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Salamanders (*Plethodon cinereus*) go for more: rudiments of number in an amphibian

Abstract Techniques traditionally used in developmental research with infants have been widely used with nonhuman primates in the investigation of comparative cognitive abilities. Recently, researchers have shown that human infants and monkeys select the larger of two numerosities in a spontaneous forced-choice discrimination task. Here we adopt the same method to assess in a series of experiments spontaneous choice of the larger of two numerosities in a species of amphibian, red-backed salamanders (*Plethodon cinereus*). The findings indicate that salamanders "go for more," just like human babies and monkeys. This rudimentary capacity is a type of numerical discrimination that is spontaneously present in this amphibian.

Introduction

Within the last decade there has been a renewed interest in applying methods common to developmental cognitive science to a comparative agenda. In this new field of inquiry, the usefulness of the methods lies in the fact that they can be used to investigate nonverbal creatures, namely, nonhuman primates and human babies. The main reason

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for this methodological success is that one can compare cognitive abilities of species in very closely matched tasks, that is, tasks that do not require any training. One of the reasons why this is relevant is because, traditionally, comparisons of different species would require language in the case of human children and training in the case of, say, chimpanzees, making the comparison difficult to interpret. The use of nonlinguistic methods drawn from the study of cognitive development in human children provides a unique opportunity to compare cognitive abilities among species, especially because these methods assess cognitive abilities that are spontaneously present in the species (for a discussion of this point, see Uller 1996 and Hauser and Carey 1999). This is particularly useful because tracking ontogenetic and phylogenetic origins of cognition can lead us to determine what minds can spontaneously generate.

Within this framework, investigations in the general domain of number cognition have proven successful in a variety of ways. Research has shown that rhesus macaques can add and subtract small numbers of objects (Hauser et al. 1996; Sulkowski and Hauser 2001) and can determine the number of objects that bear distinct properties (Uller et al. 1997; Santos et al. 2002), and cotton-top tamarins can add small numbers of objects (Uller et al. 2001). These studies make use of the *looking time* method, a method used widely in infant cognition as a powerful tool to evaluate infants' expectations about outcomes of events. Specifically in the domain of number, infants have been shown to add and subtract small entities as early as 5 months of age (Simon et al. 1995; Uller et al. 1999; Wynn 1992). In this method, infants are presented with a certain object or objects during a familiarization or habituation phase. In the test phase, they are then shown a contrast between a consistent event and an inconsistent event. An infant's attention to these displays is measured by a computer program that keeps track of the amount of time spent looking at the displays. Generally, the results show a significant difference between looking times for an inconsistent event and a consistent event, namely, looking times are longer for the inconsistent than the consistent event. These results have been taken as evidence for infant and nonhu-

man primate capacity for small number representation, in the sense that the operations performed on these sets (1+1=2 versus 1, 1+1=2 versus 3, 1+1=2 versus a big 1, 2−1=1 versus 2, etc.) happen behind a screen, and subjects have to be able to keep track of the number in the outcome, so that this representation is stored in memory.

Another line of research within this framework makes use of search methods. Here, the main question is whether infants and nonhuman primates have an understanding of ordinality, namely, that 2>1, 3>2, 4>3, and so forth. This is a relevant question for many reasons: together with the ability to represent operational relations between small numerosities (1+1=2, 2−1=1, etc.), animals should also have an ability to understand the "order" in which these numerosities are organized, because one could argue that showing an ability to discern visually that 1+1=2 and not 1 does not necessarily entail an understanding of number, but perhaps that the numbers are just visually dissimilar. Another reason is that, in ethology, theories of optimal foraging (MacArthur and Pianka 1966; Pyke et al. 1977; Stephens and Krebs 1986) predict that animals "go for more." That is, animals evolve foraging strategies that maximize their net energy gain when foraging (i.e., the energetic profit when foraging exceeds the energetic loss during foraging).

Recently, two studies in comparative cognition have addressed this issue. First, infants' ordinal choices were measured with the use of a spontaneous forced-choice method (Feigenson et al. 2002). In this experiment, 10- and 12-month-old infants were shown two buckets containing sets that differed in the number of cookies, 1 versus 2, 2 versus 3, 3 versus 4, and 3 versus 6. The procedure was as follows. Mother sat with the baby 100 cm away from the buckets. The experimenter showed the infant the cookies being placed inside each of the containers. The baby was then released to go for the bucket of choice. Each baby was tested in one condition only and received only one trial. The overall result was that both age groups successfully chose the bucket containing the larger numerosity when 1 versus 2 and 2 versus 3 were contrasted, but not in the 3 versus 4. The researchers concluded that, to succeed in the task, infants had to recognize the ordinal relationships between the two numerosities (1 versus 2, 2 versus 3), and they had to track spontaneously the number of cookies because there was no training involved and thus no opportunity for learning. Infants therefore established the ordinal relationship between the two numerosities, choosing the container that yielded "more."

Second, the same experiment was performed using rhesus macaques (Hauser et al. 2000). Monkeys were shown two buckets in which slices of apples were placed. As in the infant case, this experiment involved no training and mimicked a natural foraging problem. The researchers manipulated conditions in which 1 versus 2, 2 versus 3, 3 versus 4, 3 versus 5, 4 versus 5, 4 versus 6, 4 versus 8, and 3 versus 8 were contrasted. Each monkey was tested in one condition only and received only one trial. The monkeys chose the container with the greater number in 1 versus 2, 2 versus 3, 3 versus 4, and 3 versus 5 slices,

but not in 4 versus 5, 4 versus 6, 4 versus 8, and 3 versus 8 cases. The researchers concluded that the results show a spontaneous numerical ability for small numerosities that closely matches that attained by young human infants. They speculated that the failure to discriminate larger numerosities was in disagreement with a larger numerosity understanding shown in training experiments with rats, pigeons, and chimps. They also speculated that the small range of numerosities present spontaneously in ontogenetic and phylogenetic development seems to coincide with "number" encoded in the structure of natural languages.

These results, and the speculations derived from them, yield interesting predictions. If monkeys and infant babies have a limited system for spontaneous representation of number, or at least a limited capacity to "go for more," then it may be part of the primate lineage only, in which case we would not expect it to occur in other species. Another prediction is that this limited system seems to correspond to the system encoded in natural languages. If only primates have this ability as an evolutionary trait, then other species would not have the same ability. The investigation of similar abilities in other species proves fruitful insofar as it will shed light onto the validity of such predictions. Here we chose to investigate the spontaneous ability to "go for more" in caudate amphibians. We report a spontaneous forced-choice discrimination task with red-backed salamanders (*Plethodon cinereus*: family Plethodontidae). Red-backed salamanders employ an optimal foraging strategy in that they forage indiscriminately between two sizes of flies (*Drosophila*) when both are low in numbers but specialize on the larger flies when the numbers of prey increase (Jaeger and Barnard 1981). This ability to change foraging tactics suggests that a salamander can assess the number of prey items within its visual field (Jaeger et al. 1982).

Methods

The following is the general method for all experiments. Particulars are given separately for each experiment.

Subjects

Adult (>32 mm snout–vent length; Sayler 1966) male and female red-backed salamanders (*Plethodon cinereus*) were collected every year in the forest near Mountain Lake Biological Station, Giles County, Virginia, United States for investigation in the Salamander Laboratory in the Department of Biology, University of Louisiana at Lafayette. We transported each salamander in a separate jar. Upon arrival in the laboratory, we placed each salamander into a separate petri dish measuring 140×15 mm lined with moist (spring water) filter paper. The salamanders were each fed 20 live fruit flies (*Drosophila virilis*) once per week from the date of arrival until testing began so that they would learn to detect visually this prey type prior to experimentation. Salamanders were generally in the laboratory for approximately 1 month before being tested. The laboratory was maintained at 19±1°C with a light:dark cycle of 12:12 h. Collection and housing procedures are the same for all experiments reported here.

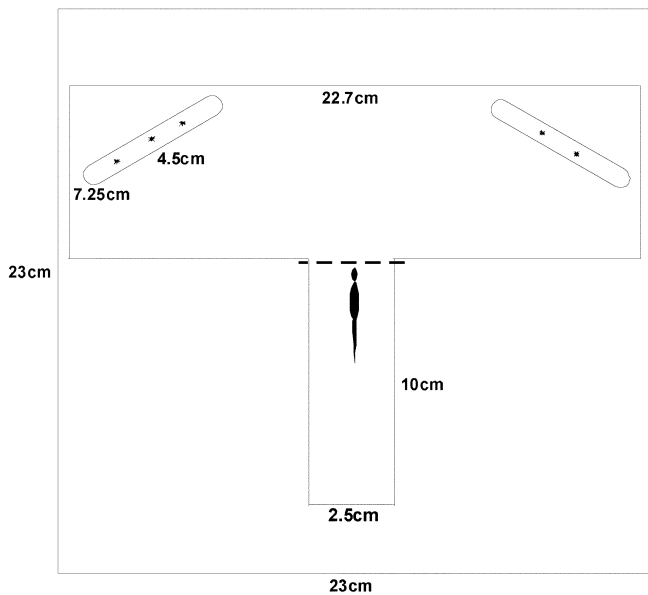record the amount of time that the salamander took to make the choice. The side of the numerosity (x, y) or (y, x) was counterbalanced across subjects.

For all experiments, we measured the salamander's choice for one numerosity (x) or the other (y). A testing session was considered over and was stopped when either (a) the salamander touched with its snout one of the tubes containing x or y flies (as if attempting to feed on the flies) or (b) the salamander did not move or moved but did not snout-touch either tube within the test trial cutoff time.

For each experiment, we used 30 animals that successfully made a choice and discarded the animals that did not move. Each animal was tested only once. Testing occurred from August 2000 to July 2002 for periods of 2–3 months for each experiment.

Some experimental sessions were recorded with a camera (Panasonic S-VHS Model AG456), placed approximately 475 cm above the testing chamber, that recorded the salamander's behavior. The testing procedure is the same for all experiments reported here, with exceptions reported as appropriate.

Experiment 1

We started our series of experiments with the discrimination of 2 versus 3 flies for a number of reasons. The primate literature has substantial evidence that monkeys discriminate between 2 and 3 apple pieces (Hauser et al. 2000), and 12-month-old human babies discriminate between 2 and 3 cookies (Feigenson et al. 2002). Second, as there is no prior evidence for this kind of discrimination in a species of amphibian, our intuitions about this ability in salamanders were poor. Third, as this is a completely new methodology, and it was unknown whether this experiment would yield interpretable data, numerosities that have yielded success in other species were taken as the appropriate candidates to start this investigation.

Subjects and procedure

Thirty adult male red-backed salamanders completed a 2 versus 3 spontaneous forced-choice discrimination test by touching with their snouts one of the two tubes within the 15-min recording cutoff time. Sixty-six animals were discarded due to no movement from the starting point of the tunnel within the 15-min trial cutoff (n=65), or movement toward a fly-baited tube but no choice within the 15-min cutoff (n=1).

Results

Data from the 30 salamanders that touched either the 2-fly tube or the 3-fly tube were coded as choice. Twenty salamanders touched the 3-fly tube and 10 touched the 2-fly tube. A binomial test revealed a significant effect (one-tailed due to the prior prediction that salamanders would prefer the 3-fly tube, alpha level=0.05): P=0.049.

The salamanders reliably chose 3 over 2. This result is original, as there are no scientific records to date showing numerical discrimination in a species of amphibian. However, because this result may be an anomaly, we proceeded

Fig. 1 Testing chamber and testing enclosures

Materials and procedure

Pretesting protocol included a phase of 3 days (72 h). On day 1, we transferred each salamander from its petri dish into a clear plastic chamber (Nunc bioassay dish) measuring 23×23×1.5 cm. This testing chamber contained a moist (spring water) sheet of paper towel on the bottom and had a transparent lid. Each salamander was then fed five live fruit flies (*D. virilis*). Because red-backed salamanders readily establish territories in such chambers by marking the towel with pheromones (Gillette et al. 2000), we placed each animal in a separate chamber.

On day 2, we placed the testing enclosure in the testing chamber (Fig. 1). The enclosure was T-shaped, constructed of transparent plastic bound by nontoxic silicon-based aquarium cement. The large end of the enclosure, which contained the prey stimuli during testing, was 22.7×7.5×1.25 cm. The narrow part of the enclosure (tunnel) measured 10×2.5×1.25 cm and served as a holding area for the salamander before the testing phase. We removed all uneaten flies from the chamber and placed on each side of the large end of the enclosure one transparent plastic tube that measured 45 mm long and 5 mm in diameter. We placed the salamander into the testing chamber and allowed it to move about.

On day 3, the last day prior to testing, the salamander was confined to the testing enclosure but still allowed to move around the entire T-shaped structure.

On day 4, the day of testing, and 2 h prior to the beginning of the session, the salamander was confined to the narrow part of the enclosure (tunnel) and was prevented from entering the large choice chamber by insertion of a piece of blue-tinted plastic measuring 3.5×1.25 cm, at the juncture of the "T".

Five minutes prior to testing, we removed the empty plastic tubes from the enclosure and replaced them with two identical tubes containing either x (e.g., 2) or y (e.g., 3) live fruit flies. The two tubes were placed 20 cm apart and equidistant from the salamander's path of approach from the tunnel. The ends of the tubes were sealed to prevent the flies from escaping and to prevent chemical cues from the flies from emanating into the enclosure. The flies could nonetheless freely move within each tube. We used live flies because salamanders will attend visually only to moving prey. A stopwatch measured 5 min so that the salamander had an opportunity to see the flies in the tubes. The testing began when we removed the blue-tinted barrier to allow the salamander to go from the tunnel into the choice chamber. When the salamander's snout entered the choice chamber, we started the stopwatch again to

to replicate this experiment. In experiment 2, we refined the procedure to make the salamanders more "enticed" to leave the tunnel.

Experiment 2

This experiment was developed with a new group of salamanders to verify that salamanders spontaneously discriminate between 2 and 3 fruit flies.

Subjects and procedure

A group of 30 adult male red-backed salamanders completed the 2 versus 3 forced-choice discrimination test by touching with their snouts one of the two tubes. Another 12 animals were discarded due to no movement from the starting point of the tunnel within the cutoff time. The procedure was exactly the same as in experiment 1, with the following differences: (a) a Dyonics model 375A narrow beam microscope lamp (175 W) was placed about 2.5 cm above the testing chamber, situated at the starting point of the tunnel. The introduction of this light into the procedure was to stimulate the salamander to leave the tunnel and move toward the fly tubes. (b) The cutoff time was reduced to 10 min because the salamanders that made a choice in experiment 1 had all done so before 10 min had elapsed.

We measured the salamander's choice for one numerosity (2) or the other (3). A testing session was considered over when either (a) the salamander touched with its snout one of the tubes containing 2 or 3 flies, or (b) the salamander did not move or moved but did not snout-touch either tube within the 10-min test trial.

Results

Data from the 30 salamanders that touched either the 2-fly tube or the 3-fly tube were coded as choice. Twenty-one salamanders touched the 3-fly tube, and 9 touched the 2-fly tube. A binomial test revealed a significant effect (one-tailed due to the prior prediction that salamanders would prefer the 3-fly tubes, alpha level=0.05): P=0.022.

The salamanders reliably chose 3 over 2 as in experiment 1, which reduces the likelihood that the salamanders randomly selected one numerosity or the other. This result represents further evidence that salamanders select the larger numerosity when it is paired with a lesser one. The positive result of this experiment also indicates that the method yields interpretable data, and that further studies should be developed to shed light on the discrimination abilities in this species of amphibian. Also, the addition of the light beam in the procedure reduced considerably the number of animals that did not make a choice.

As the animals used in experiments 1 and 2 were males, we asked if there would be sex differences for this discrimination ability. The motivations for this experiment were twofold, one theoretical and one methodological. Because female red-backed salamanders, in their natural environments, track number of eggs in their nests, females could be better than males at this discrimination task. In addition, because there were female animals available for testing, we decided to run a control experiment in which only females were tested for sex differences. In the next experiment, we chose to replicate the 2 versus 3 experiment with a new set of animals, all females.

Experiment 3

This experiment was performed with a new group of salamanders (all adult females) in the exact same forced-choice discrimination procedure as in experiment 2.

Subjects and procedure

A group of 30 adult female red-backed salamanders completed the 10-min 2 versus 3 forced-choice discrimination test by touching with their snouts one of the two tubes within the 10-min trial. Another 17 animals were discarded due to no movement from the starting point of the tunnel within the 10-min trial. The procedure used in this experiment was identical to that used in experiment 2. A testing session was considered over when either (a) the salamander touched with its snout one of the tubes containing 2 or 3 flies, or (b) the salamander did not move or moved but did not snout-touch either tube within the 10-min test trial.

Results

Data from the 30 salamanders that touched either the 2-fly tube or the 3-fly tube were coded as choice. Twenty salamanders touched the 3-fly tube and 10 touched the 2-fly tube. A binomial test revealed a significant effect (one-tailed due to the prior prediction that salamanders would prefer the 3-fly tubes, alpha level=0.05): P=0.049.

The female salamanders reliably chose 3 over 2 as did males in experiments 1 and 2. Thus, no sex difference appears to exist in the selection of the larger of two numerosities when the numerosities are 2 and 3. This result provides further evidence that salamanders select the larger numerosity when it is paired with a lesser one.

Experiment 4

The experiments so far have shown that salamanders have a capacity to discriminate 2 from 3 fruit flies in a "go for more" spontaneous forced-choice task. Evidence from rhesus monkeys (Hauser et al. 2000) and human infants (Feigenson et al. 2002) indicates that these animals also show the same discrimination ability, but not beyond a set of 4 items. Rhesus monkeys, for example, cannot discrimi-

nate between 4 and 6 apple slices because they do not select the larger numerosity when given the choice, and human infants do not succeed in selecting 4 versus 6 cookies when given two jars to choose from. These results seem to imply that there is a limit on the number of items that monkeys and young babies can discriminate, not beyond 4.

In experiment 4, we assessed the limit on the highest numerosity that a salamander will choose. We contrasted the numerosities 4 and 6 as tested in experiments with non-human primates and human infants.

Subjects and procedure

A group of 30 adult male red-backed salamanders completed the 10-min, 4 versus 6 forced-choice discrimination test by touching with their snouts one of the two tubes within the 10-min trial. Another 14 animals were discarded due to no movement from the starting point of the tunnel within the 10-min trial. The procedure used in this experiment was the same as the one used in experiment 2. A testing session was considered over when either (a) the salamander touched with its snout one of the tubes containing 4 or 6 flies, or (b) the salamander did not move or moved but did not snout-touch either tube within the 10-min test trial.

Results

Data from the 30 salamanders that touched either the 4-fly tube or the 6-fly tube were coded as choice. Sixteen salamanders touched the 6-fly tube and 14 touched the 4-fly tube. A binomial test revealed no significant effect (P=0.429, one-tailed).

The salamanders were random at selecting one numerosity over the other. This result seems to indicate that the limit on the highest numerosity chosen lies somewhere around 4. However, if the random effect were caused by the amount of movement by the flies in the tubes, it may be that the same number of flies in both tubes, four in each, were by chance moving at the time of choice, and therefore the salamanders' random selection was due to there being no difference in the amount of movement inside the tubes. We therefore replicated experiment 4.

Experiment 5

In this experiment, we replicated the discrimination between 4 and 6 with fresh fruit flies and a new group of salamanders.

Subjects and procedure

A group of 30 adult male red-backed salamanders completed the 10-min 4 versus 6 forced-choice discrimination test by touching with their snouts one of the two tubes

within the 10-min trial. Another 18 animals were discarded due to no movement from the starting point of the tunnel within the 10-min trial. The procedure used in this experiment was the same as the one used in experiment 4. A testing session was considered over when either (a) the salamander touched with its snout one of the tubes containing 4 or 6 flies, or (b) the salamander did not move or moved but did not snout-touch either tube within the 10-min test trial.

Results

Data from the 30 salamanders that touched either the 4-fly tube or the 6-fly tube were coded as choice. Twelve salamanders touched the 6-fly tube, and 18 touched the 4-fly tube. A binomial test revealed no significant effect (P=0.181, one-tailed).

The salamanders were random at selecting one numerosity over the other. This result confirms the result of experiment 4, that the limit on the highest numerosity chosen by the salamanders lies somewhere around 4.

As results in the rhesus monkey and human infant literature suggest, a limit on the highest numerosity chosen in forced-choice spontaneous discrimination conditions seems to exist. Rhesus macaques (Hauser et al. 2000) and human babies (Feigenson et al. 2002) can "go for more" only up to 3–4.

Experiment 6

In this experiment, we tested for the exact limit for salamanders of the numerosity discriminated in forced-choice spontaneous conditions. Just as in experiments with non-human primates and human infants, we contrast the numerosities 3 and 4.

Subjects and procedure

A group of 30 adult female red-backed salamanders completed the 10-min 3 versus 4 forced-choice discrimination test by touching with their snouts one of the two tubes within the 10-min trial. Another 17 animals were discarded due to no movement from the starting point of the tunnel within the 10-min trial. The procedure used in this experiment was the same as the one used in experiment 2. A testing session was considered over when either (a) the salamander touched with its snout one of the tubes containing 3 or 4 flies, or (b) the salamander did not move or moved but did not snout-touch either tube within the 10-min test trial.

Results

Data from the 30 salamanders that touched either the 3-fly tube or the 4-fly tube were coded as choice. Fifteen sala-

manders touched the 3-fly tube, and 15 touched the 4-fly tube. A binomial test revealed no significant effect ($P=0.429$, one-tailed).

The salamanders were random at selecting one numerosity over the other. This result indicates that the exact limit on the highest numerosity chosen lies at 3. Unlike nonhuman primates, and like human infants, salamanders rely on exactness of choice in such conditions up to 3.

To have a full picture of the salamanders' capacity to choose the larger numerosity under conditions of spontaneous forced choice, it remains to be shown that salamanders indeed choose between two small numerosities, namely, those contained in sets of 1, 2, and 3. We started this series of studies with the most prominent case of discrimination, 2 versus 3. Now we show that the salamanders can discriminate between 1 and 2.

Experiment 7

In this experiment, we addressed the small numerosity discrimination capacity issue to verify whether salamanders were indeed capable of choosing the highest numerosity of sets up to 3. We selected the discrimination of 1 versus 2.

Subjects and procedure

A group of 30 adult female red-backed salamanders completed the 10-min 1 versus 2 forced-choice discrimination test by touching with their snouts one of the two tubes within the 10-min trial. Another 17 animals were discarded due to no movement from the starting point of the tunnel within the 10-min trial. The procedure used in this experiment was the same as the one used in experiment 2. A testing session was considered over when either (a) the salamander touched with its snout one of the tubes containing 1 or 2 flies, or (b) the salamander did not move or moved but did not snout-touch either tube within the 10-min test trial.

Results

Data from the 30 salamanders that touched either the 1-fly tube or the 2-fly tube were coded as choice. Twenty-two salamanders touched the 2-fly tube, and 8 touched the 1-fly tube. A binomial test revealed a significant effect (one-tailed due to the prior prediction that salamanders would prefer the 2-fly tubes, alpha level=0.05): $P=0.0089$.

The salamanders reliably chose 2 over 1. This result shows that the salamanders have indeed a capacity to choose the larger numerosity in spontaneous forced-choice conditions of small sets containing 1, 2, or 3 fruit flies. These results parallel results with nonhuman primates and human infants showing comparable abilities.

Discussion

The capacity to "go for more" shown previously in non-human primates and human babies was here extended to salamanders (*Plethodon cinereus*). Salamanders were able to select the larger of two numerosities when the paired numbers were 1 versus 2 and 2 versus 3, but not 3 versus 4 and 4 versus 6. For the animals to succeed in the tasks, we infer that, at a minimum, they recognized that 2 is more than 1 and 3 is more than 2. We also infer that the animals spontaneously tracked the number of fruit flies, as there was no training involved and therefore no learning could have occurred. Finally, we conclude that the animals made a decision on which "container" to choose after spontaneously tracking the number of fruit flies. Just as in the case of nonhuman primates and human infants, salamanders "went for more" when the numerosities were smaller than 4. Therefore, we suggest that salamanders show a rudimentary ability to "go for more" that has previously only been shown in the primate lineage.

However, it is still unclear what "kind of number" is being assessed in this series of experiments. That is, it is possible that the salamanders are choosing "more" on the basis of (a) *movement* or (b) *fruit-fly stuff*. For the "amount of movement" argument, there are two different alternatives: (1) that total amount of movement of the array is driving the choice, or (2) that the tube with more flies has a higher probability of having at least one fly active than does the tube with fewer flies. We address these alternatives separately in terms of future experiments. The first experiment would test for "total amount of movement." In this experiment, salamanders would be shown a video-formatted task that mimics the original tasks described here. On one side of the monitor, a tube-like box shows 2 fruit-fly-like objects flying at speeds of 0.1 cm/100 ms and 0.5 cm/100 ms. On the other side of the monitor, a tube-like box shows 2 fruit-fly-like objects flying at a speed of 0.1 cm/100 ms. If movement determines the salamanders' choices, then they should select the tube-like box with more movement. The "probability of amount of movement" argument derives from the fact that fruit flies do not move all the time. However, if probability of movement is what is driving choice in the salamanders, then we would not expect consistent failure in 4 versus 6 conditions. Suppose that, during the 10-min choice period, 1 fly is moving in the 4-fly tube, and 2 flies are moving in the 6-fly tube, encompassing a 1 versus 2 discrimination. Salamanders succeed in a 1 versus 2 choice, but do not succeed in a 4 versus 6 choice. One way to verify the "probability of amount of movement" argument is to run a control experiment where the amount of movement of each fly is frame–frame coded. Two groups of fruit flies, one with 2 flies, the other with 3 flies, would be placed in the laboratory tubes used in these experiments. They would each be recorded for 10 min. Frame–frame coding would reveal the total and average amount of movement per numerosity. The same would be done for the other numerosities tested in these experiments, namely, 4 and 6.

Another alternative explanation of the results concerns an argument based on *fruit-fly stuff*. In this experiment, salamanders would be shown a video-formatted task in which two tube-like boxes contrast small fruit flies with fruit flies that have twice the amount of surface area. Again, if fruit-fly stuff determines the salamanders' choices, then they should select the tube-like box that contains the greater amount of fruit-fly stuff. Results of these experiments, among others, will shed more light on the salamanders' choice for "more."

The pattern of successes and failures in the present experiments, taken together with the infant and nonhuman primate results, indicates that the system underpinning this ability is limited. Just like that of nonhuman primates, salamanders' food choice discrimination capacity is reduced to 3–4 items. This is rather telling because, in food choice situations, animals in general tend to maximize total amount of food. However, something should be said about the differences among the tasks and task demands. In the infant and nonhuman primate cases, the apple slices and cookies were placed in opaque containers. In the salamander experiments, the flies were placed in transparent tubes. The difference lies in the transparency/opacity of the containment relationship – in the primate case, opaque, in the salamander case, transparent. Despite this difference, we believe the results show similar properties of the numerical system in all these creatures because of the set size limitation pointed out above. Although there are clear computational demand differences in these tasks (infant and monkey experiments require memory for object representation), for the purposes of this work the visual information present in the experimental setup was enough for the salamanders, as well as for the babies and the monkeys, to make a discrimination and "go for more."

The rudimentary numerical ability studied here is part of a precursory numerical system that can be characterized as follows:

1. This system is limited. The limit on the spontaneous number representation in monkeys and human babies seems to lie between 3 and 4.
2. This system is precise. The system precisely tracks exact small numerosities that form the representations of small sets. It does not involve estimative capacities.
3. This system is spontaneously available. The representations revealed by visual attention and reach/touch methods do not require training and thus are not learned.
4. This system is adaptively powerful. As such, these representations may be widespread in the animal kingdom.
5. This system is "entity-based." The representations are constructed on the basis of one–one correspondences. For each entity encoded, one representation is formed and stored in short-term memory.

The nature of this ability, however, remains unclear. For human infants and nonhuman primates, researchers have proposed that an object-file model would be the best candidate to account for these and other results (see, for example, Uller et al. 1999; Hauser et al. 2000). This model is one originally adopted from the literature on object-based attention (Treisman and Gelade 1980; Trick and Pylyshyn 1994). It assumes that objects are individuated according to principles of object individuation and identification and then encoded as object files maintaining one–one correspondence. For each object encountered in the world, one file is opened. A maximum of four object files can remain open simultaneously. Object files are discrete and precise. They do not rely on a capacity to estimate number. The counterpart of the object file model is an analog magnitude model that operates in concert with the former for number representation in humans and other animals and is used for larger numerosity encoding and estimation processes (see, for example, Whalen et al. 1999). Further experiments that probe the salamanders' numerical capacities will help us decide if these abilities are or are not comparable to human and nonhuman primate numerical abilities. For example, experiments that address the ratio between two numerosities will help clarify the nature of these abilities as far as a model is concerned. Contrasts between higher numbers in which the ratio is 1:2, namely, 4 versus 8, 5 versus 10, 6 versus 12, 8 versus 16, and so on, are useful in this respect. This will allow us to assess whether the salamanders "go for more" when the ratio is larger. Conversely, larger ratios that contrast a small numerosity with a rather large numerosity (e.g., 2 versus 20) will also help tease apart the salamander capacity to "go for more." That is, 2 may be an understandable/tangible numerosity within their repertoire, but 20 may be "far too much," representing not a discernable quantity, but a rather confusing one, in which case the salamander might "go for less." These are all empirical questions. In answering them, we will be on safer grounds to evaluate the kinds of numerical representations being assessed, and their nature.

The ability to "go for more" may be widespread in the animal kingdom and is observed in primates and now in salamanders. It will come as no surprise if, in the near future, research shows that there is a neural substrate for the detection of "more" the same way that there are neurons specialized for particular numbers (Nieder et al. 2002).

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