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Subproblem learning and reversal of a multidimensional visual cue in a lizard: evidence for behavioural flexibility?



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

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Social living has many benefits but can also be a demanding environment in which interactions between individuals shape their social structure (Hinde, 1987). The resulting selective pressure is thought to have led to the evolution of extensive abilities in attention, memory and learning (Byrne & Whiten, 1988; Byrne, 1994, 1998), forming the foundation of the 'social intelligence hypothesis' (Humphrey, 1976). Complex cognition has been frequently investigated through behavioural flexibility: the ability to adjust behaviour to changes in the environment (Brown & Tait, 2015) by directing attention to essential stimuli (Dias, Robbins, & Roberts, 1996; Welsh & Pennington, 1988) and adjusting existing skills to a new problem (Manrique & Call, 2015). Behavioural flexibility can be a valuable tool in the social domain. To react flexibly to a change in the social environment (addition or removal of group members) and to selectively pay attention to interactions between individuals

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can be useful for tracking relationships within a social group (social monitoring; McNelis & Boatright-Horowitz, 1998). The insights gained can then be used to adjust behaviour directed towards conspecifics according to the current state of their interindividual relationships (Byrne, 1998; McNelis & Boatright-Horowitz, 1998).

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

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A touch screen test for ID/ED attentional set shifting was first developed to compare human and nonhuman primates' attentional set-shifting ability (Dias et al., 1996; Roberts, Robbins, & Everitt, 1988). The task consists of multiple sequential visual discriminations (using shapes and lines as stimulus dimensions), designed to encourage an attentional set (through repeated exposure to consistently relevant and irrelevant information: Sutherland & Mackintosh, 1971) and then test the ability to shift away from that set. First, subjects learn a simple discrimination (SD) between stimuli of only one dimension. After reaching a predetermined learning criterion the stimulus-reward association is reversed and the other stimulus in the pair is reinforced. Next, stimuli of the irrelevant dimension are superimposed onto the SD stimuli, producing compound cues (CD), with the SD stimuli still associated with reward. After reaching criterion the reward associations are again reversed. Next, during the intradimensional acquisition (ID), new examples of shapes and lines are introduced. With dimensional relevance staying the same, subjects must maintain their attentional set and apply it to unfamiliar stimuli. After reaching criterion, the reward contingencies are again reversed. Finally, during the extradimensional shift (ED), again, unfamiliar shapes and lines are introduced. In contrast to the intradimensional acquisition, the reinforcement is now associated with the formerly irrelevant dimension. If set formation occurred during earlier stages, performance in the extradimensional shift is expected to be worse compared to the intradimensional acquisition, since the previously established attentional set no longer applies (Garner et al., 2006; Roberts et al., 1988). The extradimensional shift is again followed by a reversal.

The assumption that the number of trials to reach criterion during extradimensional shifting is higher than during the intradimensional acquisition (as a measure of attentional set shifting) does not rely on absolute values. It is therefore possible to compare shift performance in different species (Table 1). For example, marmosets, *Callithrix jacchus*, can form an attentional set and shift to a previously irrelevant second dimension (Dias et al., 1996; Roberts et al., 1988) and similar results have been obtained in rhesus monkeys, *Macaca mulatta* (Baxter & Gaffan, 2007; Weed, Bryant, & Perry, 2008). Rodents, such as rats, *Rattus norvegicus* (e.g. Birrell & Brown, 2000; Hecht, Will, Schachtman, Welby, & Beversdorf, 2014; Kim, Choi, Jeon, & Han, 2016; McAlonan & Brown, 2003; McGaughy et al., 2014) and mice, *Mus musculus* (e.g. Bissonette, Lande, Martins, & Powell, 2012; Colacicco, Welzl, Lipp, & Wuerbel, 2002; Garner et al., 2006; Janitzky et al., 2015) also show the ability to form and shift attentional sets. Comparable findings in other taxa such as birds, fishes and reptiles are scarce (Table 1). One study in great tits, *Parus major*, showed their ability to form an attentional set and shift to a new dimension (Titulaer, van Oers, & Naguib, 2012). Painted turtles, *Chrysemys picta*, show an improved performance during successive compound discrimination reversals, perhaps indicative of set formation. However, without comparison between intradimensional and extradimensional stages, this improvement could equally be evidence of learning set formation (training effect) instead of attentional set formation (Cranney & Powers, 1983).

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

We tested tree skinks, *Egernia striolata*, which are viviparous, diurnal, family-living lizards found in arboreal and rocky habitats throughout eastern Australia (Wilson & Swan, 2008). Tree skinks show complex sociality in which lizards frequently live in family groups consisting of a socially monogamous parental unit and at least one generation of offspring (Chapple, 2003; Duckett, Morgan, & Stow, 2012; Whiting & While, 2017). They are visual foragers that eat plant material (including fruits) as well as insects such as cockroaches and grasshoppers (Chapple, 2003). As a diurnal, visual forager, *E. striolata* is a good model to investigate learning in a visual discrimination task. Furthermore, flexibly adjusting behaviour to changing conditions is beneficial for survival (Manrique & Call, 2015). Finally, complex sociality can select for enhanced cognitive

Table 1

Literature comparison between studies incorporating the described methodology

Species	Age	Methodology	Dimensions	ED>ID	Study
Primates					
Common marmoset	Subadult	CANTAB ID/ED	Visual	Yes	Dias et al., 1996
Common marmoset	Subadult	CANTAB ID/ED	Visual	Yes	Roberts et al., 1988
Rhesus monkey	Juvenile	CANTAB ID/ED	Visual	Yes	Weed et al., 2008
Rhesus monkey	Adult	CANTAB ID/ED	Visual	Yes	
Rhesus monkey	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

Column ED > ID indicates whether set formation impaired performance during the extradimensional shift (yes/no). ID: intradimensional acquisition; ED: extradimensional shift: REV: reversal; CANTAB ID/ED: Cambridge neuropsychological automated test battery ID/ED attentional set-shifting test.

abilities including flexibility in learning, attention and memory (Byrne & Whiten, 1988; Byrne, 1994, 1998) which can be important tools both within and outside a social context (Byrne & Bates, 2007).

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

METHODS

Study Animals and Husbandry

We hand-captured 24 adult (snout-vent length $[SVL] \ge$ 100 mm; Chapple, 2003) E. striolata (12 males and 12 females, mean SVL \pm standard deviation: all: 106.08 \pm 3.69 mm; male: 105.58 \pm 4.14 mm; female: 106.58 \pm 3.29 mm) near Albury, New South Wales (-35.980S, 146.970E), Australia, during April 2016. SVL, total length (TL), mass and sex (presence of hemipenes) were determined on site (Appendix Table A1). Additionally, each lizard was subcutaneously injected with a PIT tag (Biomark, HPT8, 8.4 mm: this method was chosen because animals do not show distinctive markings and it is preferable to toe clipping) laterally 1.5 cm behind the front leg (no anaesthetic was applied), for individual identification. Skinks were transported to Macquarie University within 2 days of capture and transferred into individual plastic tubs (487×350 mm and 260 mm high) immediately after arrival. Lizards were housed indoors, with room temperature set at 22.7 ± 1.9 °C (mean \pm SD, depending on season), relative humidity of 30–65% and a 12:12 h light:dark cycle. We installed heat cord underneath the enclosure to create a thermal gradient between 16 and 30 °C (±4 °C). For the duration of the experiment, room temperature was monitored within enclosures using iButtons (Thermochron iButton model DS1921) which recorded temperature hourly. We used newspaper as a substrate and each enclosure had a hide, a small water bowl and a wooden ramp. We fed lizards three times a week (Monday, Wednesday and Friday): twice with crickets powdered with vitamins (aristopet Repti-vite) and calcium (URS Ultimate Calcium) and once with baby food $(2 \pm 0.1 \text{ g}, \text{Heinz})$. During experiments, skinks were fed small amounts $(0.15 \pm 0.01 \text{ g})$ of baby food daily and crickets on Fridays; animals had ad libitum access to water. To ensure that animals had acclimated to the conditions of captivity, we kept them undisturbed for 2 weeks and made sure they were feeding consistently. All subjects were naïve and had never participated in any other cognition experiments.

Learning Experiment

Habituation

To habituate the animals to the experimental set-up, we transferred them to bigger tubs (683×447 mm and 385 mm high) 12 days prior to the start of the experiment. Previous studies have shown that extensive handling and unfamiliar environments induce increased levels of stress which affects learning (Burghardt, 1978; Langkilde & Shine, 2006); therefore, animals were kept and tested in these enclosures for the entire experiment. They were identical to previous enclosures except that a second ramp was introduced (Fig. 1). Baby food was presented on top of one ramp in a small white plastic saucer (3 cm in diameter) for 2 days (counterbalanced for side).

Set-up

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

Stimuli

Cue cards with the stimuli (S) were made of pressed wooden coaster cards (rectangle coaster, Boyle Industries Pty Ltd, Mitcham, VA, Australia; 11.3×9.3 and 0.3 mm high) and sprayed with differently coloured spray paint (Appendix Table A2). Shapes were drawn onto the sprayed cards by tracing a previously created pattern made of cardboard with a black waterproof marker (Fig. 2; for information on area and circumference of the shapes see Appendix Table A3). Colour pairs were chosen to be easily discriminable based on lizards' perception (Fleishman, Loew, & Whiting, 2011) and shapes were made up of lines (e.g. X, O, H) or



Figure 1. Schematic representation of the set-up used during the set-shifting experiment. Two ramps are place at one end of the tub (approximately 15 cm apart, the water bowl in between) with the cue cards containing the stimuli attached to the inner wall of the enclosure at the top end of the ramp and the food dishes containing the reward directly in front of the cards. The start position indicates the position from where animals started in each trial.



Figure 2. Stimulus pairs and order of presentation (1–4) for both stimulus group 1 (which started with shape as the positive stimulus) and stimulus group 2 (which started with colour as the positive stimulus) during the eight stages of the set-shifting task. Tick marks indicate the rewarded (correct) choice during each stage, whereas Xs indicate that access to the reward was blocked (incorrect choice). SD: simple discrimination: SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound discrimination reversal; ID: intradimensional acquisition; IDR: intradimensional reversal; ED: extradimensional shift; EDR: extradimensional reversal.

were solid. During experiments, the left/right position was pseudorandomly predetermined and counterbalanced for side, so that each stimulus was never on the same side more than twice in a row. For compound cues, the left/right position of each stimulus dimension varied independently of each other.

Experimental procedure

At the start of a trial, each individual was ushered into its hide if not already in it and placed at the start position opposite the ramps. Next, both cue cards were simultaneously fixed with putty (Bostik Blu-Tack) to the inner wall of the tub and immediately afterwards feeding dishes were placed on the ramps in the same manner in front of the stimuli (Fig. 1). The order in which the subjects were set up was kept constant over the course of the study. After about 3 min of acclimation, the hide was removed, and the trial started, lasting for 1.5 h. We then returned the hide and removed feeding bowls and cues. Between trials both dishes were cleaned and rebaited, making sure that both bowls were touched. Cues and feeding dishes were never interchanged between individuals. Trials were conducted from May 2016 to March 2017. We tested subjects twice a day, between 0800 and 1230 hours, 5 days a week (10 trials per week) with an intertrial interval (ITI) of 40 min. All trials were videotaped (H.264 Digital Video Recorder, 3-Axis Day & Night Dome Cameras) and scored afterwards. During trials, animals were left undisturbed to minimize stress caused by the inability to hide.

Choice (correct/incorrect) was scored as the first food dish over which an animal's snout passed. Latency was scored as the time from first movement (directed, uninterrupted forward movement of the whole body ending in the examination of a food bowl; an interruption is defined as no movement for 10 s or more) to the first food dish examined. Animals were not actively corrected when making a wrong choice (noncorrection method) and had ample opportunity to visit both stimuli and feeding dishes during trials. We used a learning criterion of 6/6 or 7/8 correct choices in consecutive trials. These criteria were chosen because they have shown to be good indicators of successful learning (Leal & Powell, 2012). To avoid overtraining, an animal was allowed no more than 100 trials for each stage. If a subject showed chance or below chance performance for at least 6 consecutive weeks (60 trials) or did not show criterion performance of 6/6 or 7/8 consecutive trials correct within the 100 trials, it was removed from the experiment ('nonlearner'); as soon as an individual reached criterion, however, it moved on to the next stage.

Coding

A subset (about 17% = 809) of trials randomly chosen from all subjects and stages was rated by two researchers (M.L. and P.Y.) unfamiliar with the experiment and blind to the tested questions as well as by the first author (B.S.). Interobserver reliability was calculated based on Cohen's kappa (Falissard, 2012), which estimates the interrater agreement between two independent raters; 100% agreement equals a kappa of 1, 0% agreement a kappa of 0. It was estimated at 0.92 and 0.94 between M.L. and B.S. and P.Y. and B.S., respectively.

Simple discrimination and reversal

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

Compound discrimination and reversal

As soon as subjects reached criterion on the simple discrimination reversal, they were tested on the compound discrimination (CD), introducing a second stimulus dimension. The initially trained stimulus dimension remained relevant (e.g. triangle and X), while the second dimension acted as an irrelevant distractor (e.g. background colour). Stimulus group 1 was presented with two different shapes (triangle and X) superimposed on the dark and light green background colours and stimulus group 2 with two different colours on the background (light and dark blue; Fig. 2). To succeed at this stage, animals had to maintain their attention on the currently relevant dimension, and respond according to the already learnt stimulus-reward association (e.g. X is rewarded regardless of background colour), while ignoring the new stimulus dimension. After the performance criterion was met on the CD, subjects moved on to a reversal (CDR), again changing the former unrewarded S⁻ to S⁺ and vice versa (e.g. triangle is rewarded regardless of background colour).

Intradimensional acquisition and reversal

After the subjects had reached the learning criterion on the CDR, we introduced new examples of shapes and colours; however, the relevant dimension (stimulus group 1: shape; stimulus group 2: colour) stayed the same as in previous stages (Fig. 2). Test subjects had to apply their attentional set to novel pairs of stimuli (e.g. a square and circle), while still ignoring the second dimension (e.g. background colour). After reaching criterion at the intradimensional acquisition (ID), subjects were tested on a reversal (IDR), changing reinforcement to the alternate stimulus in a pair.

Extradimensional shift and reversal

As with the previous stage, we again introduced unfamiliar colours and shapes to the test subjects: however, S⁺ was shifted to one of the two stimuli within the former irrelevant dimension (stimulus group 1 to colours and stimulus group 2 to shapes; Fig. 2). We introduced new stimuli to avoid any partial reinforcement effects (Shanab & Mcclure, 1983), and to ensure the intradimensional (ID) and extradimensional (ED) stages were equivalent (save for the effects of the primed attentional set). Therefore, the reward contingencies changed so that the previously irrelevant dimension now contained the positive and negative stimuli (e.g. light and dark pink), whereas the former relevant dimension (shapes) became irrelevant to reinforcement. After reaching criterion at the ED, subjects were presented with a reversal (EDR): the reward was now associated with the formerly unreinforced stimulus in the new relevant dimension (e.g. ED: light pink was reinforced; EDR: dark pink was reinforced).

Statistical Analyses

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

To base estimates on as many data points as possible we included data from all animals that reached criterion in any given stage (excluding the stage they were removed) in the analysis. This means that the number of individuals decreases with stage (as they were removed after not reaching criterion) which can compromise statistical power. We applied Bayesian GLMMs (Hadfield, 2010) to test whether the probability of choosing correctly increased with the number of trials (indicative of learning), in each of the eight stages separately. We used the same approach to test whether learning performance was influenced by sex or stimulus group as well as interactions between sex and stage, sex and stimulus group, and stimulus group and stage. However, nonsignificant interactions were subsequently dropped and the best-fitting model, based on DIC (deviance information criterion), is presented (Appendix Table A4). The final global model included only sex and stimulus group as fixed effects. Our analysis did indicate a significant sex difference in one stage (SDR) and sex was therefore included in the analysis of this stage (Table 2). In all models, 'trial' was z-transformed (mean centred and scaled by the standard deviation) for better interpretability of probabilities. Models also included individual level random slopes (trial) and intercepts (individual PIT) to account for the possible autocorrelation between successive choices.

Instead of an attentional set, animals might have formed a learning set (training effect). To test this, we used a Bayesian approach, like the stage-by-stage analysis but including a random intercept for stage in the random effects term. Furthermore, we ran separate GLMMs to find out whether performance on the extradimensional shift stage differed from the intradimensional acquisition stage (shift performance) as well as between acquisition and reversal stages of compound, intradimensional and extradimensional discrimination (reversal learning) by focusing only on data from stages of interest (either ID and ED, CD and CDR, ID and IDR or ED and EDR; Table 2). Trial was included in the models as a fixed effect as a scaling variable to make estimates interpretable. Model diagnostics were performed on all models to ensure that no autocorrelation between samples of the posterior distribution occurred (correlation between lags < 0.1; Hadfield, 2010) and that sufficient mixing took place (by visually inspecting plots of MCMC chains). We used Heidelberg and Welch diagnostic tests to ensure that the chain was long enough. Lastly, to find out whether animals made perseverative errors after the initial shift (extradimensional shift stage), indicative of the formation of an attentional set (Garner et al., 2006), we investigated their choice during the first 10 trials of the extradimensional shift stage using the binomial test.

Ethical Note

Our study involved noninvasive observations of animal behaviour which were approved by the Macquarie University Animal Ethics Committee (ARA no. 2013/031). Collection of skinks was approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (license no. SL101264). Skinks were captured individually by hand and placed in cloth bags until they could be transported by vehicle to Macquarie University from Albury, New South Wales, in an insulated box. If possible both animals in a pair were collected. All animals were euthanized by injecting Lethabarb, diluted 1:1 with saline buffer solution (100 mg/kg) intrapleuroperitoneally at the end of the study to extract the brain for a comparative brain study.

RESULTS

Of the 24 animals tested, 15 were excluded because they did not reach the learning criterion in 100 trials: eight (five males and three females) during the simple discrimination, four (two males and two

Table 2	
Summary of parameter estimates and test statistics to investigate reversal and shift performance	

Parameter	Posterior mean	Lower 95% confidence interval	Upper 95% confidence interval	рМСМС
Shift performance				
Intercept	0.663	0.116	1.261	0.018
Stage	0.009	-0.480	0.505	0.969
Trial	0.391	-0.110	0.885	0.103
Stage * Trial	-0.145	-0.640	0.348	0.563
Reversal learning in com	pound stages			
Intercept	0.690	-0.005	1.391	0.032
Stage	-0.133	-0.579	0.311	0.567
Trial	0.581	-0.046	1.259	0.051
Stage * Trial	-0.144	-0.639	0.353	0.568
Reversal learning in intr	adimensional stages			
Intercept	0.886	0.195	1.671	0.011
Stage	-0.148	-0.575	0.278	0.495
Trial	0.626	0.014	1.289	0.029
Stage * Trial	-0.115	-0.556	0.343	0.613
Reversal learning in extr	adimensional stages			
Intercept	0.958	0.125	1.860	0.023
Stage	-0.108	-0.525	0.317	0.616
Trial	0.545	-0.221	1.378	0.145
Stage * Trial	-0.126	-0.539	0.287	0.549

The table shows the difference in the probability of a correct choice between the intradimensional and extradimensional shift stages (shift performance) and the acquisition and reversal stages. Significant parameters are indicated in bold. pMCMC: significance of parameter based on Bayesian modelling.

females) during the simple discrimination reversal, two females during the intradimensional reversal and one female during the extradimensional shift. Motivation was high during the experiment: in a total of 4854 trials (sum of all 24 individuals) there were only two trials (one each for two subjects) during which the reward was not eaten.

Body condition did not differ between learners and nonlearners (LM: estimate = -0.49, SE = 0.95, t = -0.52, P = 0.610). As predicted, animals that were removed (nonlearners) during the experiment made significantly more errors than learners (GLMM: estimate = 0.16, SE = 0.05, Z = 3.14, P = 0.002) showing that nonlearners were performing badly. Additionally, the probability of choosing correctly increased with trial number, indicated by a positive value, for learners in each stage confirming the robustness of our learning criteria. As sample size decreased with each stage, statistical power decreased and, consequently, the width of confidence intervals increased to cross zero leading to nonsignificant results (Table 3). Neither stimulus group nor sex affected performance within any given stage except simple discrimination reversal, in which males' probability of choosing correctly was significantly higher than females (Table 3). Furthermore, animals did not show a shift cost (increase in number of trials to learn the extradimensional shift stage compared to intradimensional acquisition, Table 2, Fig. 3) or reversal cost (increased number of trials to learn between acquisition and reversal stages, Table 2, Fig. 3) and animals did not perseverate (base their choice on the previously reinforced dimension) on the formerly relevant dimension (binomial test: N = 10, P > 0.05; Appendix Table A5) during the first 10 trials of the extradimensional shift stage. The probability of choosing correctly did not increase significantly with trial when controlling for stage as a random effect, showing that no learning set was formed either (GLMM: posterior mean = 0.23, lower 95% confidence interval, CI = -0.21, upper 95% CI = 0.66, P = 0.275).

DISCUSSION

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

The attentional set-shifting task is designed to show attentional set formation only if animals experience an increase in trials to criterion during the extradimensional shift relative to the intradimensional acquisition, after forming a set during the sequential progression from simple (in which an animal first learns what stimuli are relevant to find a reward; Baxter & Gaffan, 2007), then compound (in which the same stimuli plus a distractor in the form of a second dimension are presented; Birrell & Brown, 2000), to intradimensional discrimination (during which animals have to transfer previously acquired knowledge to unfamiliar stimuli; Brown & Tait, 2015; Dias et al., 1996). Subjects need to overcome this previously learnt attentional set and shift their attention away from one dimension to the second, formerly irrelevant, dimension. Our results do not show evidence that the tested group of lizards formed an attentional set; therefore, we are not able to conclude that their performance at the extradimensional stage reflected an attentional shift. This stands in contrast to findings in primates, rodents and a bird which all showed a decrease in learning speed during the shift stage compared to the intradimensional acquisition (Table 1), whereas our lizards showed similar levels of learning in these stages.

In addition to the extradimensional shift stage, the standard setshifting task includes reversal stages. During the acquisition (learning) of a discrimination, positive (rewarded stimulus) and negative (unrewarded stimulus) values are assigned to each stimulus (Wise, Murray, & Gerfen, 1996, cited by Manrique & Call, 2015)

Table 3
Summary of parameter estimates and test statistics calculated for each stage

Parameter	Posterior mean	Lower 95% confidence	Upper 95% confidence	pMCMC			
		interval	interval				
Simple discrimination							
Intercept	0.424	0.055	0.813	0.023			
Trial	0.373	0.068	0.704	0.018			
Simple discrimination r	eversal						
Intercept	1.383	-0.562	4.363	0.123			
Trial	1.286	-0.754	4.179	0.174			
Sex	1.704	0.453	3.015	0.008			
Compound discriminati	on						
Intercept	1.147	0.069	2.368	0.015			
Trial	1.209	0.091	2.538	0.015			
Compound discriminati	on reversal						
Intercept	1.023	-0.136	2.521	0.046			
Trial	0.781	-0.288	2.094	0.106			
Intradimensional discri	mination						
Intercept	0.915	0.083	1.896	0.020			
Trial	0.589	-0.114	1.389	0.074			
Intradimensional discri	mination reversal						
Intercept	1.196	-0.199	2.904	0.059			
Trial	0.996	-0.418	2.733	0.124			
Extradimensional shift							
Intercept	1.241	-0.175	2.971	0.054			
Trial	0.757	-0.625	2.306	0.225			
Extradimensional shift	reversal						
Intercept	1.363	0.023	2.872	0.032			
Trial	1.107	-0.267	2.463	0.095			
Global model	Global model						
Intercept	0.170	-0.034	0.380	0.100			
Sex	0.223	-0.082	0.532	0.144			

Learning performance (probability of correct choices) was analysed separately for each of the eight stages of the experiment including a global model based on data of all stages to investigate the effect of sex on performance. Sample sizes decreased with stage due to animals being removed as nonlearners: SD = 24, SDR = 16, CD = 12, CDR = 12, ID = 12, IDR = 12, ED = 10, EDR = 9. Significant parameters are indicated in bold. pMCMC: significance of parameter based on Bayesian modelling.



Figure 3. Mean + SE trials to criterion (including criterion trials) for each stage of the experiment. Sample sizes are given within bars. SD: simple discrimination: SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound discrimination reversal; ID: intradimensional acquisition; IDR: intradimensional reversal.

and the proportion of behavioural responses is increasingly directed towards the reinforced stimulus (learning). When a subject is confronted with a reversal it first must inhibit responding to the formerly positive stimulus and then form a new reward association with the formerly negative stimulus (Dias et al., 1996). Most of our lizards that could learn during acquisitions were able to reverse during the following stage, showing the ability to inhibit responding to an established stimulus–reward relationship and showing flexibility in their response behaviour. Furthermore, our lizards performed well during reversals showing no decrease in performance compared to the respective acquisition stages. This result stands in contrast to findings in rhesus monkeys (e.g. Weed et al., 2008), rats (e.g. McAlonan & Brown, 2003) and mice (e.g. Garner et al., 2006) which perform worse in reversals than acquisition.

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

In this study, colour pairs were chosen based on humanperceived brightness and shapes could be categorized into those made up of lines (e.g. X, O, H) and those that were solid (e.g. triangle, square, star). Combinations were chosen to be easily distinguishable based on the lizards' perceptual ability (they are tetrachromatic and have good visual acuity; Fleishman et al., 2011). Skinks could have experienced a sensory bias towards one or more stimuli or a dimension. For example, rhesus monkeys perform differently when shifting according to the stimulus dimension they initially encountered. Monkeys had difficulty shifting from colour to shape but not vice versa (Baxter & Gaffan, 2007). During the first stage, we started each of four subsets of lizards (stimulus groups) with one of the four stimuli (light blue, dark blue, X or triangle). However, performance did not differ between stimulus groups, indicating that our dimensions were of similar difficulty to our test animals. There is a possibility that lizards used brightness instead of chroma or hue to learn the discrimination. As the order of presentation from simple discrimination to intradimensional reversal was bright-dark-dark-bright-bright-dark this can be seen as a sequence of simple acquisition and reversal stages. Therefore, if animals had used brightness, our data would show a decrease in trials to criterion since a reversal to a previously correct stimulus is easier than a reversal to a previously not reinforced stimulus, but no such decrease was found. The same is true for shape solidity, area and circumference (line-solid-solid-line-solid-line, smalllarge-large-small-large-small and long-short-short-long-shortlong). However, there is a small chance that animals used some other property of the cue cards (surface texture or minor imperfections due to the painting process) to learn the discrimination that was not visible to a human observer.

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

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Appendix

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

Measurements were taken at time of capture. PIT: animal ID; F: female; M: male; SVL: snout vent length; TL: total length. 'Learnt' indicates whether the lizard finished the eight stages of the task.

Table A2

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

SD: simple discrimination; SDR: simple discrimination reversal; CD: compound discrimination; CDR: compound discrimination reversal; ID: intradimensional acquisition; IDR: intradimensional reversal; ED: extradimensional shift; EDR: extradimensional reversal.

Table A3

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

Shape	Stage	Area (cm ²)	Circumference (cm)
х	Simple and compound discrimination and reversal	14.08	36.80
Triangle	Simple discrimination and reversal	22.01	21.30
Circle	Intradimensional acquisition and reversal	13.85	30.47
Square	Intradimensional acquisition and reversal	26.01	22.00
Н	Extradimensional shift and reversal	13.28	35.00
Star	Extradimensional shift and reversal	17.43	28.00

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 is significant
5	Correct ~ Sex	4735.07	Best-fitting model based on DIC
6	Correct ~ Stimulus group	4736.81	Model 5 explains the data better

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

Table A5

Number of perseverative errors during the first 10 trials (677 received only eight trials) of the extradimensional shift stage of the nine individuals reaching criterion during this stage

PIT	Sex	Stimulus group	Perseverative trials (out of 10)	Stimulus	Binomial P
1469711	F	Shape 1	6/4	Star/H	0.754
1469743	F	Shape 1	4/6	Star/H	0.754
1469715	М	Shape 2	5/5	Star/H	1
1469708	Μ	Shape 2	4/6	Star/H	0.754
1469677	М	Colour 1	5/3	DP/LP	0.727
1469492	F	Colour 1	6/4	DP/LP	0.754
1469685	Μ	Colour 1	3/7	DP/LP	0.344
1469744	F	Colour 1	5/5	DP/LP	1
1469709	М	Colour 2	5/5	DP/LP	1

PIT: animal ID; F: female; M: male; DP: dark pink; LP: light pink. Significance is based on a two-tailed binomial test.