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RESEARCH ARTICLE

A cognitive map in a poison frog

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ABSTRACT

A fundamental question in cognitive science is whether an animal can use a cognitive map. A cognitive map is a mental representation of the external world, and knowledge of one's place in this world, that can be used to determine efficient routes to any destination. Many birds and mammals are known to employ a cognitive map, but whether other vertebrates can create a cognitive map is less clear. Amphibians are capable of using beacons, gradients and landmarks when navigating, and many are proficient at homing. Yet only one prior study directly tested for a cognitive map in amphibians, with negative results. Poison frogs exhibit unusually complex social and spatial behaviors and are capable of long-distance homing after displacement, suggesting that they may be using complex spatial navigation strategies in nature. Here, we trained the poison frog *Dendrobates auratus* in a modified Morris water maze that was designed to suppress thigmotaxis to the maze wall, promoting exploration of the arena. In our moat maze, the poison frogs were able to use a configuration of visual cues to find the hidden platform. Moreover, we demonstrate that they chose direct paths to the goal from multiple random initial positions, a hallmark of a cognitive map. The performance of the frogs in the maze was qualitatively similar to that of rodents, suggesting that the potential to evolve a cognitive map is an evolutionarily conserved trait of vertebrates.

KEY WORDS: Parallel map theory, Sketch map, Spatial cognition, Morris water maze, Trajectory analysis, Amphibian, Poison dart frog

INTRODUCTION

In 1948, Tolman proposed the concept of a cognitive map, which he defined as a mental representation of the external world (Tolman, 1948). Since then, the concept of the cognitive map has inspired research in biology and psychology (Jacobs and Schenk, 2003; O'Keefe and Nadel, 1978; Shettleworth, 2009), computer science and mechanical engineering (Georgopoulos et al., 2003; Kosko, 1986). While used widely, the term cognitive map is not always clearly defined or precisely applied. Herein, we define a cognitive map as flexible place mapping that depends on arrays of distal cues. Evidence of a cognitive map has been provided for some mammals (Boesch and Boesch, 1984; Foo et al., 2005; Singer et al., 2006; Wills et al., 2010) and birds (Bingman et al., 1990; Kamil and Jones, 1997). Owing to their phylogenetic position, amphibians are key to understanding the evolution of spatial cognition in vertebrates. While they retain many of the primitive traits that characterized the common ancestor of all tetrapods, they also reflect the evolution of a more complex forebrain that was associated with the evolutionary transition from an aquatic to a terrestrial lifestyle (Bingman and Muzio, 2017; Butler and Hodos, 2005; McGirr and Martin, 2017; Northcutt, 1995). Yet, whether amphibians possess a cognitive map has been virtually ignored, with the exception of a single study on the northern leopard frog (Bilbo et al., 2000).

It is widely accepted that the hippocampus is at the center of the cognitive map neural network (Jeffery, 2015; Morris et al., 1982; O'Keefe and Nadel, 1978). According to the parallel map theory, an integrated map is formed in the hippocampus via two mapping systems (Jacobs, 2003; Jacobs and Schenk, 2003). The bearing map encodes cues that provide directional information such as environmental gradients or distant beacons. Evidence for bearing maps in amphibians has been broadly found in field and laboratory experiments, including use of magnetic fields (Phillips, 1996; Shakhparonov and Ogurtsov, 2017), sensory beacons (Daneri et al., 2011, 2015; Kundey et al., 2016; Liu and Burmeister, 2017; Liu et al., 2016; Ogurtsov et al., 2018; Sinsch, 1987, 1990, 2007, 2014) and arena geometry (Sotelo et al., 2015, 2017). The sketch map, in contrast, stores topographical information by recording geometric relationships of position cues and corresponds to the classic definition of the cognitive map. A hallmark of sketch maps is that they enable animals to use geometric spatial relationships among allocentric cues to configure the shortest pathway from any novel location to a goal (Bennett, 1996; Gallistel, 1990; Jacobs and Menzel, 2014; O'Keefe and Nadel, 1978; Shettleworth, 2009). This hallmark of the sketch map is not easy to demonstrate and is the focus of much debate (Bennett, 1996; Cheeseman et al., 2014a,b; Cheung et al., 2014; Shettleworth, 2009). One widely accepted method to test for the sketch map is use of the Morris water maze (Jacobs and Menzel, 2014; Shettleworth, 2009); however, a swimming task is not suitable for the majority of vertebrates. Various tasks have been designed to test some aspects of the sketch map in other vertebrates (Fremouw et al., 1997; Kamil and Jones, 1997; LaDage et al., 2012; López et al., 2000; Mayer et al., 2010; Rodriguez et al., 1994). The only study, to our knowledge, to directly test for a sketch map in amphibians showed that leopard frogs did not utilize a sketch map in a classic Morris water maze (Bilbo et al., 2000). Whether these results were due to maze design, choice of species, or overall lack of a sketch map in amphibians is unknown.

The poison frogs (Dendrobatidae family) are an unusual group of anurans that have evolved sophisticated parental care that requires complex use of space. In most species, mothers deposit eggs on leaves on the forest floor and parents periodically return to hydrate the clutches. Once eggs hatch, parents transport tadpoles, one or two at a time, to pools of water that form in tree holes and in epiphytes in the forest canopy (Roithmair, 1992; Summers, 1989; Wells, 1978, 2010; Weygoldt, 1980). Since the pools are ephemeral and unpredictable, frogs spend considerable time locating them (Summers, 1989; 1990; Summers et al., 1999; Weygoldt, 1987). In order to successfully reproduce, a major daily task is to travel

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among shelters, egg clutches, water pools and feeding locations (Ringler et al., 2013; Summers, 1989; Ursprung et al., 2011). Using a sketch map would allow efficient travel among these locations.

There is a growing understanding of the abilities of poison frogs to navigate in their natural environment. *Oophaga pumilio* use place cues (and not tadpole identity) to locate their tadpole deposition sites (Stynoski, 2009) and can accurately orient towards their territories after displacement (Nowakowski et al., 2013). *Allobates femoralis* has accurate homing abilities, navigating in a straight trajectory after displacement independent of egocentric path integration and route learning (Pašukonis et al., 2018, 2014a,b, 2013, 2016). These studies suggest that poison frogs are able to use a sketch map to navigate in nature, but the specific cues used for navigation have yet to be identified. Evidence of a sketch map requires that alternative cognitive mechanisms, such as the use of beacons and vectors, are excluded (Bennett, 1996; Shettleworth, 2009). Given the difficulty of controlling the necessary cues and the subjects' prior experiences in a natural environment, a laboratory experiment is necessary to establish the existence of a sketch map in poison frogs (Jacobs and Menzel, 2014).

A major challenge for laboratory experiments on cognition is accommodating a species' natural tendencies. While the Morris water maze is quite successful for testing the sketch map in rats (D'Hooge and De Deyn, 2001; Jacobs, 2003; Morris, 1984; Vorhees and Williams, 2006), it does not translate well to other species, even mice (Vorhees and Williams, 2006), and has failed to reveal a sketch map in anurans (Bilbo et al., 2000). Both the leopard frog and *Dendrobates auratus* (see Results) show a strong tendency to touch the walls of the maze (i.e. thigmotaxis), a common initial response of many vertebrates (Bilbo et al., 2000). As a consequence, the frogs spend little time in the center of the arena and they apparently fail to attend to distal visual cues (Bilbo et al., 2000), making it impossible to use the classic Morris water maze to test spatial memory in anurans. Therefore, we modified the Morris water maze by creating a shallow area in the center and a deep area on the edge to reduce thigmotaxis to the wall, allowing the frogs to explore the arena and attend to cues in the environment. Using our moat maze, we were able to ask whether *D. auratus*, which expresses a pattern of parental care typical of many poison frog species (Summers, 1989) and possesses remarkable flexibility in place learning (Liu et al., 2016), is able to use a sketch map to locate a hidden platform.

MATERIALS AND METHODS

Animals

We trained five sexually mature *Dendrobates auratus* (Girard 1855) (three male and two female) that were bred and raised in captivity (Indoor Ecosystems, LLC) with snout–vent length around 4 cm. They were likely two to three generations removed from the wild, yet these frogs remain attentive parents even in captivity. We maintained the animals under conditions that approximated their natural habitat: 25°C, 80% relative humidity (RH), 12 h:12 h light: dark cycle (lights on at 07:00 h). We housed the frogs individually in terraria and fed them fruit flies fortified with calcium and vitamins three times per week; all frogs were in a non-breeding state. The University of North Carolina's Institution for Animal Use and Care Committee approved all procedures (protocol 14-026).

Apparatus

We used a white polyethylene cylindrical tank (diameter=84 cm, height=72 cm) as the arena. A white round table (diameter=62 cm) divided the maze into two areas: a shallow area created by the table with 2 cm depth of water and a moat, which was the annular area between the table and the wall, with 8 cm deep water (Fig. 1A). Because the frogs prefer the shallow area, thigmotaxis to the wall was reduced by pretraining. In addition, because the frogs could explore the shallow area by walking or hopping (instead of swimming), it allowed them to raise their heads and attend to the visual cues.

We divided the shallow area into four quadrants indicated by the cardinal directional terms NE, SE, SW, NW, and we provided four visual cues 5 cm above water level: red flashing light, yellow artificial flower, blue spinning fan, and green artificial leaves on the east, south, west and north walls of the tank, respectively (Fig. 1A). We provided a white platform (diameter=5 cm, height=1.2 cm), which was submerged in milk-opacified water, in the center of the SE quadrant. We increased the water temperature to approximately 35°C to motivate the frogs to use the visual cues to find the platform in order to escape the water. We used a white curtain surrounding the maze to exclude cues outside of the arena. We recorded the behavior of the frogs from a camera above the arena.

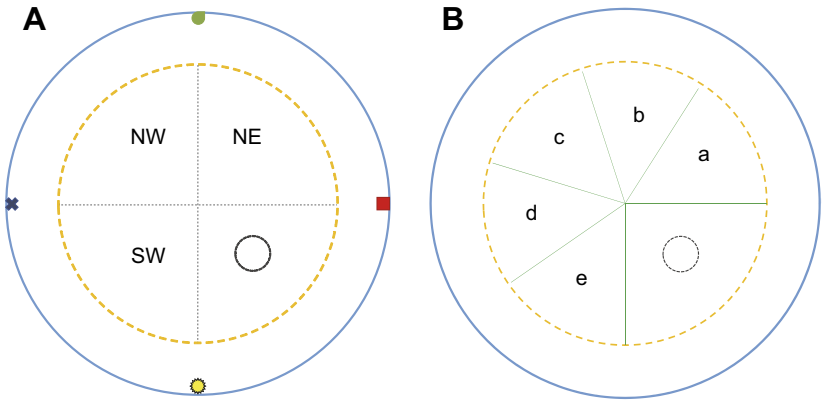

Fig. 1. Diagram of the maze. Schematic of maze (A) during training and (B) showing the five sections (a–e) without the platform (i.e. NE, NW, SW quadrants combined) that we used to ensure that release points in the maze were randomly distributed. We provided visual cues on the east (red flashing light), south (yellow artificial flower), west (blue spinning fan) and north (green artificial leaves) walls of the maze. We included kinetic cues (red flashing light and blue spinning fan) because frogs may attend better to moving visual stimuli than static stimuli. The blue spinning fan was potentially multi-modal, possibly generating auditory and/or somatosensory (air flow) cues in addition to the visual cue. However, these non-visual cues, which could only provide directional information, would be insufficient for a frog to navigate accurately to the platform in this maze. The solid blue circle indicates area of arena, the dashed yellow circle represents shallow area, and the dashed black circle shows the invisible platform.

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Procedure

Pretraining

Before training frogs in the spatial task, we pretrained them in three trials per day for 10 days. During pretraining, the water was 1 cm above the table and there were no visual cues or platform. For each trial, we released the frog in the shallow area and allowed 3 min for exploration. Gradually, the frogs learned to swim back to the shallow area after falling into the moat. By the end of pretraining, frogs spent most of the time in the shallow area.

Acquisition

We trained the frogs in five trials per day. We divided the area without the platform (i.e. NE, NW, SW quadrants combined) into five equal sections (Fig. 1B). For each trial in a day, we released the frogs in a different section and the order of sections was changed each day. We transported the frogs to the maze in a transparent cup that we rotated during transport to ensure that orientation at release varied unpredictably. We then released the frog into one of the above-mentioned sections on the table. As a result, release points and head direction were unpredictable and evenly distributed in the maze.

After the frogs' first movement, we allowed 3 min to find the platform. If a frog climbed onto the platform and stayed on it for 20 s, the trial was counted as a successful trial. Latency in successful trials was the duration between the first movement and climbing onto the platform. When frogs did not find the platform within 3 min, we covered them with the transparent cup, moved the cup slowly to the platform, and kept the frog on the platform for 20 s. Latency for these unsuccessful trials was recorded as 180 s. After 20 s on the platform, we transferred frogs to their home cage. We stirred the water after every trial to prevent the frogs from using olfactory cues to learn the task. Inter-trial intervals were around 40 min.

We tracked the proportion of successful trials per day for each individual to determine when each frog learned the task. We defined our criterion for learning as four successful trials within one day (80%). After 10 days' training, four of the five frogs had reached the criterion and maintained their performance between 60 and 100% successful trials in later trials. The last frog reached the criterion on the 13th day. We monitored group performance by determining when the proportion of successful trials and latency reached asymptotic performance across three successive days (Fig. 2, days 12–14, <10% variation among days). We stopped training on day 14. We used repeated-measures ANOVA in SPSS 20 to test for changes in latency and proportion of successful trials (after arcsine transformation) across days.

Probe trial

We conducted the probe trial on day 15 by removing the platform and moving the visual cues 180 deg from their original position, leaving the rest of the maze unchanged. We released each frog in the SW or NE quadrant and tracked its movement for 3 min (Fig. 1A). We recorded the proportion of total time spent in each of the four quadrants and used repeated-measures ANOVA in SPSS 20 to test whether frogs were biased to particular quadrants. If the frogs used the spatial configuration of visual cues to locate the platform which was located in quadrant SE during training, they should prefer the NW quadrant during the probe trial. (Fig. 1A).

Pathway analysis

We determined the pathway of each frog in each trial using the MultiTracker plugin (rsbweb.nih.gov/ij/plugins/multitracker.html)

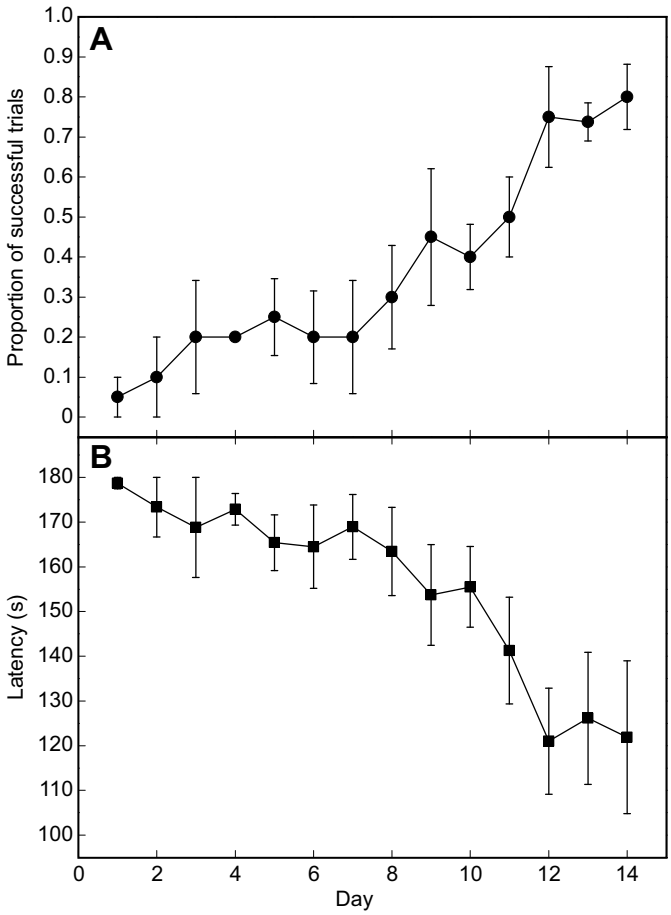

Fig. 2. Performance of frogs across training days. (A) Frogs (n=5) had increasingly greater success finding the platform (repeated measures ANOVA, $F_{13,52}$=8.8, P<0.0001) and (B) found the platform more quickly (repeated measures ANOVA, $F_{13,52}$=5.7, P<0.0001) across 14 days of training with performance reaching asymptote on day 12. Values are means±s.e.

in ImageJ (Abràmoff et al., 2004) to extract coordinate data of the frogs' locations that, in turn, we used to generate vectors of each pathway. We then used circular statistics to examine the frogs' orientation toward the platform following a strategy used by Domenici et al. (2008), as follows. The frogs' pathways consisted of discrete movements (i.e. hops). We assessed orientation of a pathway by analyzing the angles between the vector of actual hops and the vector of perfect direction toward the center of the platform (Fig. S1). For pathways in successful trials, we averaged the angles from every hop in that pathway to determine whether the frogs as a group showed significant orientation using Hotelling's one sample second order test (Batschelet, 1981; Zar, 1999). Hotelling's test reflects whether frogs are significantly oriented (i.e. non-random directions) but does not directly test the hypothesis that they are oriented toward the platform itself. Therefore, we also calculated a Straightness Index (Mahan, 1991) that reflects whether or not the frogs were moving directly toward the platform, as follows.

Straightness index (SI) can be represented by circular standard deviation (Batschelet, 1981; Mahan, 1991; McCarthy et al., 2010):

$$\mathrm{SI} = \sqrt{2(1-r)}, \quad (1)$$

in which r is the length of mean vectors (Batschelet, 1981). However, this equation only tests if vectors are concentrated to any direction; it does not test whether vectors are concentrated toward a

predicted direction which, in this study, is the direction to the platform. Thus, we calculated R to represent the deviation of each hop to the most efficient direction toward the platform (Fig. S1) as (Batschelet, 1972):

$$R = r\cos(\theta). \quad (2)$$

Next, we substituted R for r in the calculation of SI shown by Eqn 1:

$$\mathrm{SI} = \sqrt{2(1-R)}. \quad (3)$$

Thus, this revised equation (Eqn 3) represents the deviation of each hop relative to the predicted direction straight toward the platform. SI will decrease as concentration (R) increases. Therefore, a lower SI indicates a straighter path.

Finally, we did a V-test plus 95% confidence interval (CI) (Aneshansley and Larkin, 1981; Batschelet, 1981; Fisher, 1995; Mardia and Jupp, 2009) to determine if each pathway of every frog was significantly oriented toward the platform during the last 3 days of training. In the V-test (unlike Hotelling's test), the angle of each hop was the statistical unit (Fig. S1). For Hotelling's test and the V-test, we used Oriana 4 (Kovach Computing Services). For SI, we used repeated measures ANOVA in SPSS 20 after feature scaling and arcsine transformation.

RESULTS

Our moat maze significantly reduced thigmotaxis during pretraining, enabling all the frogs to learn to locate the hidden platform during acquisition of the spatial task. After 10 days of training, four of the five frogs reached 80% success. The last frog reached the criterion on the 13th day. As a group, learning was demonstrated by increasing success (Fig. 2A; $F_{13,52}$=8.8, P<0.0001) and decreasing latency to find the platform (Fig. 2B; $F_{13,52}$=5.7, P<0.0001).

Use of a sketch map is characterized by an animal learning the location of a goal based on a configuration of cues in the environment. Therefore, we conducted a probe trial on the 15th day to directly test whether the frogs used the provided visual cues by rotating the cues 180° from their original position. The frogs spent significantly more time searching in the quadrant indicated by the rotated cues ($F_{3,12}$=18.5, P<0.0001; Fig. 3).

A sketch map is characterized by the ability to take direct routes to a goal regardless of starting position, a prediction we tested by quantifying the pathways of the frogs during training. The frogs found the platform with random orientations in their first successful trial (Hotelling's test: F=2.1, P=0.26, n=5; Fig. 4A,B; Table S1), showed increasingly more direct paths across training (repeated measures ANOVA: $F_{13,52}$=4.2, P<0.0002; Fig. 4C) and, by the end of training, they took significantly direct paths to the platform (Hotelling's test: F=24.4, P=0.014, n=5; Fig. 4D,E; Table S2). However, a straight path from release point to the platform could be attributed to route learning that reflects learning a series of stimulus-response associations on particular tracks (O'Keefe and Nadel, 1978; Shettleworth, 2009). In contrast, a sketch map enables animals to take a straight pathway from any release point to the platform. To distinguish these two possibilities, we confirmed that the release points of frogs were distributed throughout the maze in the last 3 days when learning had reached an asymptote (Fig. 5A). Frogs took significantly direct pathways to the platform in 86.4% of these trials (V test: P<0.05 and mean vector ε 95% CI; Fig. 5A; Table S3) and, as a group, showed significant orientation to the platform (Hotelling's test: F=594.6, P=0.0001, n=5; Fig. 5B).

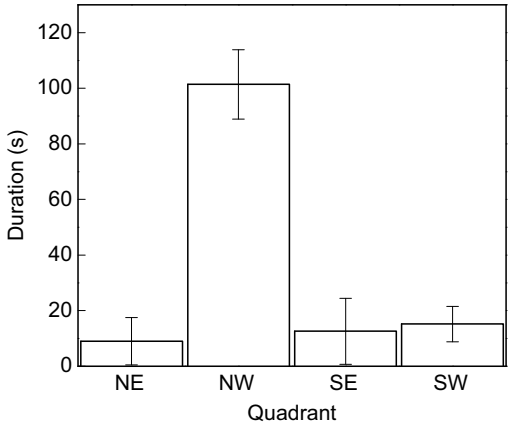

Fig. 3. Time spent by frogs in each quadrant during probe trial. During the probe trial, frogs (n=5) spent significantly more time searching for the platform in the NW quadrant (repeated-measures ANOVA, $F_{3,12}$=18.5, P<0.0001), demonstrating that they relied on the spatial configuration of visual cues to find the platform during training. Values are means±s.e.

DISCUSSION

Our moat maze enabled poison frogs to overcome their tendency toward thigmotaxis to the maze wall in order to learn to find the hidden platform. The probe trial, in which the platform was removed, confirmed that frogs did not use a beacon associated with the platform, or any salient cue near the platform, to learn the task. Furthermore, the configuration of visual cues, which were distal to the platform, ensured that the frogs would not have been able to use a single cue as a beacon to navigate accurately to the platform, ruling out the use of any single vector to navigate in the maze. Finally, we demonstrated that the frogs were able to take a direct pathway from multiple unpredictable locations. The performance of poison frogs is qualitatively similar to that of rodents in the classic Morris water maze (Morris, 1984). Together, these findings represent the first demonstration of a sketch map (topographic information) in an amphibian. Combined with the results of field experiments in *O. pumilio* and *A. femoralis* (Nowakowski et al., 2013; Pašukonis et al., 2018, 2014a,b, 2016; Stynoski, 2009) and evidence of bearing maps (directional information) in other amphibians (Sinsch, 1990, 2014), we can conclude that poison frogs are likely to have an integrated cognitive map that includes both bearing and sketch mapping systems. Our study provides the first conclusive evidence of an integrated cognitive map in an amphibian.

An important breakthrough in the present study was maze design. Although the Morris water maze is the most powerful task to test the cognitive map of rodents, it does not work well with frogs because of strong thigmotaxis (Bilbo et al., 2000). Thigmotaxis, a common response of animals to the water maze, can inhibit successful learning (Bilbo et al., 2000; Day and Schallert, 1996; Vorhees and Williams, 2006). Furthermore, lesions and pharmacological disruption of the hippocampus promote thigmotaxis in rats (Devan et al., 1999; Hostetter and Thomas, 1967; Morris et al., 1982; Saucier and Cain, 1995). Together, these results indicate that, to solve the Morris water maze, an animal must first switch from thigmotaxis to open search. Therefore, one possible reason for the success of our maze might be that our modification helped to release frogs from thigmotaxis and allowed learning before overtraining effects occurred (e.g. loss of motivation, exhaustion) (Dickinson, 1998; Hosono et al., 2016).

Several aspects of the natural history of poison frogs likely select for complex spatial cognition, including territoriality and mate guarding (Roithmair, 1992; Summers, 1989), but it is their parental

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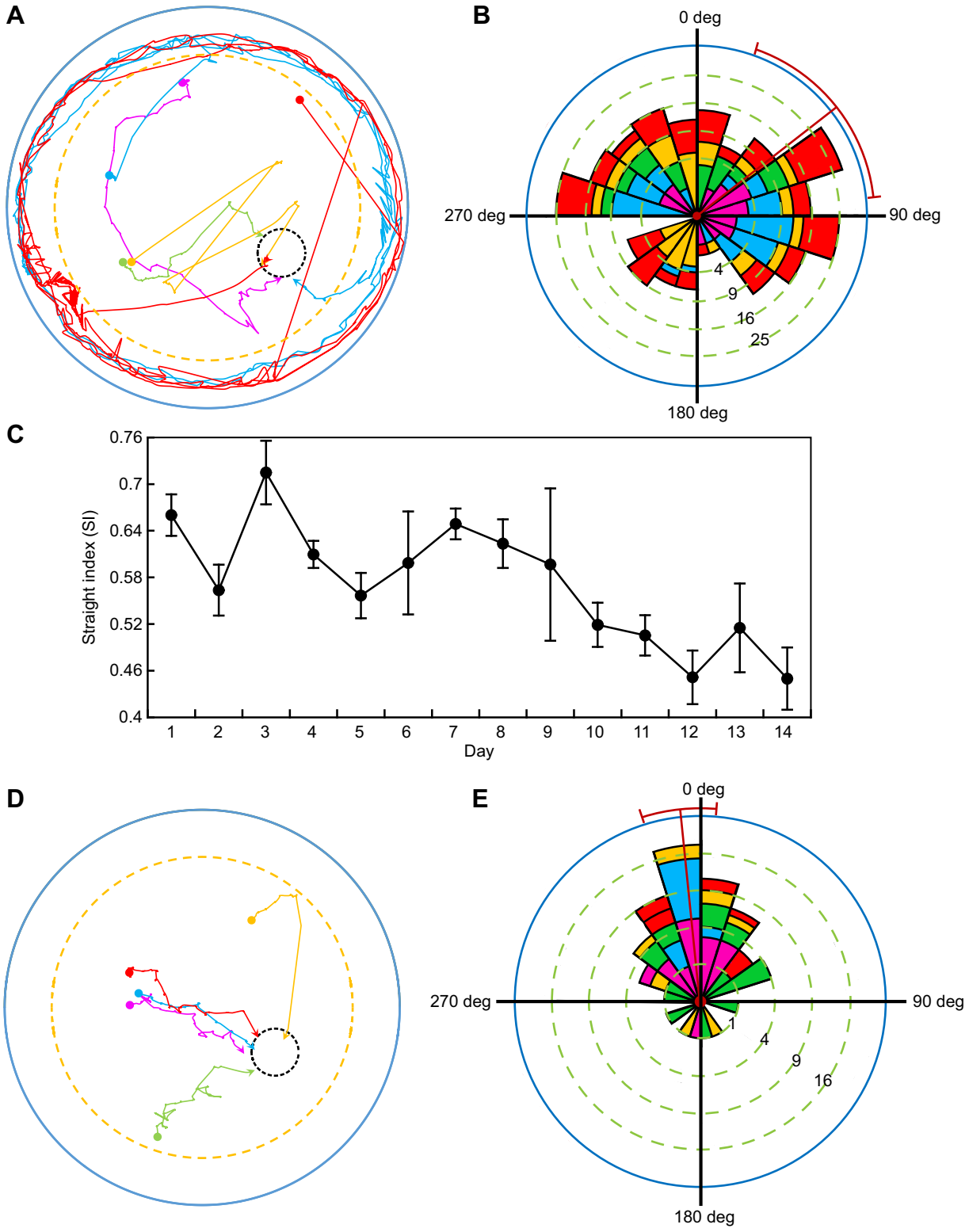

Fig. 4. Pathway analysis of successful trials across training. Pathway analysis shows that the frogs (n=5) gradually established a mental representation of visual cues to solve the task. (A) Poison frogs took indirect paths to the platform in their first successful trials. The solid blue circle indicates area of arena, the dashed yellow circle represents shallow area, and the dashed black circle shows the invisible platform. Colors represent different individuals, filled circles indicate start positions and arrows mark the final position. (B) Rose diagram shows that poison frogs did not orient toward the platform for their first successful trials to approach the platform (Hotelling's test: F=2.1, P=0.26). The circular axis indicates movement direction, 0 deg is the direction to the platform. The radius axis shows number of movements in certain range of directions. Color represents different individuals. The red curve indicates 95% confidence interval. (C) Decreasing straightness index indicates the frogs took increasingly direct paths to the platform across training (repeated measures ANOVA, $F_{13,52}$=4.2, P<0.0002). (D,E) At the end of training, the frogs chose direct pathways to the platform (Hotelling's test: F=24.4, P=0.014) .

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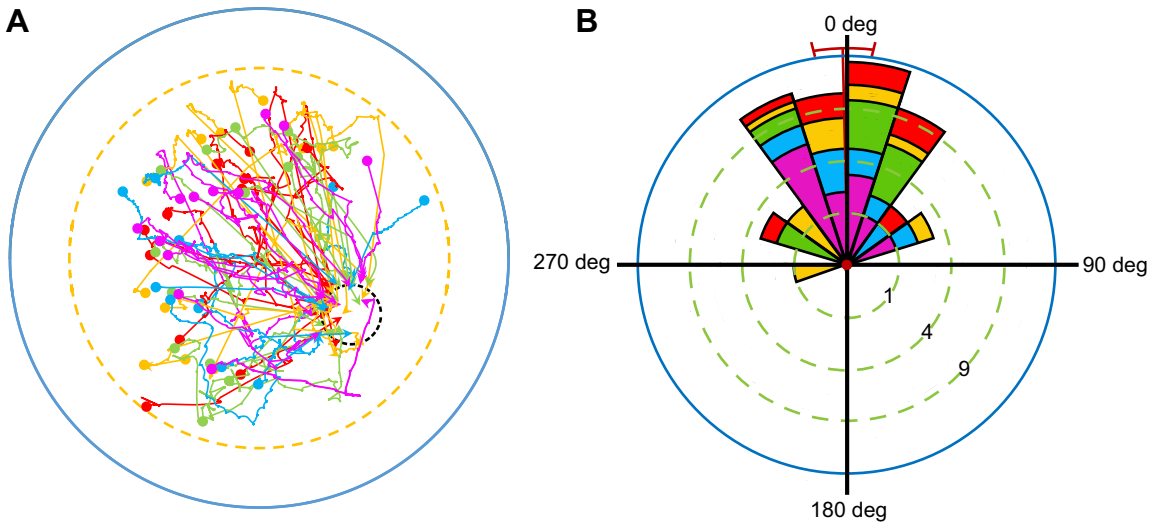

Fig. 5. Pathway analysis of successful trials after reaching asymptotic performance. Pathway analysis demonstrates that the frogs (n=5) took direct paths to the platform regardless of release point (V test: P<0.05) (A) and that they were significantly oriented to the platform (Hotelling's test: F=594.6, P=0.0001) (B) after reaching asymptotic performance (days 12–14). Each color represents a different frog; dots indicate release points. The circular axis indicates movement direction, 0 deg is the direction to the platform. The radius axis shows number of movements in certain range of directions. The red curve indicates 95% confidence interval around 0 deg.

care that would appear to depend most heavily on a cognitive map. Males maintain the clutches throughout their development and must locate suitable tadpole deposition sites (typically tree holes) in the forest canopy tens of meters or more away from their territories (Summers, 1989, 1990; Ursprung et al., 2011). Because tadpole deposition sites can dry out or become unsuitable for other reasons, poison frogs have to spend considerable time locating available sites (Summers, 1989, 1990; Summers and Tumulty, 2013; Wells, 2010; Weygoldt, 1987). Environmental events (e.g. rainstorms) can dramatically change the landscape, causing rearrangements of leaf litter, branches, etc., which may affect normal routes and/or beacons to known sites. Thus, as competent parents, poison frogs are required to locate and relocate tadpole deposition sites in a changing landscape. An integrated cognitive map is likely to be the most efficient way to solve this task, suggesting that the sketch map demonstrated here by *D. auratus* had adaptive value as poison frogs evolved a terrestrial lifestyle. Among amphibians, the only other species tested for a sketch map is the northern leopard frog. While the Northern leopard frog has the ability to home toward natal ponds (Dole, 1968; Mazerolle and Desrochers, 2005), which likely utilizes a bearing map, they failed to use allocentric cues to locate a platform in a Morris water maze (Bilbo et al., 2000). Why this might be so requires further study.

Evidence suggests that an elaboration of the hippocampus in response to specific selective pressures correlates with the evolution of a sketch map (Healy, 2006; Jones et al., 2003; Sherry et al., 1992). Work from corvids, parids, and lineages of rock doves demonstrate that species, populations, or sexes that experience particularly strong demands on their ability to remember locations in a more flexible manner (e.g. caching food for later retrieval in order to survive the winter) will evolve neural and cognitive systems that enable a sketch map, which is typically associated with a larger relative hippocampal volume (Bond et al., 2007; Ebinger and Löhmer, 1984; Healy and Krebs, 1992; Rehkämper et al., 2008). One contribution of parallel map theory to the study of cognitive maps in mammals is to associate the bearing and sketch mapping systems to subdivisions of the hippocampal formation (Jacobs, 2003; Jacobs and Schenk, 2003). Yet, whether this model applies to other vertebrates with evidence of a sketch map, such as birds or poison frogs, requires further comparative analyses (Bingman and Muzio, 2017; Day, 2003). Nonetheless, evidence to date indicates that the medial pallium, which is the amphibian homolog of the mammalian hippocampus, contributes functionally to aspects of spatial navigation (Sotelo et al., 2016). Understanding the neural basis of the integrative cognitive map in a broader range of vertebrates could provide important insight into the constraints on, and evolutionary potential of, cognitive maps.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: S.S.B., L.B.D.; Methodology: Y.L., S.S.B., L.B.D.; Formal analysis: Y.L., S.S.B.; Investigation: Y.L.; Resources: S.S.B., K.S.; Writing - original draft: Y.L.; Writing - review & editing: S.S.B., L.B.D., K.S., Y.L.; Visualization: Y.L.; Supervision: S.S.B.; Project administration: S.S.B.; Funding acquisition: S.S.B.

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