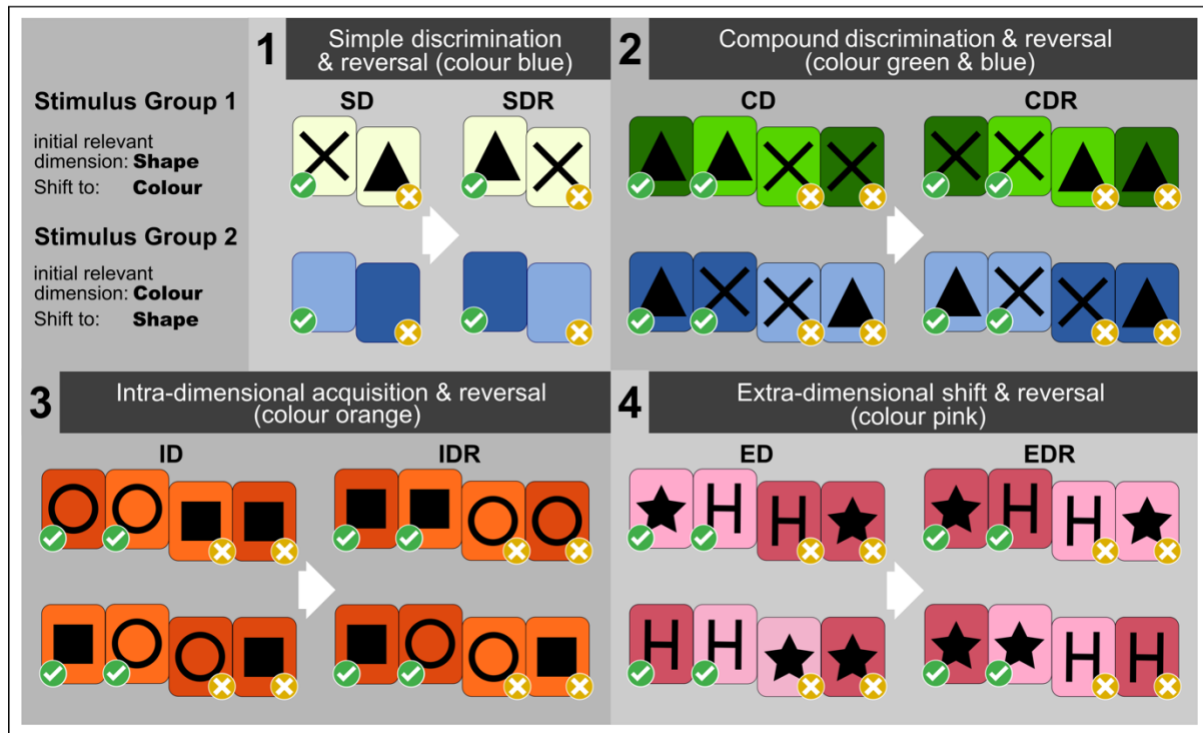
667 Two ramps are placed at one end of the tub (approximately 15 cm apart, the water bowl in

668 between) with the cue cards containing the stimuli attached to the inner wall of the enclosure

669 at the top end of the ramp and the food dishes containing the reward directly in front of the

670 cards. The start position indicates the position from where animals started in each trial.

671



672

673 **Figure 2.** Stimulus pairs and order of presentation (1 to 4) for both stimulus group 1 (which

674 started with shape as the positive stimuli, top row) and stimulus group 2 (which started with

675 colour as the positive stimuli, bottom row) during the eight stages of the set-shifting task.

676 Tick marks indicate the rewarded (correct) choice during each stage, whereas Xs indicate

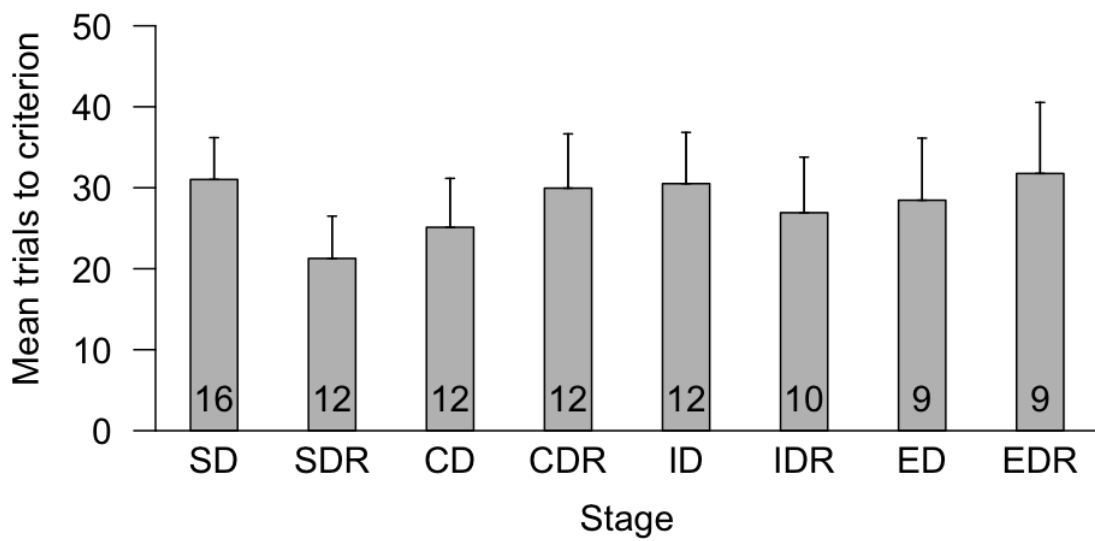
677 that access to the reward was blocked (incorrect choice). SD – simple discrimination, SDR –

678 simple discrimination reversal, CD – compound discrimination, CDR – compound

679 discrimination reversal, ID – intra-dimensional acquisition, IDR – intra-dimensional reversal,

680 ED – extra-dimensional shift, EDR – extra-dimensional reversal.

681



682

683 **Figure 3.** Mean + SE trials to criterion (including criterion trials) for each stage of the
684 experiment. Sample sizes are given within bars. SD – simple discrimination, SDR – simple
685 discrimination reversal, CD – compound discrimination, CDR – compound discrimination
686 reversal, ID – intra-dimensional acquisition, IDR – intra-dimensional reversal, ED – extra-
687 dimensional shift, EDR – extra-dimensional reversal. Stages were not significantly different
688 from each other.

689

690 APPENDIX A

691