

Learning to learn: advanced behavioural flexibility in a poison frog



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Behavioural flexibility is essential for survival in a world with changing contingencies and its evolution is linked to complex physical and social environments. Serial reversal learning, in which reward contingencies change frequently, is a key indicator of behavioural flexibility. While many vertebrates are capable of serial reversal learning, only birds and mammals have previously been shown to use rule-based decision strategies (e.g. win-stay/lose-shift) to become better at learning changes in reward contingencies across reversals. While the lifestyles of many amphibians have a degree of complexity, the evidence to date suggests limited levels of behavioural flexibility. Here, we show that the poison frog *Dendrobates auratus*, which has evolved complex parental behaviours that likely depend on remembering locations in a flexible manner, can use a win-stay/lose-shift strategy to increase their behavioural flexibility across sequential changes in the reward contingencies in a visual discrimination task. Furthermore, probe trials demonstrate that the frogs used the provided visual cues to spatially orient in the maze in a manner reminiscent of complex spatial cognition. Our study provides the first evidence of serial reversal learning in frogs and is the first to demonstrate the use of a rule-based learning strategy in a nonavian, nonmammalian species.

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Behavioural flexibility is the ability to change one's behaviour according to variation in the environment, and it can enable animals to increase survivorship and reproductive success (Fagen, 1982; Snell-Rood, 2013). For example, species with greater levels of behavioural flexibility are more likely to successfully invade a new environment (Tebich, Sterelny, & Teschke, 2010; Wright, Eberhard, Hobson, Avery, & Russello, 2010). Serial reversal learning, in which animals progressively improve their performance in a task with frequently changing reward contingencies, is a standard laboratory method for measuring behavioural flexibility (Bitterman, 1965; Roth & Dicke, 2005), and the ability to perform serial reversals is more often found in animals that live in complex physical and social environments (Bond, Kamil, & Balda, 2007; Godfrey-Smith, 2002; de Waal & Tyack, 2003).

There are several mechanisms that allow animals to learn serial reversal tasks (Gonzalez, Behrend, & Bitterman, 1967; Mackintosh, 1974; Parker et al., 2012; Shettleworth, 2009; Strang & Sherry, 2014). Among them, lower-order processes, such as proactive interference (Bitterman, 1965; Mackintosh, 1974), involve

involuntary learning and hence are thought to represent a lower level of behavioural flexibility (Parker et al., 2012; Shettleworth, 2009). These mechanisms have been discovered across a broad range of vertebrate taxa (Gaalema, 2011; Gonzalez et al., 1967; Mackintosh, McGonigle, & Holgate, 1968). In contrast, rule-based strategies, which indicate the ability of an animal to learn and use the underlying rule of the reversal task, represent a greater degree of behavioural flexibility (Parker et al., 2012; Shettleworth, 2009). For example, using a win-stay/lose-shift rule requires animals to make their current choice based on the reward from their previous choice (Mackintosh et al., 1968; Shettleworth, 2009). The optimal outcome of this strategy is the one-trial reversal in which animals make an error on the first trial of a reversal followed by all correct choices on subsequent trials of that reversal (Mackintosh et al., 1968). This type of rule-based strategy has only previously been found in mammals and birds (Mackintosh et al., 1968; Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013; Rumbaugh, Savage-Rumbaugh, & Washburn, 1996; Shettleworth, 2009).

Amphibians, which include both aquatic and terrestrial stages in their life cycle, have to handle environments with a high degree of complexity. Yet, they were once thought to lack behavioural flexibility (Bitterman, 1965; Bitterman, 1975), and have been considered inflexible in learning tasks in artificial laboratory environments

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(Maier & Schneirla, 1935). More recent studies, however, show that amphibians can solve mazes using local visual cues (i.e. visual cues that are directly associated with a goal or are part of the goal), body-centred motor strategies (remembering a place by learning to turn left or right) and geometric cues (i.e. the shape of the space) (Crane & Mathis, 2011; Daneri, Casanave, & Muzio, 2011; Ellins, Cramer, & Martin, 1982; Heuring & Mathis, 2014; Sotelo, Bingman, & Muzio, 2015). Furthermore, in simple discriminations, amphibians are capable of single reversals (Daneri et al., 2011; Ellins et al., 1982; Schmajuk, Segura, & Reboresda, 1980). Nevertheless, we still know relatively little about the cognitive strategies used by amphibians in reversal tasks and whether they are capable of the types of behavioural flexibility observed in mammals and birds.

While many frogs have relatively simple social behaviours, the poison frogs (Dendrobatidae) have evolved complex social and spatial behaviours reminiscent of many mammals and birds (Summers, 1989; Summers & Tumulty, 2013): they are territorial, show mate guarding and pair bonding (some are even monogamous; Brown, Morales, & Summers, 2010), and the parents of some species transport tadpoles to deposition sites (small pockets of water) in the forest canopy after hatching. Some species show homing abilities in the field that suggest advanced spatial cognition (Pasukonis, Warrington, Ringler, & Hödl, 2014). However, whether poison frogs can use spatial cues in a flexible manner and whether they use cognitive strategies similar to birds and mammals is unknown.

We trained the poison frog *Dendrobates auratus* in a two-arm maze in which the position of the correct arm was associated with visual cues in the starting chamber. The visual cues could be reliably associated with the goal based on spatial relationships, but they could not be used for direct guidance (e.g. an animal could not simply approach the visual cues to locate the goal). Our study was designed to (1) determine whether poison frogs could use visual cues to learn a complex spatial discrimination task, (2) investigate whether poison frogs are capable of serial reversal learning and (3) identify the behavioural mechanisms underlying improvement during serial reversal.

METHODS

Animals

We used 10 sexually mature *D. auratus* (four males, six females) that were bred in captivity and were likely several generations removed from the wild (Indoor Ecosystems, LLC, Whitehouse, OH, U.S.A.). In this species, males maintain territories and provide parental care (egg attendance, tadpole transport); females maintain territories and perform mate guarding but do not provide parental care (Summers, 1989). We maintained the animals under conditions that approximated their natural habitat: 25 °C, 80% relative humidity (RH), 12:12 h light:dark cycle (lights on at 0700 hours). We housed the frogs individually in terraria and fed them fortified fruit flies three times per week. The University of North Carolina's Institution for Animal Use and Care Committee approved all procedures (protocol 14-026).

Apparatus

The maze consisted of a central starting chamber and two arms (Fig. 1). The maze arms were uniformly white, but the starting chamber had visual cues on each side (Fig. 1). The frogs were required to use the visual cues in the starting chamber to spatially orient to the goal. We blocked the exits at the end of the arms with identical white doors, only one of which could be opened during a given trial. We attached a rope to the reverse side of the correct

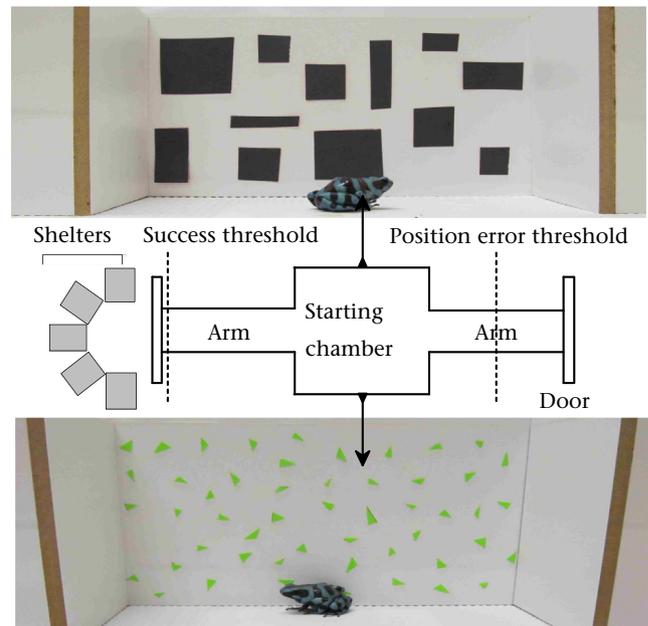


Figure 1. Schematic drawing of the two-arm maze (54 cm (L) × 18 cm (W) × 9.5 cm (H)) and photos of the visual cues on the interior walls of the starting chamber.

door and we blocked the other door from behind with a brick that was not visible to the frog in the maze. We used white absorbent paper, which was replaced every day, as the floor of the maze. Thus, any potential olfactory cues on the floor would be disrupted each day and would not be reliably associated with the goal. We covered the maze with Plexiglas and surrounded the maze with a 1.4 m high white curtain in order to isolate extraneous visual cues in the room. We recorded trials using a camera above the arena (1.5 m high). Experimenters, who were blind to the progress of each individual, sat outside the white curtain to record each training trial and open the door on the correct side. We provided five shelters outside the maze in which the frogs could find refuge after exiting the maze (Fig. 1). To motivate the frogs to locate the exit in order to find shelter, we created a bright, hot (37 °C) and dry (10% RH) environment inside the maze. The frogs are accustomed to a moist environment with ample shelter, similar to the forest floor, and, as such, they find the bright, open environment of the maze to be aversive. Therefore, the reward for finding the correct door was to gain access to a shelter and then the home cage.

Procedure

Acclimation

Before training, we acclimated the frogs to the maze in two trials approximately 24 h apart. During acclimation, both doors were open and no shelters were provided. We used a small, overturned pot with a cardboard floor to transfer and release the frogs in the middle of the starting chamber, resulting in an unpredictable orientation of the frog at the start of each trial. All frogs appeared highly motivated to leave the maze and successfully exited within 2 min.

Acquisition

For the initial learning trials (acquisition), we arbitrarily determined which door was correct. We trained the frogs with three trials per day with an intertrial interval greater than 1 h (from 60 min to 80 min). We wiped the apparatus with alcohol after all individuals had finished one trial. As frogs could be in any position

within the release chamber when trials began, the orientation of the frog at the start of each trial was unpredictable.

We defined three possible behavioural outcomes for each trial (successful trials without error, successful trials with error, or unsuccessful trials). Successful trials without error were those in which the frog approached within 0.5 cm of the correct door within 2 min of release without first moving halfway down the incorrect arm (i.e. committing a position error). Successful trials with error were those in which the frog first advanced at least halfway towards the incorrect door (a position error) before approaching within 0.5 cm of the correct door within 2 min of release. Unsuccessful trials were those in which the frogs failed to complete the task after 2 min. In unsuccessful trials, we opened the correct door and allowed the frogs one additional minute to exit, after which we guided them to the exit by orienting them to face the exit and touching them to make an initial hop in the correct direction. After exiting, the frogs entered one of five small shelters that we used to return them to their home cage.

We operationally defined a learning criterion in order to determine when an individual frog's performance demonstrated sufficient evidence of learning. Because the threshold for success (within 0.5 cm of the correct door) and the threshold for a position error (halfway towards the incorrect door) were not equidistant, their probabilities were not equally likely. Therefore, as is standard in similar studies (Landau & Spelke, 1988; Le Bourg & Buecher, 2002), we used the outcomes on the first day of training (i.e. in naïve animals) to estimate the random probability of success. This approach provides a more accurate measure of learning than using chance probability of turn choice or an arbitrary benchmark. In our case, we required that the animals perform a successful trial without error, and, in naïve animals, the probability of such an outcome was 17%. We then defined our learning criterion as seven successful trials without error in nine sequential trials ($7/9 = 77.8\%$). Based on a binomial test, this performance criterion differs significantly from that of naïve frogs ($P = 1.1 \times 10^{-4}$). Thus, we could be confident that animals that reached the criterion had learned the task.

Reversal

Each time a frog reached criterion, we reversed the reward contingencies by switching the location of the correct door for five sequential reversals. We recorded the number of trials required for each frog to reach the criterion and used repeated measures ANOVA to determine whether the number of trials to criterion decreased across reversals. The experimenters performing the trials were blind to the identity of the animal and the experimental expectation. Furthermore, they did not know which stage of the experiment each individual was in (acquisition, reversal 1, etc.) for a particular trial. After the trials were run, one of us (Liu) collected additional data from the videos. During data collection, Liu was blind to the identity of the frog, the training session (acquisition, reversal 1, etc.) and which side was correct (that is, until the end of the trial when the door opened).

Probe trial

Although we only intended to provide the visual cues in the starting chamber, frogs could potentially use any available cue, including visual cues invisible to humans, olfactory cues and so on, which are unpredictable and hard to control. Therefore, to determine whether the frogs used the visual cues in the starting chamber when solving the maze, we ran two probe trials for each individual once that frog achieved the learning criterion in acquisition and on the fifth reversal. In the probe trials, we blocked both doors and switched the two walls of the starting chamber to opposite sides. Thus, the contingency between the visual cues and

the correct turning response was reversed from that during training. Because we left all other potential cues intact, the probe trials determine whether the frogs' behaviour was guided by the provided cues, and not by other, uncontrolled cues. During the 3 min probe, we quantified the time spent in each arm. We refer to the arm as spatial-correct if it was the correct side indicated by the visual cues, and as original-correct if it was the correct arm during acquisition. We used paired samples *t* test to compare the duration in each arm in the probe trials. After the first probe trial, we retrained individuals to criterion before proceeding with the first reversal.

Error Analysis

To examine the behavioural mechanisms underlying the improvement in reversal learning, we analysed the types of errors committed during each reversal. We defined position errors as cases in which a frog advanced half the length of the incorrect arm. We defined noncontingent errors as cases in which the frogs failed to approach either door. This error may reflect familiarity with the task (that is, an understanding that the task is to approach a door in order to exit) or a lack of motivation to complete the task. We defined perseverative errors as the number of position errors before the first success after a particular reversal. Perseverative errors reflect poor extinction (i.e. the inhibition of previously learned responses; Mackintosh et al., 1968; Strang & Sherry, 2014). Extinction is a critical step in learning a reversal task because an animal must inhibit previously learned responses in order to learn new associations, and rapid extinction suggests that the animal has learned the overall rule of the task (i.e. that serial reversals are taking place).

To test whether the frogs used a rule-based strategy (i.e. win-stay/lose-shift) to solve the serial reversal task, we created a choice matrix to categorize the choice pair of every two successive trials within individuals. For each trial, there were four types of choices: position error, noncontingent error, success (no error), and a position error in a successful trial (position error + success). We labelled each cell in the matrix with win-stay, lose-shift, win-shift, lose-stay, or excluded (Table 1).

We recorded the frequency of each category and calculated the win-stay rate and the lose-shift rate by taking their proportions out of the trials with win and lose as the previous choices, respectively. Because the win-stay and lose-shift data are proportions that cannot be normally distributed, we used an arcsine transformation before statistical analysis. We used repeated measures ANOVA to determine whether errors (noncontingent, perseverative) or decision strategies (win-stay rate and lose-shift rate) changed across reversals. All of the statistics were run in SPSS (v.20, IBM, Armonk, NY, U.S.A.).

RESULTS

All frogs learned to find the correct door, reaching the criterion for learning in 7–22 days (Fig. 2a). Furthermore, the first probe trial demonstrated that they used the visual cues in the starting chamber when remembering the location of the correct door ($t_9 = 2.30$, $P = 0.047$; Fig. 2b). The second probe trial showed that they continued to rely on the provided visual cues to solve the maze after five reversals ($t_9 = 3.20$, $P = 0.011$; data not shown). During five sequential reversals, the poison frogs reached the learning criterion more quickly each time they reversed, indicating a grasp of the experimenter-imposed rule of the task (i.e. that serial reversals were taking place) ($F_{4,36} = 4.14$, $P = 0.007$; Fig. 2c).

A combination of mechanisms contributed to the increased flexibility across reversals. First, we found a decrease in the

Table 1
Choice matrix to categorize the choice pair of every two successive trials within individuals

Current choice	Previous choice			
	Position error	Noncontingent error	Success	Position error+success
Position error	Lose-stay	Excluded ¹	Win-shift	Win-shift
Noncontingent error	Excluded ¹	Lose-stay	Win-shift	Win-shift
Success	Lose-shift	Lose-shift	Win-stay	Win-stay
Position error+Success	Lose-stay	Excluded ¹	Win-shift	Win-shift

¹ These choice pairs were excluded from the error analysis because both the previous choice and the current choice involved an error.

perseverative errors ($F_{4,36} = 3.31$, $P = 0.021$; Fig. 3a), reflecting the frogs' ability to inhibit responses to the previously correct door. Second, noncontingent errors declined ($F_{4,36} = 2.19$, $P = 0.090$; linear contrast: $F_{1,9} = 6.62$, $P = 0.030$; Fig. 3b), suggesting that increased motivation or familiarity with the task contributed to the improved performance. Third, we found that the frogs increased the rate of lose-shift trials across reversals ($F_{4,36} = 3.12$, $P = 0.026$), while the rate of win-stay trials remained stable ($F_{4,36} = 1.62$, $P = 0.190$; Fig. 3c), indicating that the frogs used a rule-based decision strategy similar to that of birds and mammals.

DISCUSSION

We found that the poison frog *D. auratus* learned to find the maze exit by associating the correct orientation with the visual cues

in the starting chamber, demonstrating that they are capable of complex spatial learning. Furthermore, we found that they were able to reverse their associations in a highly flexible manner, improving their performance across five reversals. To our knowledge, this is the first evidence of serial reversal learning in frogs. Importantly, we also found that they increased the lose-shift rate across reversals, which indicates they could use a rule-based decision strategy to flexibly respond to changing reward contingencies. While previous studies indicate that amphibians (Ellins et al., 1982), fish (Woodward, Schoel, & Bitterman, 1971) and reptiles (Gaalema, 2011; Kirkish, Fobes, & Richardson, 1979) are capable of serial reversal, none have demonstrated the use of a rule-based strategy as shown here in *D. auratus*. Thus, our study is the first to demonstrate this greater level of behavioural flexibility outside birds and mammals.

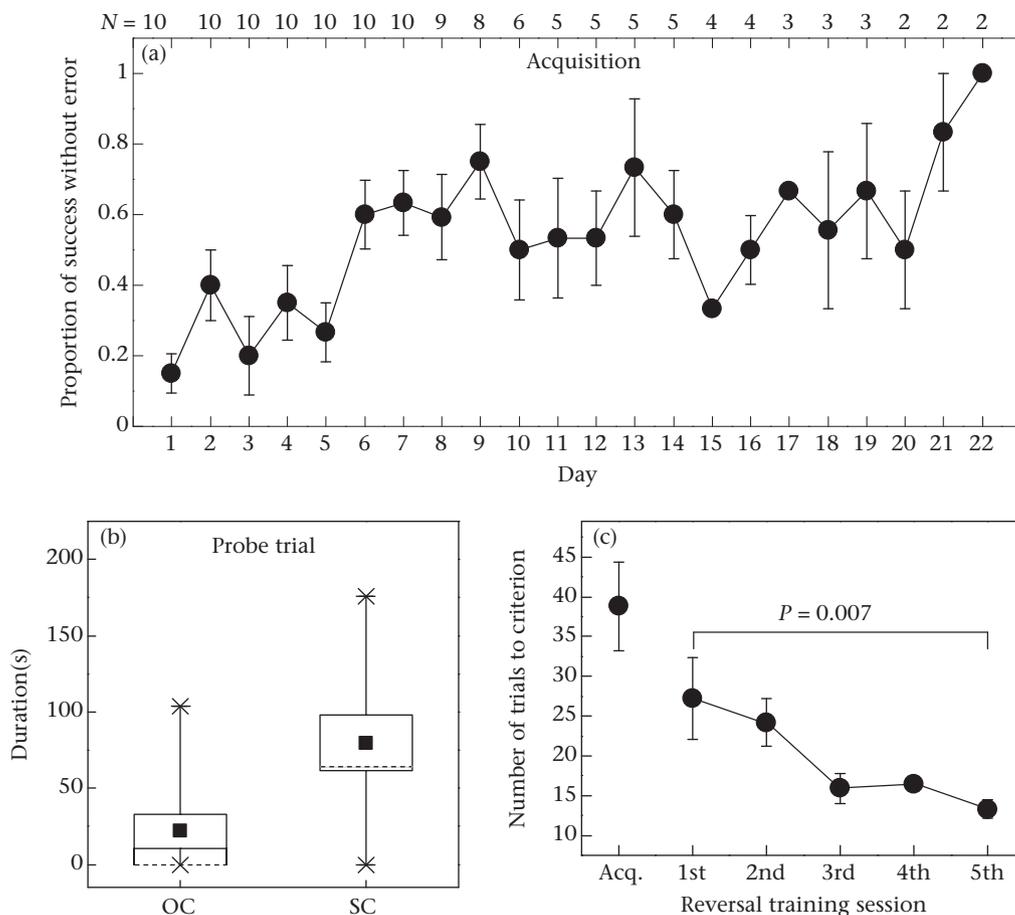


Figure 2. (a) Variation in the mean \pm SE proportion of successful trials without error over successive days for individual frogs during the acquisition training period. (b) Duration that frogs spent in the original-correct arm (OC) and the spatial-correct arm (SC) during the first probe trial. Stars represent maximum and minimum values, solid squares represent the mean, dashed lines represent the median, and the upper and lower border of the open rectangle represent the standard error. (c) Number of trials (mean \pm SE) to criterion during acquisition (Acq.) and across five reversals.

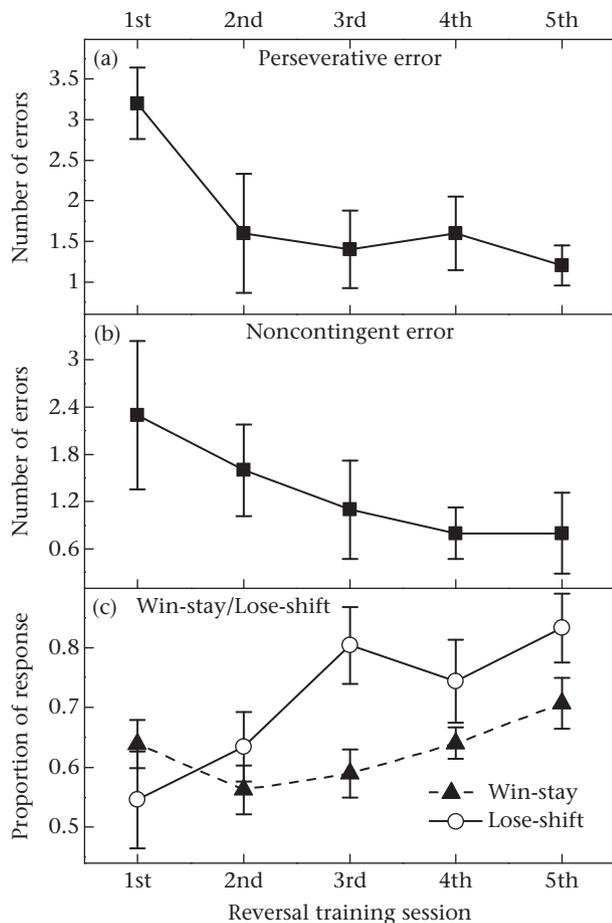


Figure 3. (a) Perseverative errors (mean \pm SE) across five reversals; (b) Noncontingent errors (mean \pm SE) across five reversals; (c) Mean (\pm SE) proportion of win-stay and lose-shift responses across five reversals.

In addition to using a rule-based strategy (i.e. win-stay/lose-shift), we found that noncontingent errors declined across reversals, indicating that increased motivation and/or familiarity with the task contributed to the improved performance. This change in motivation and/or familiarity is consistent with attentional processes previously described in rodents (Mackintosh, 1974; Mackintosh et al., 1968), indicating that the frogs also used lower-order processes to increase flexibility during the serial reversal task. Therefore, we conclude that *D. auratus* is able to use both attentional processes and a rule-based strategy to flexibly adapt to an unpredictable world.

One of the hallmark behaviours in dendrobatid frogs is tadpole transportation, in which a parent transports recently hatched tadpoles from the clutch site on the forest floor to small pockets of temporary standing water in the forest canopy (Summers, 1989). Dendrobatids tend to deposit only one tadpole in one water pocket in order to increase survivorship (Summers, 1990). Since the pockets of water are a highly unpredictable resource, frogs spend considerable time locating them (Summers, 1989, 1990). However, pools can dry out or become unsuitable for other reasons, creating a highly dynamic landscape. Hence, an essential element of reproductive success is the ability of an individual to update its memory of the available deposition sites in real time. The most efficient way to maintain an accurate mental map of useful deposition sites would be to use spatial memory in a flexible manner, not unlike that demonstrated by our serial reversal task. Thus, the high level of behavioural flexibility demonstrated by *D. auratus* in this serial

reversal task is likely to have adaptive significance in nature and suggests that greater behavioural flexibility might have evolved in dendrobatids as they adapted to a terrestrial lifestyle.

The ability of dendrobatids to revisit tadpole deposition sites based on location (Stynoski, 2009) and to return to home territories after displacement (Pasukonis et al., 2014) have led to the speculation that poison frogs have spatial memory; that is, memory for locations based on the spatial relationships among distal visual cues. However, up until now, whether poison frogs could use visual cues in such a complex manner was unknown. Previous work has shown that anurans are able to use local visual cues, but, like most other vertebrates (Bitterman, 1965; Day, Ismail, & Wilczynski, 2003; Morris & Hagan, 1986; Murray & Ridley, 1999), they prefer to use a body-centred motor strategy (e.g. turn left or right) when visual cues and turn cues are in conflict (Daneri et al., 2011). Leopard frogs in a water maze appear to be incapable of using, or prefer not to use, distal spatial cues for orientation (Bilbo, Day, & Wilczynski, 2000). While our task is not as spatially complex as those using multiple distal cues in a configuration to cue the goal, such as the Morris water maze, our study is among the first, to our knowledge, to show that an amphibian can use nonlocal visual cues in such a complex manner when orienting in space.

In summary, we found that *D. auratus* could use visual cues in a complex spatial discrimination and they were able to update their visual associations in five sequential reversals using a rule-based decision strategy (win-stay/lose-shift). Their ability to learn the underlying rule of the serial reversal task demonstrates an advanced cognitive ability (Brown & Bowman, 2002) and indicates a degree of behavioural flexibility that until now was exclusively associated with birds and mammals.

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