Animal Cognition (2022) 25:27–32
https://doi.org/10.1007/s10071-021-01528-x

SHORT COMMUNICATION

Quantity discrimination in a spontaneous task in a poison frog

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Received: 9 June 2020 / Revised: 14 April 2021 / Accepted: 16 June 2021 / Published online: 28 July 2021

Abstract

The use of quantitative information underlies a range of animal behaviors. There are thought to be two parallel systems for judging quantity: a precise representation of small numbers of objects, typically less than 4, that can be tracked visually (object tracking system) and an imprecise system for larger quantities (approximate number system) governed by Weber's law. Using a spontaneous discrimination task with live prey, we examined the ability of the poison frog *Dendrobates auratus* to discriminate quantities of low (1–4) or high (4–16) numerosity over a range of ratio contrasts (0.33, 0.5, 0.67, 0.75). Similar to a previous study in treefrogs, we found that the poison frogs chose the larger quantity of flies when choosing between 1 and 3 and between 1 and 2. However, their performance was near chance when choosing between 2 and 3 and below chance when choosing between 3 and 4. When the numerosity of flies was higher, they did not discriminate between the larger and smaller quantity. Our findings are consistent with the ability of poison frogs to discriminate small quantities of objects using an object tracking system, but could also reflect a singular vs. plural discrimination. We did not find evidence of an approximate number system governed by Weber's law, nor evidence of a speed–accuracy tradeoff. However, total set size was associated with lower accuracy and longer latencies to choose. Future studies should explore quantity discrimination in additional contexts to better understand the limits of these abilities in poison frogs.

Keywords Numerical cognition · Quantity discrimination · Amphibian · Anuran

Introduction

The ability to discriminate quantities is relevant to many aspects of animals' life history, including the selection of foraging sites, social groups, and mates. For example, female preferences for larger tail patches in rock sparrows (Griggio et al. 2011) depends on the ability to discriminate larger from smaller patches, the tendency of tadpoles to associated with larger groups to avoid predator cues requires an ability to compare quantities of conspecifics (Balestrieri et al. 2019), and many aspects of foraging or prey selection are made more efficient by the ability to discriminate quantities or sizes of potential food items or patches (e.g., Hunt et al. 2008; Lucon-Xiccato et al. 2015).

The abilities of animals to discriminate numerical information is thought to emerge from two complementary systems. The precise representation of small quantities of objects, typically less than 4, that can be tracked visually is referred to as the object tracking system and is defined by the limits of working memory (Trick and Pylyshyn 1994). For larger quantities, animals typically utilize an imprecise system that is referred to as the approximate number system (Gallistel and Gelman 2000). The approximate number system is governed by Weber's law such that discriminability is constrained by the ratio of compared quantities (Fechner et al. 1966). The two systems have been described in a broad range of species, including primates, mammals, and birds (reviewed in Shettleworth 2009). Species may utilize one or both systems during discrimination and which system predominates can be influenced by task or context (Hyde 2011). However, both systems are not always evident in the discrimination abilities of animals (e.g., Al Aïn et al. 2009; Jones and Brannon 2012). For example, some studies have found that the total number of objects to be discriminated is a better predictor of performance than ratio of items (Bogale et al. 2011; Garland et al. 2012). In addition, under conditions when the two systems are not readily utilized, animals may use set representations to discriminate between singular

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and plural or between sets and subsets (e.g., all vs. sum) (Barner et al. 2008).

While the field of numerical cognition has a long history, these abilities are rarely explored in amphibians (Agrillo and Bisazza 2017). What is known so far is that, in the fire-bellied toad (Stancher et al. 2015), Italian treefrog (Lucon-Xiccato et al. 2018), and Plethodon salamanders (Uller et al. 2003), the threshold for discrimination is around 3 or 4 objects for small quantities (1–4). For larger quantities (> 4), work in the fire-bellied toad (Stancher et al. 2015) and salamanders (Krusche et al. 2010) suggest that the threshold for discrimination is below the ratio contrast of 0.67. To better understand quantity discrimination in amphibians, we tested the poison frog *Dendrobates auratus* in a spontaneous discrimination task that spanned low and high numerosity. Poison frogs are territorial and express parental care (Brown 2013). In *D. auratus*, males attends to developing clutches of 5–7 eggs in their territories (Summers 1990). When tadpoles hatch, the father transports them, one to two at a time, to water sources in the forest canopy, where they complete development (Summers 1990), a task that may incorporate tracking the quantity of tadpoles and distances to sites (Ringler et al. 2013). We tested the ability of *D. auratus* to discriminate between small and large quantities of flies in a spontaneous task, testing both the object tracking system and the approximate number system across ratio contrasts of 0.33 to 0.75.

Materials and methods

We used 24 *D. auratus* acquired from Indoor Ecosystems, LLC (Whitehouse, OH, USA). Frogs were housed in pairs under conditions similar to their natural environment at 25 °C and 75% relative humidity with a 12:12 light:dark cycle and fed fruit flies (flightless *Drosophila hydei* or wingless *D. melanogaster*) dusted with calcium and vitamins every 1–2 days. During testing, frogs were only fed in the test arena. All procedures were approved by UNC's Institutional Animal Care and Use Committee (19.285).

We used a white poster board to construct a semi-circular arena of 40 cm in diameter and 30 cm in height (Fig. 1). We established three zones within the arena: a holding zone (4 × 4 cm), where we released subjects and two stimulus zones (4 cm radius) located equadistant and 45° from the holding zone. The stimulus flies (*D. melanogaster*) were contained in a sealed, transparent 8-cm glass tube in the stimulus zones. Before trials began, we acclimated test individuals to the arena with 3 trials per day (5 min each) for 2 consecutive days. To facilitate acclimation, we released a small number of *D. melanogaster* into the arena during the acclimation trials.

For each discrimination trial, we transported frogs from their home cage to the holding zone in a 2 × 2 × 3 cm box. We allowed the frogs at least 20 s to settle in the holding zone and began the 10-min trial once all stimulus flies were in motion by lifting the box. At the time the trial began, frogs could have been in any orientation. However, the lateral position of the eyes in amphibians allows them to see in virtually all directions (Stebbins and Cohen 1997). Furthermore, once the frogs oriented toward the stimuli, both stimuli would have been simultaneously visible.

The discrimination tests spanned numerosity (1–4 and 4–16) and ratio contrasts (0.33, 0.50, 0.67, 0.75; Table 1). For each pair of discriminations representing a ratio contrast (Table 1), we tested 6 frogs in both the low and high numerosity conditions (for example, 1 vs. 3 and 4 vs. 12). Thus, there were a total of 20 frogs in the study (6 frogs for each of the four pairs of discriminations). Each test consisted of 5 trials each day for 4 days for a total of 20 trials per individual. We alternated the location of the larger quantity of flies in a psuedorandom manner. We ended the trial when the frog approached within 5 cm of a tube or made a strike. If frogs chose the larger quantity, we allowed them to consume

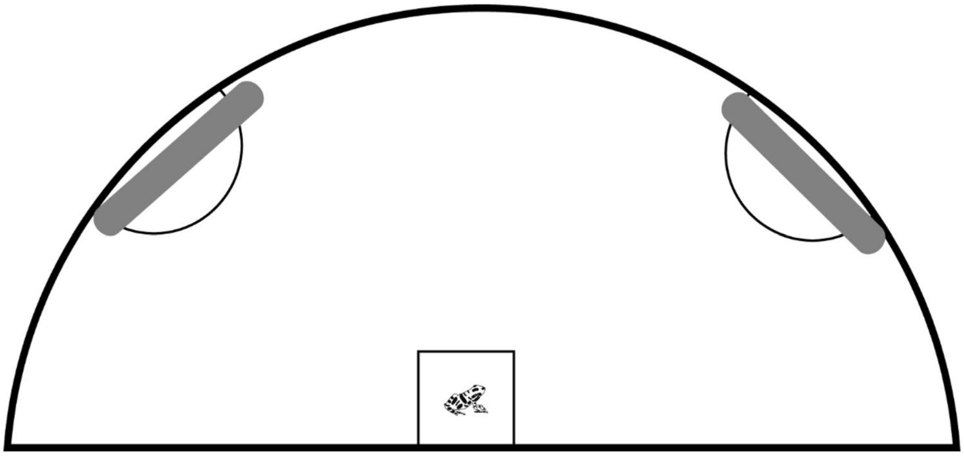

Fig. 1 Diagram of the experimental apparatus (40 cm diameter). Frogs were released in a 4 × 4 cm holding zone and allowed to approach one of two quantities of flies contained in transparent test tubes in the stimulus zones

Table 1 Results for one sample Wilcoxon signed rank tests; all $n = 6$

	Low numerosity				High numerosity			
Ratio contrast	Choice	Statistic	z	p	Choice	Statistic	z	p
0.33	1 vs. 3	10.5	– 2.10	0.03	4 vs. 12	– 7.5	– 1.33	0.18
0.50	1 vs. 2	10.5	– 2.11	0.03	4 vs. 8	– 0.5	0.00	1.0
0.67	2 vs. 3	8.5	– 1.89	0.06	8 vs. 12	– 5.0	– 0.82	0.40
0.75	3 vs. 4	1.0	– 0.27	0.78	12 vs. 16	– 5.0	– 1.05	0.29

approximately 5–6 flies in the arena to maintain motivation in the task. After 10 trials, we replaced stimulus flies to reduce their habituation.

For each individual, we calculated the proportion of times the frog chose the larger quantity out of 20 trials and recorded the latency to choose (reaction time). For latency data, we log transformed scores before analysis when latency was a response variable to reduce skew. For each discrimination, we used a one sample Wilcoxon sign rank test to determine if frogs chose the larger number of flies greater than chance. For low numerosity, we used the results of the Wilconox sign rank tests to determine the threshold of discriminability of the object tracking system.

Prey capture is generally assumed to be a spontaneous response but, because we fed frogs on trials in which they chose the larger quantity of flies, there was an opportunity for them to learn. Therefore, we used mixed effects linear models to examine whether experience (across trials and/or days) influenced the number of times the animal chose the larger quantity or latency to choose, as follows: we nested observation within day as a random intercept and random coefficient for trial, day within numerosity (low, high) as a random intercept and random coefficient for day, and numerosity within individual as a random intercept.

We used a mixed effects linear model to examine the effect of total combined set size on mean number of choices for the larger quantity with observation nested within frog as a random intercept and random coefficient for total set size. We similarly used a mixed-effects linear model to examine effect of total set size on mean latency to choose by nesting observation within numerosity as a random intercept and numerosity within individual as a random intercept and random coefficient for total set size.

To explore whether there was evidence of a tradeoff between accuracy and speed, we tested for an effect of latency on choices in first trials. We narrowed this question to first trials to eliminate variation in latency due to changes in motivation, as we found that latency increased across trials (see results). We aggregated data across first trials for individuals (resulting in sum of choices for larger quantity in first trials and mean latency for first trials) and used a general linear model.

Analyses were performed in R (version 1.1.463) and Stata (15.1).

Results

For low numerosity (1–4), *D. auratus* chose the larger quantity of flies when choosing between 1 and 3 or 1 and 2. For 2 and 3, the quantities neared discriminability ($p = 0.06$), but not for 3 and 4 (Table 1), consistent with an object tracking system with a limit around 3. When numerosity was higher (4–16), the frogs failed to choose the larger quantity of flies for any ratio (Table 1; Fig. 2). Because frogs could discriminate in some low numerosity tests, but not high numerosity tests, we asked whether combined total set size predicted performance. Indeed, total set size was associated with lower accuracy ($z = -4.7$, $p < 0.001$; Fig. 3A) and longer latency to choose ($z = 7.01$, $p < 0.001$; Fig. 3B).

We found no evidence that the probability of choosing the larger number of flies changed across days ($z = -0.91$, $p = 0.37$). We did find an increase in latency across trials within a day ($z = 2.75$, $p = 0.006$), indicating that there was a decrease in motivation with repeated testing, but no change in latency across days ($z = 1.0$, $p = 0.30$). Finally, we found no relationship between speed and accuracy for first trials in

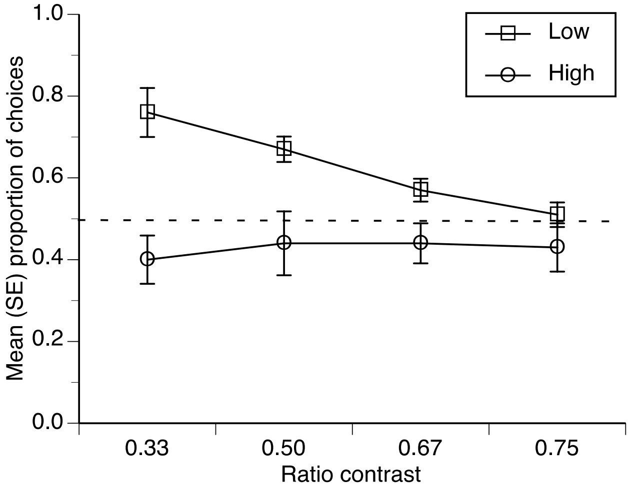

Fig. 2 Proportion of choices for the larger quantity of flies in low and high numerosity tests of different ratio contrasts. Frogs chose the larger quantity of flies when numerosity and ratio contrast were low, but they failed to do so in high numerosity tests. Dashed line indicates chance performance. Sample sizes are 6 frogs for each ratio contrast

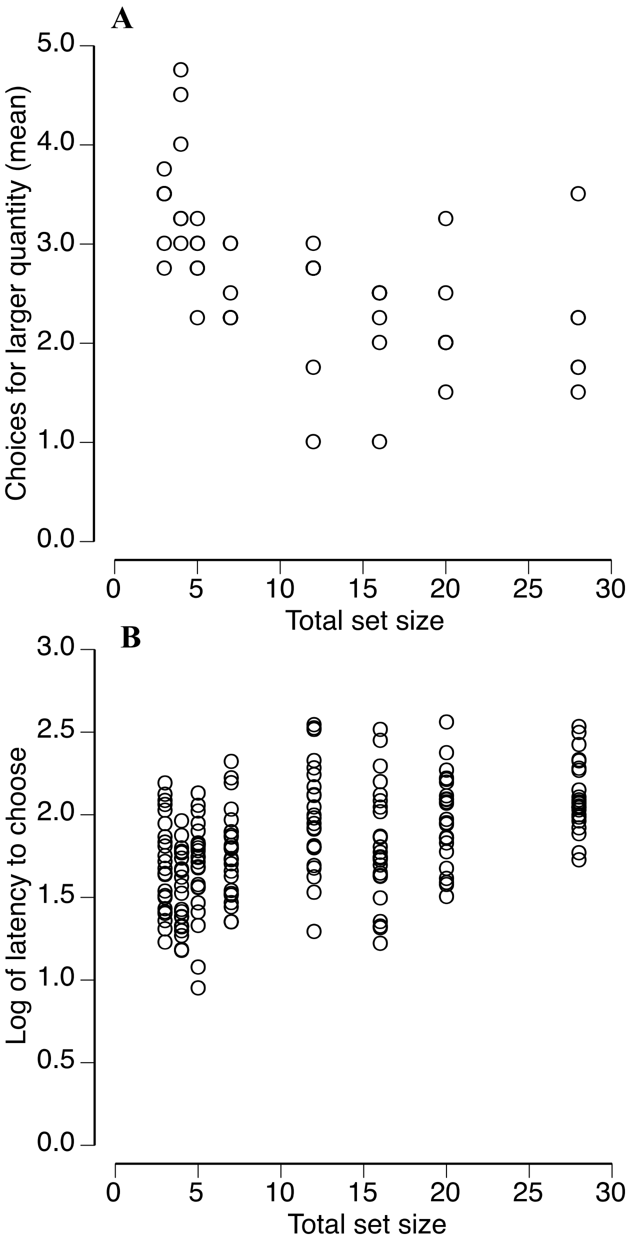

Fig. 3 Effects of combined total set size on performance in numerical discrimination tasks. We found that total set size was associated with lower accuracy ($z=-4.7$, $p<0.001$; **A**) and longer latencies to choose in individual trials ($z=7.01$, $p<0.001$; **B**). Circles represent performance of individuals within a day (**A**) or trials (**B**)

low ($z=-1.5$, $p=0.14$) or high ($z=0.15$, $p=0.88$) numerosity conditions (Fig. 4).

Discussion

Using a spontaneous discrimination task, we found that poison frogs chose the larger quantity of flies when numerosity was low, consistent with an object tracking system. The limits of discriminability appear to be around 3 objects, similar to human infants (Feigenson and Carey 2005), some fish (Stancher et al. 2013) and *Plethodon* salamanders (Uller et al. 2003). However, the poison frogs failed to discriminate in any choice when numerosity was high (4–16). These results suggest lower accuracy in high numerosity discrimination compared to the fire-bellied toad (Stancher et al. 2015) and *Plethodon* salamanders (Krusche et al. 2010).

While ratio of objects to be discriminated affects performance in many species, total combined set size can also be a factor in discriminability (Bogale et al. 2011; Garland et al. 2012). Since our frogs did not show evidence of ratio-dependent discrimination abilities, we examined whether total combined set size could explain their performance. We found that higher total set sizes were associated with lower accuracy and longer latencies. This may reflect a relationship between speed and difficulty of the task as animals may take longer to choose when discrimination is difficult, and they have lower accuracy on difficult discriminations. Alternatively, it could reflect motivation to complete the task; when choosing between large quantities of flies, there would be little cost to making an error.

Animals sometimes face a tradeoff between speed and accuracy when searching for resources. The more time an animal takes gathering information before choosing, therefore, should result in greater accuracy (e.g., Dyer and Chittka 2004; Wright et al. 2009). However, whether a speed–accuracy tradeoff is evident depends on several factors, including the difficulty of the task and the costs of inaccurate decisions (Chittka et al. 2009; Trimmer et al., 2008). In our task, there was no evidence that latency to choose varied with accuracy. Most likely, this can be explained by low cost of errors (we did not punish frogs for choosing the lower quantity of flies) and the apparent difficult of the task. Under these conditions, speed–accuracy tradeoffs may not be apparent as the best solution for the animal might be to guess (Chittka et al. 2009).

The idea that animals use two complementary systems—the object tracking system and approximate number system—has been highly influential and evidence for the two systems has been found in a range of vertebrates (Butterworth et al. 2017). However, the two systems are not always evident, nor do they always account for behavior (Hyde and Wood 2011). For example, quantity discrimination in some species of fish, birds, and primates are consistent with a single number system that span both small and large numerousness (Stancher et al. 2013; Rugani et al. 2013; Barnard et al. 2013; Al Aïn et al. 2009) and some birds are capable of object tracking for high numerosity (Garland et al. 2012). Furthermore, when sets are perceived as a unit (e.g., objects in set moving together) animals may utilize a singular vs. plural discrimination (Barner et al. 2008). In our spontaneous prey-capture task, poison frogs were most successful at

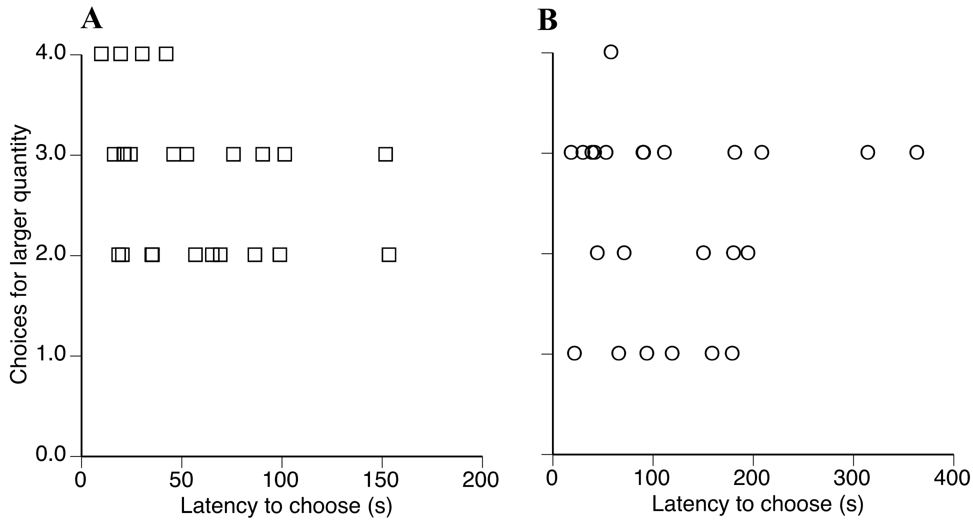

Fig. 4 Relationship between reaction time (latency to choose) and accuracy (number of choices for the larger quantity) was not evident in low ($z = -1.5$, p 0.14; **A**) or high ($z = 0.015$, $p = 0.88$; **B**) numerosity conditions. Symbols represent individual mean latencies and sums of choices for first trials

discriminating 1 vs. 2 and 1 vs. 3. While consistent with an object tracking system with a limit of about 3, an alternative interpretation is that they are discriminating singular vs. plural. In either case, past studies taken together with our results, emphasize that the ability, and strategy used, to discriminate quantities varies among species and contexts and the existence of two numerical discrimination systems may not be universal.

The apparent inability of our poison frogs to discriminate in any choice in the large numerosity trials was surprising. Based on these results, one might conclude that *D. auratus* lack an approximate number system. Alternatively, and perhaps more likely, they may possess an approximate number systems but we were simply unable to reveal it due to aspects of the conditions or context of the study. First, while our task was based on the motivation to capture prey, we did not food-deprive the animals. Thus, the failure of the frogs to discriminate in the high numerosity trials could reflect that choosing the smaller quantity of flies was associated with little cost. Second, at the time of testing, our subjects were young adults and age and/or experience may influence quantity discrimination abilities (Anderson et al. 2005; Bisazza et al. 2010). Finally, choice context can influence performance in quantity discrimination tasks. For example, guppies discriminate up to 0.83 ratio contrast when choosing shoal size (Lucon-Xiccato et al. 2017) and up to 0.75 when choosing the larger food item, but only up to 0.5 when choosing the greater number of food items (Lucon-Xiccato et al. 2015). Poison frogs are adept at a number of tasks that could be made more efficient through quantity discrimination abilities, particularly tadpole transport. Tadpole transport is associated with potentially high costs, as it requires a parent to leave territories undefended, requires time that cannot be given to other tasks (e.g., feeding), and exposes the parent to potential predators (Pašukonis et al. 2016). Thus, tracking the numbers of tadpoles, the numbers and sizes of tadpole deposition sites, and the relative distance among them, would enable poison frogs to more efficiently care for their offspring. Indeed, in the poison frog *Allobates femoralis*, males carry more tadpoles at a time when traveling to more distant deposition sites, suggesting an ability to represent quantities of tadpoles and distances (Ringler et al. 2013). Thus, future studies should examine whether the apparent quantity discrimination abilities of poison frogs are more accurate in the context of parental care compared to prey capture.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10071-021-01528-x.

Acknowledgements We thank Keith W. Sockman and James Umbanhowar for assistance with statistical analyses.

Author contributions Conceptualization SK; methodology SK and SSB; formal analysis and investigation SK; writing—original draft preparation SK; writing—review and editing SSB; funding acquisition SSB; resources SSB; supervision SSB.

Funding Not applicable.

Data availability Data are available as electronic supplementary material.

Declarations

Conflict of interest S. Khatiwada and S. S. Burmeister declare no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Consent for publication All authors consent to publication.

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