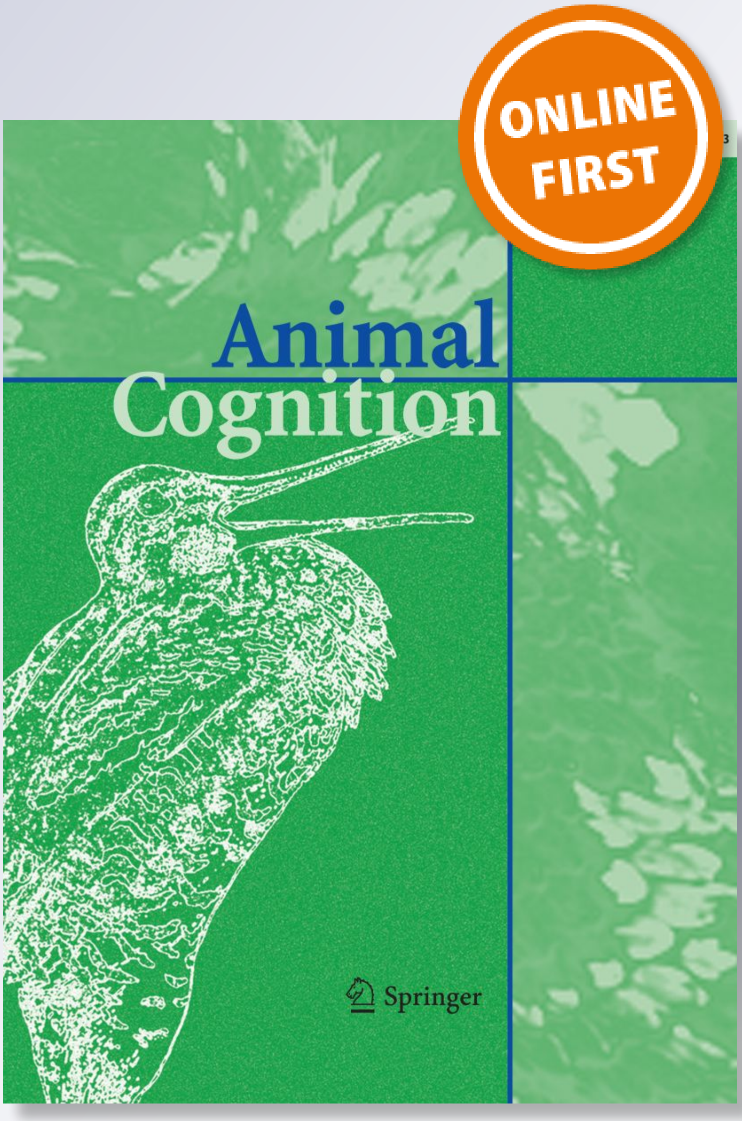
Context-specific response inhibition and differential impact of a learning bias in a lizard

Birgit Szabo, Daniel W. A. Noble & Martin J. Whiting

Animal Cognition

ISSN 1435-9448

Anim Cogn
DOI 10.1007/s10071-019-01245-6



Springer

Animal Cognition
https://doi.org/10.1007/s10071-019-01245-6

ORIGINAL PAPER

Context-specific response inhibition and differential impact of a learning bias in a lizard

Birgit Szabo[1] · **Daniel W. A. Noble**[2,3] · **Martin J. Whiting**[1]

Received: 5 July 2018 / Revised: 30 December 2018 / Accepted: 24 January 2019

Abstract

Response inhibition (inhibiting prepotent responses) is needed for reaching a more favourable goal in situations where reacting automatically would be detrimental. Inhibiting prepotent responses to resist the temptation of a stimulus in certain situations, such as a novel food item, can directly affect an animal's survival. In humans and dogs, response inhibition varies between contexts and between individuals. We used two contextually different experiments to investigate response inhibition in the eastern water skink (*Eulamprus quoyii*): reversal of a visual two-choice discrimination and a cylinder detour task. During the two-choice task, half of our lizards were able to reach an initial learning criterion, but, thereafter, did not show consistent performance. Only two individuals reached a more stringent criterion, but subsequently failed during reversals. Furthermore, half of our animals were not able to inhibit a pre-existing side preference which affected their ability to learn during the two-choice task. Skinks were, however, able to achieve a detour around a cylinder performing at levels comparable to brown lemurs, marmosets, and some parrot species. A comparison between the tasks showed that reaching the initial criterion was associated with low success during the detour task, indicating that response inhibition could be context-specific in the water skink. To the best of our knowledge, this is the first study to examine inhibitory control and motor self-regulation in a lizard species.

Keywords Cognition · Executive function · Non-avian reptile · Squamate

Introduction

Inhibitory control is one of three core control processes encompassing executive function. These are activated in novel situations to achieve a more beneficial outcome when responding automatically or instinctively would be disadvantageous (Diamond 2013). A predator, for example, must wait for the right moment to strike to capture its prey. Controlling attention and behavioural responses to overcome the pull of an external lure, such as a premature strike at a potential prey item, require inhibitory control (Santos et al. 1999). Inhibiting prepotent motor responses and going against instinct, however, takes effort (Diamond 2013).

Inhibitory control can be further broken down into distinct contextual classes such as inhibitory processes controlling attention (i.e., attentional inhibition) or motor responses (i.e., motor–response inhibition). In humans, studies show that inhibitory control has a common neural basis (e.g., Diamond 2013) which supports the view that inhibition is consistent across different contexts (Bray et al. 2014). Some research in humans, however, points to a more context-specific control which varies even between individuals (Tsukayama et al. 2011; Bray et al. 2014).

From the human literature, a plethora of methods exists to test for executive function. Some have been adopted to investigate animal cognitive abilities and associated evolutionary history. Simple two-choice discrimination and reversal learning, for example, test an animal's ability to associate one of the two stimuli with a reward. As soon as

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10071-019-01245-6) contains supplementary material, which is available to authorised users.

✉ Birgit Szabo
birgit.szabo@gmx.at

[1] Department of Biological Sciences, Macquarie University, NSW 2109 Sydney, Australia

[2] Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia

[3] Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, Australia

this stimulus–reward relationship is established, a reversal is applied during which the previously unrewarded stimulus becomes rewarded. When a subject is confronted with the reversal, it first needs to inhibit responding to the formerly rewarded stimulus and then to form a new stimulus–reward association with the formerly unrewarded stimulus (Dias et al. 1996). Although discrimination reversal is a common test used in animal cognition (Sutherland and Mackintosh 1971), only a fraction of these studies have focused on reptilian reversal learning in the visual domain. For example, rough-necked monitor lizards (*Varanus rudicollis*; Gaalema 2011), green anoles (*Anolis evermanni*; Leal and Powell 2012), and three-lined skinks (*Bassiana duperreyi*; Clark et al. 2014) all learnt to discriminate between two colour stimuli and, thereafter, successfully reversed this initial discrimination, providing evidence for response inhibition (for further reading see Burghardt 1978; Wilkinson and Huber 2012).

Another widely used method to investigate motor–response inhibition is a detour task. During a detour, animals need to either reach or move their entire body around a barrier to gain access to a reward. Different barrier shapes, such as V-shaped or cylindrical tubes, are made of a range of materials. These include mesh or glass through which the reward inside is visible during testing. The reward elicits strong motivation to approach, making it more difficult to detour compared to an invisible reward (Diamond 1981, 1990). Cylinder tasks combine both opaque and transparent barrier stages (Bray et al. 2014; MacLean et al. 2014). First, animals learn the motor action of detouring around an opaque cylinder without touching its surface. After a performance criterion is met, animals are presented with a transparent cylinder of the same shape and size. The number of successful detours (without touches to the transparent barrier) out of 10 to either entrance is used to gain insight into a subject's ability to inhibit motor responses (Diamond 1981, 1990; MacLean et al. 2014). The cylinder task has been tested in different mammals and birds, and the results indicate that great apes (MacLean et al. 2014) and corvids (Kabadayi et al. 2016) possess superior inhibitory skills (making fewer mistakes during the transparent cylinder phase) compared to the other primates and birds (Kabadayi et al. 2017b), respectively. Furthermore, only one study has applied the cylinder task in fish (Lucon-Xiccato et al. 2017) and, so far, tests of inhibition using the cylinder task in reptiles are completely absent. Therefore, to better understand response inhibition across all vertebrates, and its evolution, we need more data that include reptiles.

Discrimination reversals and cylinder detours require subjects to inhibit automatic responses to either the formerly positive stimulus or visible reward within the transparent cylinder. The basic properties of both tasks, however, are fundamentally different. Most importantly, during visual discrimination, the reward itself is not visible, only the stimulus associated with the reward can be seen while making a choice, whereas during detours around transparent barriers, the reward is visible, exerting a strong pull towards a direct approach and an error (while direct approaches during reversals do not necessarily lead to an error). Testing animals on both tasks can, therefore, give insight into how inhibition is exercised in different contexts and whether there is a trade-off or a correlation between these cognitive processes. Bray and colleagues (2014) tested dogs on three contextually different response inhibition tasks: a social task, an A-not-B task, and the cylinder task. Their aim was to investigate if dogs exhibit context-general or context-specific inhibitory skills. The dogs' performance did not correlate between the three tasks which led the authors to conclude that dogs possess context-specific inhibitory skills.

Here, we report the results on two experiments investigating response inhibition in the eastern water skink (*Eulamprus quoyii*), a reversal of a visual discrimination task as well as a detour task. *Eulamprus quoyii* is a medium-sized, Australian skink species (Cogger 2014), common in suburban areas. These lizards are primarily visual foragers (Veron 1969; Daniels 1987), making them suitable candidates for testing inhibition using visual stimuli. Previous studies in the water skink have shown their ability to use visual cues to escape a simulated predator attack in semi-natural (Noble et al. 2012) and laboratory conditions (Carazo et al. 2014) as well as socially (Noble et al. 2014) and individually (Qi et al. 2018) learn a simple colour discrimination.

Our aim was to test this species' inhibitory control in two different tasks, a simple visual two-choice discrimination reversal learning task and a detour task around a cylinder (Bray et al. 2014; MacLean et al. 2014). Based on the previous studies (e.g., Gaalema 2011; Leal and Powell 2012; Clark et al. 2014), we expected lizards to learn the visual discrimination and exhibit inhibitory control when responding during reversals. This is the first study testing a lizard on the cylinder task, allowing their performance to be compared to the results in mammals (Bray et al. 2014; MacLean et al. 2014), birds (Kabadayi et al. 2016, 2017b; MacLean et al. 2014), and fishes (Lucon-Xiccato et al. 2017).

General methods

Study animals and husbandry

During October 2017, 20 adult (snout–vent length [SVL] ≥ 100 mm; Cogger 2014) *Eulamprus quoyii* (10 males and 10 females, mean SVL ± SD all: 107.6 ± 5.8 mm; male: 106.3 ± 5.2 mm; female: 108.9 ± 6.4 mm, Online Resource, Table 1) were captured at Macquarie University campus, New South Wales, Australia, by noosing. Skinks were transported to Macquarie University Fauna Park within 2 h of capture and moved indoors into individual plastic tubs (683 L × 447 W × 385 H mm). The room temperature was set at 24 ± 2 °C (mean ± SD, depending on season) and animals were kept on a 12:12 h light:dark cycle. Heat cord was installed underneath each enclosure, thereby elevating the temperature on one side to 32 °C. We established sex (presence of hemipenes) and measured snout–vent length (SVL), total length (TL), and weight on the day of capture, and each lizard was PIT-tagged (passive integrated transponder) for individual identification (Online Resource, Table 1). For the duration of the experiment, the room temperature was monitored within enclosures using iButtons (Thermochron iButton model DS1921) which recorded temperature hourly. Newspaper was used as a substrate and each enclosure included a hide, a small water bowl, and two wooden ramps. We fed lizards three times/week (Monday, Wednesday, and Friday); twice with dog food (20 g) and once with crickets powdered with vitamin (aristopet Repti-vite) and calcium (URS Ultimate Calcium). During experiments, skinks were fed small pieces (0.1–0.2 g; amounting to less food than what was fed before the experiment to ensure motivation to participate) of cat food (Purina Supercoat® Adult chicken) soaked in water (to make them soft and easy to cut into six pieces, these were made three times a week to make sure that they were fresh) and crickets on Fridays; animals had ad libitum access to water. All subjects were naïve and had never participated in any cognitive experiments. All lizards were used in both experiments (details below).

Habituation

Animals were tested in their home enclosure to reduce stress from regular handling and thereby reduce or prevent stress-related learning impairments (Langkilde and Shine 2006). Lizards were left undisturbed for 2 weeks prior to the start of experiment 1. During this time, we made sure that animals were feeding consistently and were habituated to captivity.

Experiment 1: visual discrimination learning

Methods

Setup

Within each enclosure, masking tape secured newspaper substrate to the tub floor during trials to prevent animals from crawling underneath and out of sight from our cameras. Two ramps were place at one end of the enclosure with the water bowl in between and the hide at the opposite end at the starting position (Fig. 1b). At the start of a trial, cue cards containing the stimuli were attached to the inner wall of the enclosure at the top end of the ramp and the food dishes (55 mm diameter and 12 mm height) containing the reward (0.1–0.2 g) were placed directly in front of the cards. Dishes were covered on the outside with black electrical tape and inside with re-usable adhesive putty (Bostik Blu-Tack) to be able to stick mesh onto the top. Each dish was covered with a round piece of fine polyester window screen; however, we cut a hole into one of the pieces of mesh to provide access to the reward in one dish (Online Resource, Fig. 4). To prevent animals from associating one of the food dishes with the reward instead of the stimuli, the side each dish was presented during the experiment followed a random predetermined order. Cue cards (for more details, see Szabo et al. 2018) containing the stimuli (colour/shape) were visible to the lizards from any position within their enclosure and lizards were unable to see into the food dish before making a choice. Half of the subjects ($N = 10$; $N = 5$ females and $N = 5$ males) were trained on a shape discrimination and the other half ($N = 10$; $N = 5$ females and $N = 5$ males) were trained on a colour discrimination (Fig. 1a). All groups were counterbalanced for sex and mean SVL (± 0.1 mm).

Experimental procedure and coding

At the start of a trial, lizards were ushered into their hide at the starting position (Fig. 1b). After about 30 s the hide was removed and the lizard exposed to the setup. A trial lasted for 1.5 h after which the hides were replaced and feeding bowls and cards removed. Between trials, we cleaned both dishes and refilled them with food, making sure that both bowls were touched in the same manner (to ensure that both dishes smelled the same). The order in which subjects were set up was alternated over the course of the study to prevent order effects and cue cards and dishes were never swopped between individuals. Trials were conducted from October 2017 to February 2018, three times a day, between 08:00 and 14:00 h, 5 days a week (= 15 trials per week) with an inter-trial interval (ITI) of 40 min. All trials were videotaped (H.264 Digital Video Recorder, 3-Axis Day and Night Dome Cameras) with no experimenter present in the room (to minimize stress experienced by the inability to hide) and scored afterwards by two researchers.

We scored the lizard's choice (correct/incorrect) as the first food dish which a subject looked into (by raising its head high enough to see inside). We also recorded the time from the start of the trial and 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 choice (trial latency and choice latency in seconds). Choice latency was measured separately because the time from trial start to first movement can be quite long (range = 0–4731 s). A non-correction method was used during which lizards were

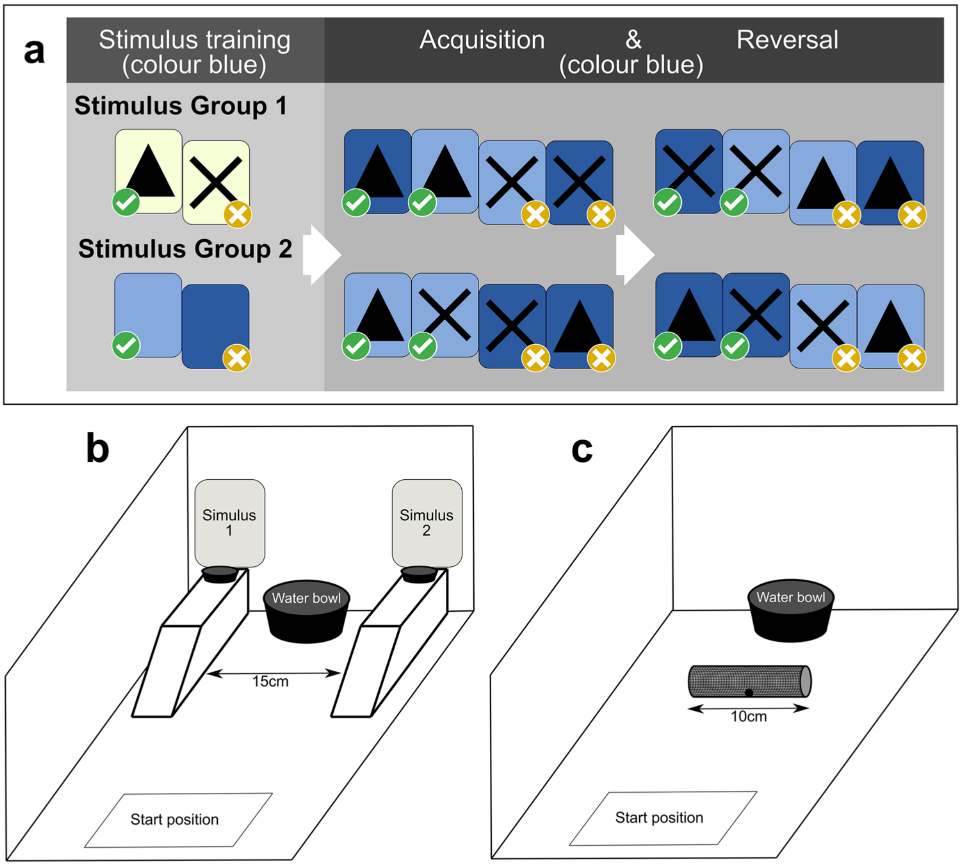


Fig. 1 **a** Stimulus pairs and order of presentation (left to right) for both stimulus group 1 (which was tested on a shape discrimination, top row) and stimulus group 2 (which was tested on a colour discrimination, bottom row) during stimulus training as well as acquisition and reversal of the discrimination learning task. Tick marks indicate the rewarded (correct) choice during each stage, whereas Xs indicate that access to the reward was blocked (incorrect choice). **b** Schematic representation of the setup used during the visual discrimination learning experiment. Two ramps are placed at one end of the tub (about 15 cm apart) with the cue cards containing the stimuli at the top end of each ramp and the food dishes directly in front of the cards. The water bowl was placed between the ramps and animals started each trial from the starting position. **c** Schematic representation of the setup used during the cylinder task. The ramps were removed and replaced with a 10 cm-long opaque or transparent cylinder (Online Resource, Fig. 5) attached to the enclosure floor (Bostik Blu-Tack). After the hide was removed, a reward was placed at its centre with tweezers in full view of the animal (the side was based on a predetermined pseudo-random order). **a**–**c** Created with Inkscape

able to correct their errors by visiting both dishes within the same trial. The initial learning criterion was defined as either 6/6 or 7/8 consecutive trials chosen correctly. However, to ensure the robustness of these criteria, animals received 12 post-criterion trials during which they were allowed to make a maximum of two errors. If they had successfully learned the task animals should make no, or only very few, mistakes, by chance, after reaching criterion. If an animal made more than two errors, it was moved to a more stringent learning criterion of 8/8 or 9/10 correct trials in a row (criteria were chosen based on a binomial choice pattern with the probability of choosing correctly six times in a row being 0.016, 7/8 being 0.035, 8/8 being 0.0039, and 9/10 being 0.011) and tested until it either learned or was removed. These more stringent criteria were also implemented during the reversal. To avoid trial fatigue (reduced motivation to participate), each individual was given a maximum of 60 trials in each stage, however, as soon as an individual reached criterion, it moved on to the next stage. If a subject did not reach criterion within 60 trials in either stage of experiment 1, it was removed from the experiment ('non-learner').

Pre-training

We pre-trained animals to habituate them to the experimental procedure, to familiarise them with the food dishes and the reward and ensure high food motivation. Pre-training consisted of three trials/day (15 trials total) one week prior to stimulus training, and was divided into three phases. During phase 1 (five trials), a dish with open mesh including a reward was introduced in front of the water bowl for 1.5 h. Two dishes were available and each was used equally often in a random order throughout the pre-training stage. An animal moved on to phase 2 if it ate the reward in at least four out of the five trials. During phase 2 (six trials), one randomly chosen food dish was placed on top of one ramp (either the left or right ramp) in a pseudo-random order. Again, lizards that ate in at least four out of the six trials moved on to phase 3. Phase 3 (four trials) was similar to phase 2; however, the hide was removed during the 1.5 h of the trial. Only animals that ate during all four trials moved on to the stimulus training.

Stimulus training

Before introducing compound stimuli with two dimensions (shapes as well as colours), we trained lizards on a simple one-dimensional task between either different shapes (Group 1, Fig. 1a) or colours (Group 2, Fig. 1a). We conducted a simple associative learning test with one stimulus (e.g., triangle) being positively reinforced (S^+) and the other (e.g., X) being unrewarded (S^-). This stage required subjects to associate one of the shapes or colours with a reward. Our lizards showed very poor performance during training and to ensure that this poor performance was not due to insufficient habituation to the captive environment (and to rule out prolonged negative effects on behaviour due to captivity) but an inability to learn the discrimination, we tested 14 animals that were able to learn during the response inhibition task (experiment 2) on a second batch of 30 trials.

Acquisition and reversal learning

As soon as subjects reached criterion in the stimulus training stage, they were tested using complex cues (introducing a second-stimulus dimension) in an acquisition and reversal stage. The initially trained stimulus dimension remained reinforced (e.g., triangle and X), while the second dimension acted as an irrelevant distractor (e.g., background colour). Group 1 was presented with two colours (light and dark blue) at the background and Group 2 with two different shapes (triangle and X) superimposed on the dark and light blue background colours (see Fig. 1a). To succeed at this stage, animals had to maintain their attention on the already learnt stimulus–reward association (e.g., triangle is rewarded regardless of background colour), while ignoring the new stimulus dimension. After the performance criterion was met, animals moved on to a reversal, changing the formerly unrewarded S^- to S^+ and vice versa (e.g., X becomes rewarded regardless of background colour). To successfully reverse a previously learnt stimulus–reward relationship, lizards needed to inhibit responding to the former S^+ and reassociate the former S^- with reward.

Statistical analyses

All statistical analyses were performed in R version 3.4.2 (R Development Core Team 2008) and all p values are two-tailed. All data sets generated and analysed during the current study are available at Zenodo https://doi.org/10.5281/zenodo.1304460. We used the packages *lme4* (version 1.1–14; Bates et al. 2015), *lmerTest* (version 2.0–36; Kuznetsova et al. 2017), *markovchain* (version 0.6.9.7; Spedicato 2017), *MASS* (version 7.3; Venables and Ripley 2002), *ggplot2* (version 2.2.1; Wickham 2009), and *psy* (version 1.1; Falissard 2012) during analysis.

No statistical comparison of the learning performance between acquisition and reversal was done, because lizards were not able to reach criterion during the reversal stage. Close inspection of our data, however, revealed that the reason why our lizards did not learn was due to an inability to inhibit a strong side bias. Consequently, we investigated if animals started out with this bias or developed a bias over time. We calculated a bias index (BI) using the number of right and left choices:

$$\frac{\text{right choice} - \text{left choice}}{\text{right choice} + \text{left choice}},$$

for each block of ten trials during stimulus training batch 1 and applied a generalised linear mixed-effects model (GLMM) with the BI as the response variable. Block was included as the fixed effect and the random effect contained a random intercept for each animal and a random slope for block. Furthermore, we wanted to know if animals that reached the initial learning criterion of 6/6 or 7/8 correct trials were able to inhibit responding to their preferred side by showing less of a side bias than those that did not learn. For this purpose, we calculated BI for 'learners' and 'non-learners' using all trials from batch 1. Due to the small sample sizes, we used non-parametric bootstrapping to draw 1000 bootstrap samples from our original data set and calculated the mean difference between the groups for each sample. The 95% confidence interval (CI) of these means was then used to quantify significance; if the CI does not cross 0 the difference between the groups is significant. Finally, we wanted to know if being rewarded during trials (stimulus training batch 1 only) would affect our lizards' choice behaviour. We applied a discrete time Markov chain (DTMC) based on which side was chosen by each lizard during each trial and if this choice was rewarded or not. Our data included four discrete states: (1) left-rewarded, (2) left-unrewarded, (3) right-rewarded, and (4) right-unrewarded. We modelled the transition probabilities of a right-side choice following

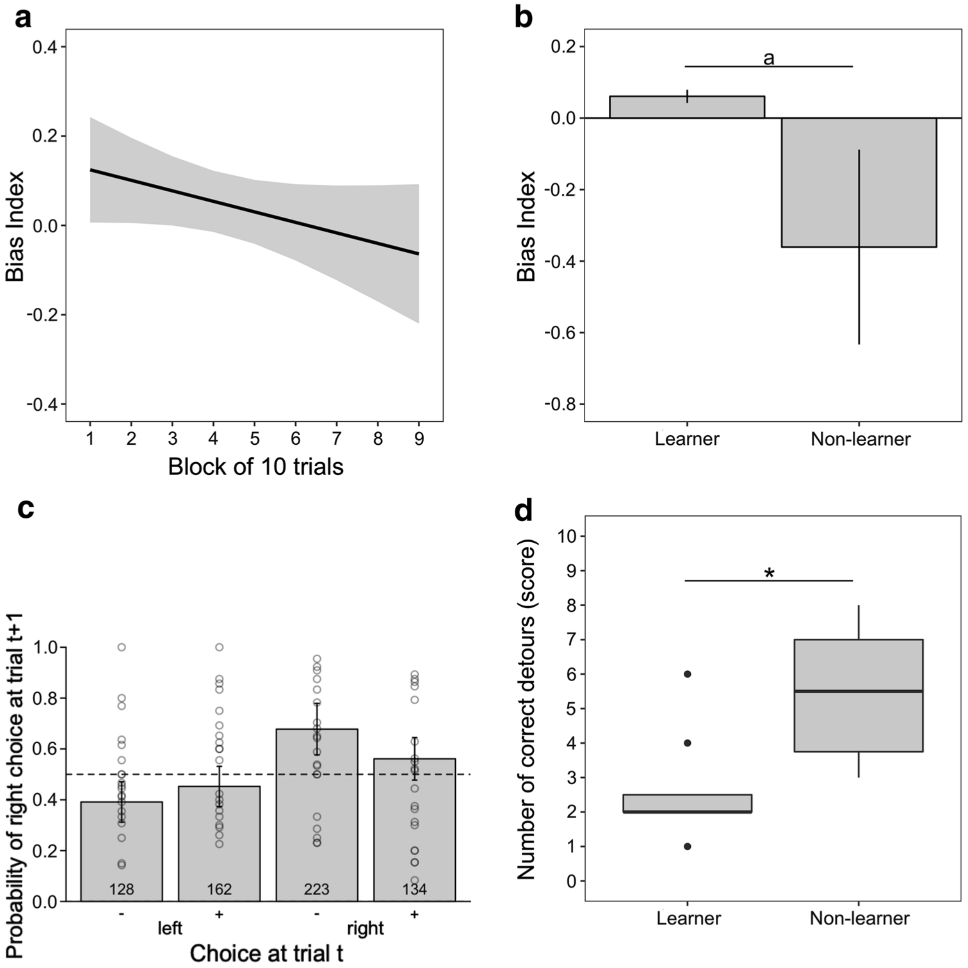


Fig. 2 **a** Change in group Bias Index from block 1 (trials 1–10) to block 9 (trials 81–90) ± 95% confidence interval. The relationship was not significant. A positive index indicates a bias to the right side and a negative index indicates a bias to the left. **b** Mean Bias Index (±95% confidence interval) calculated for 'learners' ($N=10$) and 'non-learners' ($N=10$). The distance from 0 indicates the strength of the bias. a Significant difference. **c** Transition probability (±95% confidence interval) of a response to the right side following one of four discrete states (stimulus training batch 1): a response could either be made to the left or right and, depending on the setup, was either rewarded (+) or non-rewarded (−). Superimposed points represent data from each of the 20 individuals tested in the task. Numbers within bars indicate the number of events which transition probabilities were based on the dashed line indicates 50%. **d** Number of correct detours in the transparent cylinder phase. 'Learner': lizards that were able to inhibit their side bias and reach the initial learning criterion during stimulus training batch 1, and 'Non-learner': animals that did not inhibit their bias and did not reach criterion. $*p<0.05$. **a, b, d** Created with R ggplot2. **c** Created with R baseplot

either one of these four discrete states. The resulting transition matrix was used to create Fig. 2c.

To test for inter-observer reliability, a subset (57% = 1107/1924) of trials was scored by one researcher (SH) unfamiliar with the experiment and blind to the tested questions as well as another researcher (ML) involved in data collection. Inter-observer reliability was calculated based on Cohen's kappa, which estimates the inter-rater agreement between two independent scorers; 100% agreement equals a kappa of 1, 0% agreement a kappa of 0.

Results

Of the 20 tested individuals, only 50% reached the initial learning criterion of 6/6 or 7/8 and were given 12 post-criterion trials, the other ten lizards were removed from the experiment after not reaching this criterion within 60 trials ('non-learners'). All of the ten 'initial learners', however, made more than two errors (mean ± SD = 5.5 ± 2) during the post-criterion phase, and testing was continued until they reached the new, stricter criterion of 8/8 or 9/10 consecutive trials correctly. Consequently, their maximum number of trials was increased to 90 until they were removed from the experiment. Of the ten 'initial learners', only two reached the new learning criterion and were tested in the acquisition; both did not learn within 60 trials and were therefore removed from the experiment (Online Resource, Table 1).

Contrary to our expectations, only two additional animals reached the stricter learning criterion during the second batch of stimulus training (conducted after experiment 2) and moved on to acquisition (increasing the number to a total of four individuals) and thereafter reversal. However, both individuals were not able to reverse the previously learned association and were also removed from the experiment after receiving 60 trials (Online Resource, Table 1). Motivation to participate was high; animals failed to make a choice in only 6 out of 1762 trials (sum of trials from all 20 animals during experiment 1).

Close inspection of the data revealed a side bias: some of our lizards preferred the left side and others the right side. However, only less than 40% persevered to respond to the same side during both experiments 1 and 2 (Online Resource, Table 3). Animals showed a bias from the start of the experiment instead of developing a bias with time (GLMM, block = 0.004, std. error = 0.017, $p = 0.208$; Fig. 2a). The average BI for those animals that did reach the initial learning criterion (6/6 or 7/8) was very close to 0, indicating no bias, whereas the average BI for animals that were classified as 'non-learners' was smaller than − 0.3, indicating a bias to the left (Fig. 2b); the difference was significant (bootstrapping, $\mathrm{CI}_{\mathrm{low}} = -0.671535$, $\mathrm{CI}_{\mathrm{up}} = -0.138180$). Furthermore, our analysis showed that animals that responded to the left were more likely to respond to the left in the subsequent trial and animals that initially chose to go to the right were more likely to do the same in the following trial (Fig. 2c). This pattern persisted irrespective of the choice being rewarded or not; the probability of choosing the same side was marginally higher after not being rewarded compared to being rewarded. Finally, inter-observer reliability was estimated at 0.86 indicating high agreement between independent scorers.

Discussion

Half of our lizards were able to reach our initial learning criterion ('initial learners'), but did not show consistent performance when testing continued to a more stringent criterion. With this new criterion, only 2 out of 20 lizards learned to discriminate between two compound visual stimuli, but, subsequently, did not reverse this discrimination. The low learning rate was due to a strong side bias present from the first week of testing. 'Initial learners' were able to inhibit this bias, whereas 'non-learners' were unable to overcome their pre-existing side preference. Based on the order of stimulus presentation during the two-choice discrimination task, responding to only one side made reaching the learning criterion impossible, explaining the high dropout rate.

The two-choice learning experiment was designed to test stimulus–response inhibition through reversal learning. Previously, *E. quoyii* showed reversal learning in two spatial tasks and a social learning task based on a colour discrimination. Skinks were able to learn the spatial location (side) of a randomly determined 'safe' refuge to escape a simulated predator attack and show flexibility in learning during a spatial reversal (Noble et al. 2012, 2014). In a study using males (Noble et al. 2014), lizards were first trained to remove coloured lids from food wells. Then, using lid colour to find a reward, they were tested on their use of social information to learn an acquisition and reversal task. Side was kept constant for each individual, side-confounding the task, and making it impossible to determine which stimuli (colour/side) animals used to find the reward. If this species makes particularly high use of spatial cues to learn, it may explain the divergence from our results given that we deliberately chose to disassociate colour and spatial cues by presenting stimuli as well as dishes on top of the left ramp or right ramp in a random order to be able to rule out side effects. Surprisingly, our lizards showed a side bias from the first week of testing and persisted in choosing the same side in subsequent trials no matter if they were rewarded or not. This indicates that at least half of our lizards were not able to inhibit their innate side preference. The other half were able to reach our initial learning criterion (6/6 or 7/8 correct trials) showing only a negligible bias but fell back to a one-sided response after testing continued to the more stringent criteria (8/8 or 9/10). Recent findings show, however, that *E. quoyii* males are able to successfully learn to discriminate colour when side is not confounded in a simple discrimination task involving the removal of coloured lids from food wells (Qi et al. 2018). This finding indicates that our method of using cue cards instead of food wells with lids might have been less well suited for this particular species or study population. Furthermore, using a correction method, by removing the food dish not chosen by the animals may have led to stronger learning, however, logistical constraints made implementing this approach challenging given the need to simultaneously monitor all animals. Future work exploring whether correction methods are able to remove side biases may be particularly elucidating.

The high dropout rate of our lizards might be explained by animals not being able to solve the presented task or trial fatigue. Our analysis showed that lizards were not able to learn the discrimination due to an inability to inhibit a bias to one side. This bias might be a fall-back/alternative strategy applied due to an inability to solve the learning rule. This strategy might have, in turn, strengthened a pre-existing bias increasing the effort to inhibit a one-sided response. Studies in lizards investigating brain lateralisation and associated laterality in behaviour have revealed a left-eye preference for exploring unfamiliar environments (e.g., Bonati et al. 2013), escape behaviour (e.g., Bonati et al. 2010), and aggression (e.g., Hews and Worthington 2001), and a right-eye bias for detecting moving prey (e.g., Robins et al. 2005). One advantage of cerebral lateralisation and the specialisation of specific areas to perform one or a few specific tasks is faster processing, less interference during processing and energy conservation (Vallortigara and Rogers 2005). Our findings are in accordance with the results from other studies in lizards (Csermely et al. 2010; Lustig et al. 2013) that indicate a balanced distribution of left/right preferences within a population. Empirical data suggest that an asymmetry in side preference might be an evolutionary stable strategy (EES) with an equal benefit/cost (e.g., predator escape or foraging strategy) to both left- and right-biased individuals (Vallortigara and Rogers 2005). Tree skinks (*Egernia striolata*), tested on a similar paradigm, showed no side bias or trial fatigue despite being tested in 100 trials per stage (Szabo et al. 2018). Although we do not know if water skinks are more prone to trial fatigue, we would not expect to find such differences between species.

Experiment 2: response inhibition

Immediately after animals either learned or were removed from the visual discrimination learning experiment, they were presented with a two-stage detour task testing response inhibition using a cylinder (hereafter referred to as 'cylinder task'). The same cohort of animals as in experiment 1 was used.

Methods

Setup

The general setup was adopted from experiment 1, the ramps, however, were removed, and a 10 cm-long tube (opaque for Phase 1 or mesh for Phase 2) was fixed (with re-usable adhesive putty, Bostik Blu-Tack) to the enclosure floor in front of the water bowl (Fig. 1c). Trials were conducted between November 2017 and January 2018.

Pre-training

Pre-training was used to ensure high food motivation and to train lizards to associate tweezers with getting a food reward, without showing a stress response (running away or trying to climb up the walls of their enclosure). This method was implemented, because, in previous studies on this task, the reward was presented in the experimenters' hand. Lizards commonly associate human hands with capture. Lizards were, therefore, trained to positively associate tweezers with reward and reduce stress during reward presentation. One of the already familiar food dishes was placed in front of the water bowl, the hide was removed, and a small piece of cat food was slowly placed into the food dish, using tweezers. The animal was allowed 1.5 h to retrieve the food. After this time period, the hide was replaced and the animal was left undisturbed for another 40 min (ITI). This procedure was repeated three times a day until ten trials were concluded. Criterion for completion of the pre-training was retrieving the reward in all ten trials without showing a stress response during food presentation.

Phase 1: response inhibition (opaque cylinder task)

During phase 1, animals were presented with an opaque cylinder (Online Resource, Fig. 5); a 10 cm-long opaque PVC tube covered in fine polyester window screen to make it more similar to the transparent cylinder (Phase 2). A trial lasted for 1.5 h during which time the lizard was allowed to retrieve the reward from either opening of the cylinder. A trial was scored correct if the lizard retrieved the reward without touching the exterior surface of the cylinder with its head. We repeated this procedure for three trials a day, 5 days a week, until lizards performed correctly on 4/5 consecutive trials (criterion based on MacLean et al. 2014) or a maximum of 30 trials. Animals that reached the learning criterion moved on to phase 2, whereas animals that did not reach criterion within 30 trials were removed from the experiment.

Phase 2: response inhibition (transparent cylinder task)

During phase 2, lizards were presented with a transparent cylinder (Online Resource, Fig. 5); a 10 cm-long tube made of fine Aluminium insect screen. The material was chosen to facilitate even odour diffusion and prevent animals from using the smell of the reward to make a detour. Furthermore, animals were already familiar with the mesh properties form experiment 1; we, therefore, were able to eliminate the possibility of poor performance due to inexperience with the novel object properties. Lizards were able to see the reward through the mesh holes (but could not reach it). For a trial to be scored as correct, lizards had to inhibit responding in a direct trajectory to the reward but instead detour to the side openings to retrieve the food from inside the cylinder without touching the surface of the cylinder with their head. We repeated this procedure for ten trials and calculated the mean proportion of correct detours out of ten trials for the whole group.

Coding

We scored lizard behaviour from video recordings of trials. We scored if a lizard made a correct (1) or incorrect (0) detour (Bernoulli variable) as well as trial and choice latency (for details, see experimental procedure above).

During response inhibition phase 1, animals were presented with the cylinder for the first time and might have shown some neophobia/neophilia towards the unfamiliar object, which, in turn, could have had an effect on their learning speed and performance. We, therefore, scored the time that a lizard spent within 2 cm of the cylinder (association time) as well as the number of times that the lizard moved within 2 cm of the cylinder during the first trial of phase 1 (association frequency). Due to the long trial length (1.5 h), we did not score any of the later trials because of the possibility that habituation could have occurred within the first trial.

Statistical analyses

We used the association time (time a lizard spent with 2 cm of the novel cylinder) to investigate if neophobia/neophilia affected performance during the cylinder task. We applied a linear mixed-effects model (LME) with log-transformed association time as the response variable and trials to criterion (in cylinder task phase 1), score (in cylinder task phase 2), and sex as fixed effects. We also included the association frequency as a random effect to account for any differences due to baseline activity level (animals might differ in their activity level which could bias results towards animals with very high or very low activity). To test if animals that learned faster during phase 1 were better at detouring during phase 2, we applied a generalised linear model (GLM, based on a negative binomial distribution) with trials to criterion (phase 1) as the response variable and score (phase 2) as a fixed effect. Again, we were interested if sex was a predictor for performance during phase 1 and 2 and included sex and an interaction between sex and score as fixed effects. To find out if 'initial learners' (animals that reached the learning criterion of 6/6 or 7/8 in experiment 1) were performing better/worse in the transparent cylinder task compared to "non-learners", we included the interaction between learnt (yes or no) with score (phase 2) in the model. Finally, to ensure that performance on the transparent cylinder task was not affected by the number of trials performed during stimulus training of experiment 1 (and the number of times lizards were exposed to the mesh blocking the reward), we calculated the sum of trials performed in the learning experiment before exposure to the cylinder for each lizard and compared these to the score achieved during the cylinder task phase 2. We applied a Spearman rank-order correlation to investigate if the number of trials performed was positively correlated with the achieved score.

Results

Sixteen of twenty (80%) animals reached the predetermined learning criterion of 4/5 correct detours during the opaque cylinder phase (phase 1; $\text{mean}_{\text{trials to criterion}} = 13.4$, $\text{SD}_{\text{trials to criterion}} = 6.9$, $\text{range}_{\text{trials to criterion}} = 5\text{–}29$) and subsequently performed ten trials of phase 2 (transparent cylinder). Motivation to participate was high; all animals retrieved the reward during pre-training and only one animal did not retrieve the reward in one trial in phase 2. Some animals were able to detour the transparent cylinder already during the first trial (Fig. 3), whereas the other animals gradually accumulated correct detours around the cylinder to reach the reward ($\text{mean}_{\text{score}} = 0.44$, $\text{CI}_{\text{up}} = 0.51$, $\text{CI}_{\text{low}} = 0.29$, $\text{range}_{\text{score}} = 0.1\text{–}0.8$).

Neither learning time (trials to criterion) during phase 1 (LME, estimate = − 0.0019, SE = 0.0246, *df* = 10.68, *t* value = − 0.078, *p* = 0.939) nor score on phase 2 (LME, estimate = 0.0188, SE = 0.0769, *df* = 11.23, *t* value = 0.244, *p* = 0.811) was correlated with the time animals spent near the cylinder during the first trial of phase 1, indicating that the novelty of the cylinder had no lasting effect on animals' performance. Furthermore, males and females did not differ in the time spent close to the cylinder (LME, estimate = − 0.1505, SE = 0.3309, *df* = 11.05, *t* value = − 0.455, and *p* = 0.658).

Learning speed did not predict the correct tally accumulated in phase 2 (score). We found no correlation between the time (trials to criterion) which it took lizards to learn to detour in phase 1 and the score of correct choices during phase 2 (GLM, estimate = − 0.004, SE = 0.059, *z* value = − 0.072, *p* = 0.943). Males and females did not differ in the time which it took them to learn to detour (GLM, estimate = − 0.002, SE = 0.467, *z* value = − 0.004, *p* = 0.997) or the number of correct detours around the transparent cylinder (GLM, estimate = − 0.056, SE = 0.104, *z* value = − 0.533, *p* = 0.594). We found a significant interaction between reaching the initial learning criterion during discrimination training and the number of correct detours around a transparent cylinder. The 'initial learners' made less correct detours compared to animals that did not reach the learning criterion during stimulus training batch 1 (GLM, estimate = − 0.183, SE = 0.081, *z* value = − 2.247, *p* = 0.025; Fig. 2d). The number of trials performed in experiment 1 did not significantly improve the score achieved during the transparent cylinder phase (Spearman's rank-order correlation, *t* = − 0.211, *df* = 14, $r_s = -0.056$, *p* = 0.836).

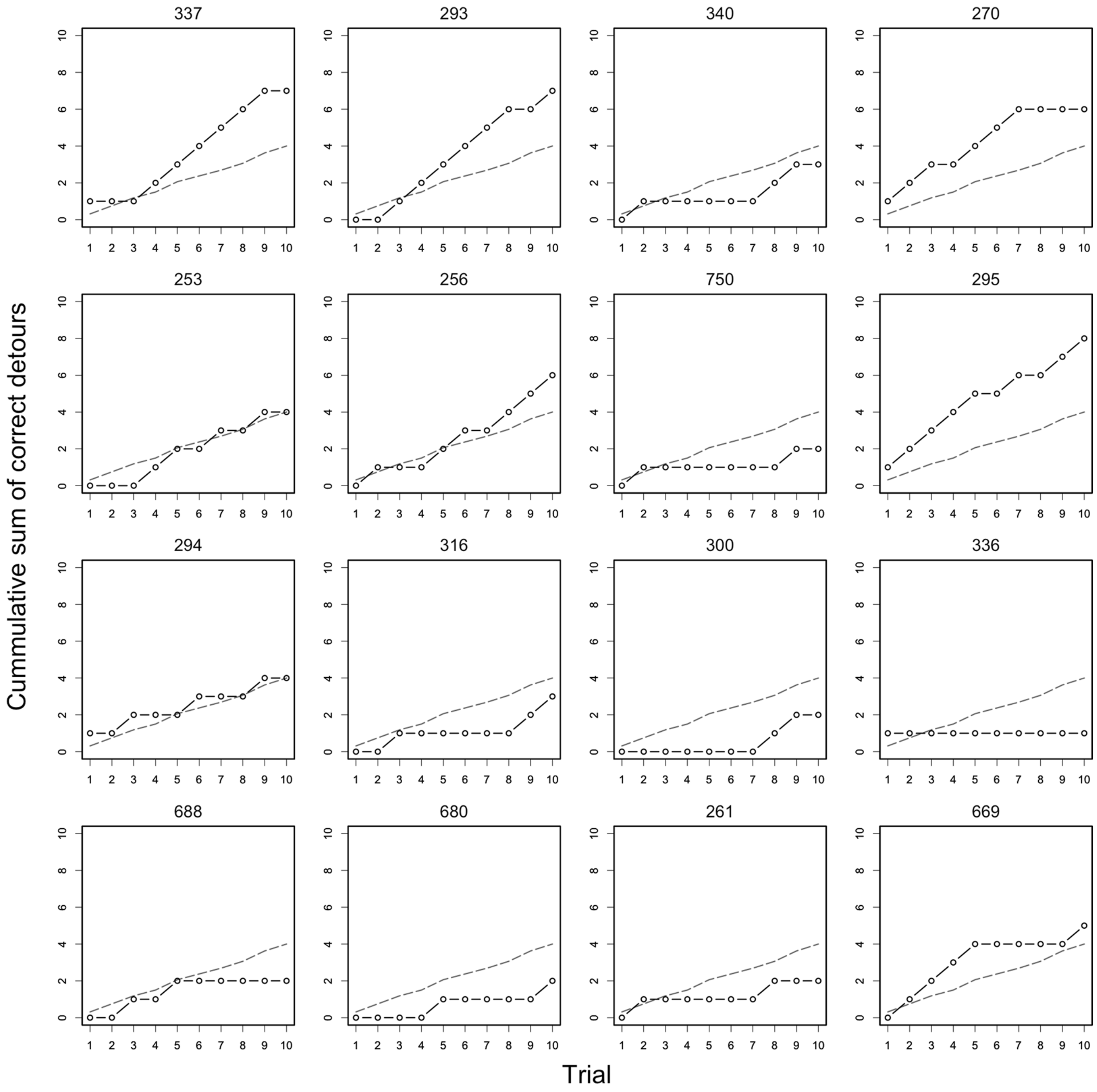


Fig. 3 Cumulative sum of correct detours during phase 2 (transparent cylinder) of the response inhibition task. Each graph shows the performance for 1 of the 16 individuals (identification number is given on top of each graph) that learned to detour during phase 1 (opaque cylinder task). The cumulative group mean is given as a dashed grey line in each graph. Created with R baseplot

Discussion

Lizards were able to detour around a transparent barrier to obtain a food reward. Importantly, a comparison between the experiments revealed that the 'initial learners', who successfully inhibited their side bias, were significantly less successful in inhibiting prepotent responses towards a visible reward within the mesh cylinder compared to 'non-learners', who failed to surpass their bias.

Some of our lizards were able to solve the detour around a mesh cylinder already on the first trial. This performance might demonstrate these individuals' ability to transfer insights about how to perform the detour from either being trained with mesh during the learning experiment or training to detour the opaque cylinder beforehand (Koehler 1925 cited by; Kabadayi et al. 2017a). Cotton top tamarins (Santos et al. 1999) tested on a transparent box only were unable to inhibit direct responses. If trained on an opaque box first, monkeys had no problems performing the detour during transparent box trials. The authors argue that the initial failure of the transparent-only group to make a detour was not due the inability to resist the strong pull of the visible reward but due to a failure to find an alternative motor response. After receiving an additional training on an opaque box, the same animals were able to perform at high levels even if more desirable rewards were used. Our analysis showed, however, that the amount of experience with mesh did not affect detour performance. Finally, learning might have improved performance over trials due to the repeated nature of the task.

Performance in cylinder tasks can be affected by different non-cognitive factors such as the type of stimulus cue, the distance to the cylinder, neophobia exhibited towards the unfamiliar object, experience with the transparent material and general food motivation (Kabadayi et al. 2017a). Water skinks rely on odour as well as vision to capture prey (Veron 1969; Daniels 1987). We used a mesh cylinder to allow even odour distribution and prevent lizards from following an odour trail around a closed, transparent cylinder. Some of our lizards might have followed the smell, instead of using visual cues, to locate the reward. No matter if they followed visual or olfactory cues; however, solving the task required inhibiting direct responses and instead detouring to one of the side openings to access the reward. The distance to the cylinder was constrained by the length of the enclosure and the setup; however, animals started as far away from the cylinder as possible, which amounted to at least 1.5 times their snout–vent length (minimum 20 cm). Furthermore, our results show that if neophobia affected lizards in some way, it did not show in their performance during the task. We were not able to find a correlation between the time spent close to the novel cylinder (first encounter only) and their learning performance or score in the subsequent test. Importantly, all our animals had the previous experience with the transparent mesh material after being tested in experiment 1. Studies show that domesticated animals or animals frequently tested with transparent objects outperform inexperienced species (Kabadayi et al. 2016, 2017a; van Horik et al. 2018). Mesh was used to cover up the incorrect food dish and block access to the reward during the two-choice task which gave lizards ample opportunity to learn its properties. We also covered the opaque cylinder with mesh to add additional experience and make both phases as similar as possible. Furthermore, our results show that more experience with the mesh during experiment 1 did not improve or decrease the score received in the cylinder task. Finally, motivation was high during the task; animals consistently retrieved the reward during the trials. Overall, the above-mentioned factors were kept constant across all individuals and our data should, therefore, represent true individual differences as opposed to confounding factors that affect learning and inhibition.

In the cylinder inhibitory control task, brain size and dietary breadth are some of the best predictors of performance (Bray et al. 2014; MacLean et al. 2014; van Horik et al. 2018). Unfortunately, no data currently exist for brain size in *E. quoyii*, and to properly understand how diet affects performance in the cylinder task we need additional data on reptiles with a variety of dietary preferences. We know, however, that water skinks are opportunistic, insectivorous, visual foragers (Veron 1969; Daniels 1987; McElroy et al. 2008), and inhibiting prepotent responses during prey capture could be an advantageous trait for this species.

Conclusions

Although we are not able to compare reversal learning performance with the performance of detouring around a transparent barrier, our results, nonetheless, show that half of our lizards were not able to inhibit a one-sided response during discrimination learning. The ten lizards that were able to inhibit their pre-existing bias and reached our initial learning criterion made fewer correct detours and more direct responses towards a visible reward within a transparent cylinder. If response inhibition is truly context-general, we would expect these ‘initial learners’ to perform well and be skilled at inhibiting both a side bias and prepotent responses towards a visible reward. All our lizards had the same basic experience and these differences in performance cannot be explained by non-cognitive factors. We can, therefore, conclude that response inhibition is context-specific, at least in our tested group of lizards. Furthermore, our study is the first to test a non-avian reptile in the cylinder task and our lizards performed at comparable levels to brown lemurs, and even outperformed marmosets, song sparrows, swamp sparrows (MacLean et al. 2014), African grey parrots, and blue-headed macaws (Kabadayi et al. 2017b). The gathered data add a new taxon to the already existing body of knowledge on how evolution has shaped inhibitory control processes.

Ethical note All experimental manipulations were non-invasive behavioural observations approved by the Macquarie University Animal Ethics Committee (ARA # 2013/031) and the collection of the animals was approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (License # SL101972). Skinks were individually captured at Macquarie University campus, New South Wales, by noosing and transported in cloth bags to their indoor enclosures.

Acknowledgements We would like to thank Maiana Lenoir (ML) for her help catching skinks and helping collect data; Sebastian Hoefer (SH) for his time coding videos and Catarina Vila Pouca for her help with the analysis of the side bias. This project was funded by Macquarie University.

Funding The study was funded by Macquarie University.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practise at which the studies were conducted.

References

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Bonati B, Csermely D, Lopez P, Martin J (2010) Lateralization in the escape behaviour of the common wall lizard (*Podarcis muralis*). Behav Brain Res 207:1–6. https://doi.org/10.1016/j.bbr.2009.09.002

Bonati B, Csermely D, Sovrano VA (2013) Advantages in exploring a new environment with the left eye in lizards. Behav Process 97:80–83. https://doi.org/10.1016/j.beproc.2013.04.002

Bray EE, MacLean EL, Hare BA (2014) Context specificity of inhibitory control in dogs. Anim Cognit 17:15–31. https://doi.org/10.1007/s10071-013-0633-z)

Burghardt GM (1978) Learning Processes in Reptiles. In: Gans C, Tinkle DW (eds) Biology of the reptilia. Ecology and behaviour A (Vol. 7). Academic Press, London, pp 555–681

Carazo P, Noble DW, Chandrasoma D, Whiting MJ (2014) Sex and boldness explain individual differences in spatial learning in a lizard. Proc R Soc B Biol Sci 281:20133275. https://doi.org/10.1098/rspb.2013.3275

Clark BF, Amiel JJ, Shine R, Noble DWA, Whiting MJ (2014) Colour discrimination and associative learning in hatchling lizards incubated at 'hot' and 'cold' temperatures. Behav Ecol Sociobiol 68:239–247. https://doi.org/10.1007/s00265-013-1639-x

Cogger HG (2014) Reptiles and amphibians of Australia, 7th edn. ed.). CSIRO PUBLISHING, Victoria

Csermely D, Bonati B, Romani R (2010) Lateralisation in a detour test in the common wall lizard (*Podarcis muralis*). Laterality 15:535–547. https://doi.org/10.1080/13576500903051619

Daniels CB (1987) Aspects of the aquatic feeding ecology of the riparian skink *Sphenomorphus quoyii*. Aust J Zool 35:253–258

Diamond A (1981) Retrieval of an object from an open box: The development of visual-tactile control of reaching in the first year of life. Soc Res Child Dev Abstr 3:78

Diamond A (1990) Developmental time course in human infants and infant monkeys, and the neural basis of the inhibitory control of reaching. In: Diamond A (ed) The development and neural bases of higher cognitive functions, Academy of Sciences, New York, pp. 637–676

Diamond A (2013) Executive functions. Annu Rev Psychol 64:135–168. https://doi.org/10.1146/annurev-psych-113011-143750

Dias R, Robbins TW, Roberts AC (1996) Primate analogue of the Wisconsin card sorting test-effects of excitotoxic lesions of the prefrontal cortex in the marmoset. Behav Neurosci 110:872–886

Falissard B (2012) psy: various procedures used in psychometry. R package version 1.1. https://CRAN.R-project.org/package=psy

Fleishman LJ, Loew ER, Whiting MJ (2011) High sensitivity to short wavelengths in a lizard and implications for understanding the evolution of visual systems in lizards. Proc R Soc B Biol Sci 278:2891–2899. https://doi.org/10.1098/rspb.2011.0118

Gaalema DE (2011) Visual discrimination and reversal learning in rough-necked monitor lizards (*Varanus rudicollis*). J Comp Psychol 125:246–249. https://doi.org/10.1037/a0023148

Hews DK, Worthington RA (2001) Fighting from the right side of the brain: left visual field preference during aggression in free-ranging male tree lizards (*Urosaurus ornatus*). Brain Behav Evol 58:356–361

Kabadayi C, Taylor LA, von Bayern AM, Osvath M (2016) Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. R Soc Open Sci 3:160104. https://doi.org/10.1098/rsos.160104

Kabadayi C, Bobrowicz K, Osvath M (2017a) The detour paradigm in animal cognition. Anim Cognit 21:21–35. https://doi.org/10.1007/s10071-017-1152-0

Kabadayi C, Krasheninnikova A, O'Neill L, van de Weijer J, Osvath M, von Bayern AMP (2017b) Are parrots poor at motor self-regulation or is the cylinder task poor at measuring it? Anim Cognit 20:1137–1146. https://doi.org/10.1007/s10071-017-1131-5

Koehler W (1925) The mentality of the ape. Kegan Paul Trench Trubner and Co. LTD, London

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. J Stat Softw 82(13):1–26. https://doi.org/10.18637/jss.v082.i13

Langkilde T, Shine R (2006) How much stress do researchers inflict on their study animals? A case study using a scincid lizard. Eulamprus heatwolei. J Exp Biol 209(Pt 6):1035–1043. https://doi.org/10.1242/jeb.02112

Leal M, Powell BJ (2012) Behavioural flexibility and problem-solving in a tropical lizard. Biol Lett 8:28–30. https://doi.org/10.1098/rsbl.2011.0480

Lucon-Xiccato T, Gatto E, Bisazza A (2017) Fish perform like mammals and birds in inhibitory motor control tasks. Sci Rep 7:13144. https://doi.org/10.1038/s41598-017-13447-4

Lustig A, Ketter-Katz H, Katzir G (2013) Lateralization of visually guided detour behaviour in the common chameleon, *Chamaeleo chameleon*, a reptile with highly independent eye movements. Behav Process 100:110–115. https://doi.org/10.1016/j.beproc.2013.08.002

MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, Aureli F, Baker JM, Bania AE, Barnard AM, Boogert NJ, Brannon EM, Bray EE, Bray J, Brent LJ, Burkart JM, Call J, Cantlon JF, Cheke LG, Clayton NS, Delgado MM, DiVincenti LJ, Fujita K, Herrmann E, Hiramatsu C, Jacobs LF, Jordan KE, Laude JR, Leimgruber KL, Messer EJ, Moura AC, Ostojic L, Picard A, Platt ML, Plotnik JM, Range F, Reader SM, Reddy RB, Sandel AA, Santos LR, Schumann K, Seed AM, Sewall KB, Shaw RC, Slocombe KE, Su Y, Takimoto A, Tan J, Tao R, van Schaik CP, Viranyi Z, Visalberghi E, Wade JC, Watanabe A, Widness J, Young JK, Zentall TR, Zhao Y (2014) The evolution of self-control. Proc Natl Acad Sci USA 111:E2140–E2148. https://doi.org/10.1073/pnas.1323533111

McElroy EJ, Hickey KL, Reilly SM (2008) The correlated evolution of biomechanics, gait and foraging mode in lizards. J Exp Biol 211:1029–1040. https://doi.org/10.1242/jeb.015503

Noble DW, Carazo P, Whiting MJ (2012) Learning outdoors: male lizards show flexible spatial learning under semi-natural conditions. Biol Lett 8:946–948. https://doi.org/10.1098/rsbl.2012.0813

Noble DWA, Byrne RW, Whiting MJ (2014) Age-dependent social learning in a lizard. Biol Lett 10:20140430. https://doi.org/10.1098/rsbl.2014.0430

Qi Y, Noble DWA, Fu J, Whiting MJ (2018) Testing domain general learning in an Australian lizard. Anim Cognit. https://doi.org/10.1007/s10071-018-1194-y

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org. Accessed Sept 2017

Robins A, Chen P, Beazley LD, Dunlop SA (2005) Lateralised predatory responses in the ornate dragon lizard (*Ctenophorus ornatus*). NeuroReport 16:849–852

Santos LR, Ericson BN, Hauser MD (1999) Constraints on problem solving and inhibition: object retrieval in cotton-top tamarins (*Saguinus oedipus oedipus*). J Comp Psychol 113:186–193

Spedicato GA (2017) Discrete time Markov chains with R. R J 9:84–104

Sutherland NS, Mackintosh NJ (1971) Mechanisms of animal discrimination learning. Academic Press, New York

Szabo B, Noble DWA, Byrne RW, Tait DS, Whiting MJ (2018) Subproblem learning and reversal of a multidimensional visual cue in a lizard: evidence for behavioural flexibility? Anim Behav 144:17–26. https://doi.org/10.1016/j.anbehav.2018.07.018

Tsukayama E, Duckworth AL, Kim B (2011) Resisting everything except temptation: evidence and an explanation for domain specific impulsivity. Eur J Personal 26:318–334

Vallortigara G, Rogers LJ (2005) Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. Behav Brain Sci 28:575–633

van Horik JO, Langley EJG, Whiteside MA, Laker PR, Beardsworth CE, Madden JR (2018) Do detour tasks provide accurate assays of inhibitory control? Proc R Soc B Biol Sci 285:20180150. https://doi.org/10.1098/rspb.2018.0150

Venables WN, Ripley BD (2002) Modern applied statistics with S. 4th edition. Springer, New York

Veron JEN (1969) Ab analysis of stomach content of the water skink, *Sphenomorphus quoyii*. J Herpetol 3:187–189

Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer, New York

Wilkinson A, Huber L (2012) Cold-blooded cognition: reptilian cognitive abilities. In: Vonk J, Shackelford TK (eds) The oxford handbook of comparative evolutionary psychology. Oxford, New York, pp 129–141