

## Discrimination of small quantities by fish (redtail splitfin, *Xenotoca eiseni*)

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**Abstract** Discrimination of quantity has been argued to rely on two non-verbal representational systems: an object file system (OFS) for representing small values ( $\leq 3-4$ ) and an analog magnitude system (AMS) for representing large magnitudes ( $>4$ ). Infants' ability to discriminate 1 versus 2, 1 versus 3, 2 versus 3, but not 1 versus 4 or 2 versus 4 seems to prove the independence of such systems. Here, we show that redtail splitfin fish (*Xenotoca eiseni*) performed relative quantity estimations preferring to approach the location previously occupied by the larger in number between two groups of conspecifics (no longer visible at test) in sets of 1 versus 2 and 2 versus 3 items, but failed at 3 versus 4 items, thus showing the same set-size limit as infants for discrimination of small quantities. However, when tested with quantities that spanned the boundary of the two systems, that is, 1 versus 4 and 2 versus 4, fish succeeded. These results thus point to either the use of continuous physical variables and/or the use of the AMS also for small numerosness in fish in this task.

**Keywords** Number cognition · Object file system · Analog magnitude system · Fish · Chick · Infant

### Introduction

Evidence suggests that in humans numerosness judgments are based on two separate systems: one for representing small numbers (the object file system, OFS) and one for representing large numerical magnitudes (the analog magnitude system, AMS). According to this hypothesis, OFS would be an object-based attention mechanism, representing each element present in a real scene as a discrete file in working memory (indeed such a system would not be dedicated to number representation per se, for number would be only implicitly represented in the files opened in the working memory). The signature of OFS is represented by a set-size limit on the number (usually  $\leq 3$  or 4) of object-files that can be simultaneously attended to and held in the working memory (Trick and Pylyshyn 1994; Ross-Sheehy et al. 2003; Le Corre and Carey 2007). The discrimination of larger sets (i.e.  $\geq 4$ ) would be supported by the AMS, which signature is represented by a ratio limit in accordance with the Weber's law (the abilities to discriminate between two numerosness would increase as the ratio between them increases, Gallistel and Gelman 1992). According to several authors, however, the AMS is probably not limited to large numbers (e.g. Cordes et al. 2001) but when operating on small numbers the imprecision related to Weber's law would become negligible making difficult to disentangle which one of the two systems is actually operating (Gallistel and Gelman 1992).

In non-human animals, the evidence for two independent numerical systems is less clear cut. On one hand, there is clear evidence for an analog magnitude system (AMS) that, when required to discriminate the larger of two sets of elements, provide approximate responses which are strikingly affected by the numerical ratio (see for a review Hyde 2011). It has also been proposed that non-human primates

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may share with humans an OFS mechanism for precisely representing quantities up to three–four. Chimpanzees show an increase in reaction times to estimate the number of dots in a large numerical range but not in a small (<3–4) numerical range (Tomonaga and Matsuzawa 2002). Similarly, rhesus monkeys appeared to be able to select the greater group of apple slices with comparisons of 1 versus 2, 2 versus 3, and 3 versus 4 but fail with 4 versus 5. Chicks in operant-conditioning tasks involving discrimination between patterns with different number of dots, with controls for continuous physical variables, show a set-size limit of 3 (Rugani et al. 2008; and see also Rugani et al. 2010).

Other experimental evidence, though, suggests continuity in the processing of small and large numbers. Rhesus monkeys (*Macaca mulatta*; Brannon and Terrace 1998; Cantlon and Brannon 2007), hamadryas baboons (*Papio hamadryas*), squirrel monkeys (*Saimiri sciureus*; Smith et al. 2003), and brown capuchin monkeys (*Cebus apella*; Judge et al. 2005) all proved able to master a numerical task involving numbers from 1 to 9, showing the same ratio effect both with small and large numbers. Continuity in processing small and large numbers seems to exist even in avian species. In domestic chicks (*Gallus gallus*), tasks involving addition and subtraction of small numerosness seem to imply abilities that extend to at least 5 items (Rugani et al. 2009). A gray parrot (*Psittacus erithacus*) named Alex was proved able to sum two sets of items (up to 6) and to use English labels to order numbers from 1 to 8 (Pepperberg 2012). Interestingly, Alex had exact number representations (Pepperberg and Carey 2012).

The more important set of data regarding the independence of the two systems comes, however, from studies on human infants that involve estimation of quantities that may stay in the opposite domains of large and small numerosness systems. Human infants seem to process small numbers via OFS (Feigenson and Carey 2005) and large numbers via AMS (Xu et al. 2005), with a gap in the processing of values at the boundary of the two domains. For instance, when 12–14-month-old infants were required to choose between two quantities of crackers, visibly placed, one cracker after the other, in one of two opaque buckets, they succeeded and chose the larger set with 1 versus 2, 1 versus 3, and 2 versus 3 but failed with 1 versus 4. Infants' failure to discriminate between numbers 1 versus 4, even though the ratio is within the limit of the AMS, coupled with their failure to track more than 3 objects, indicates that a different representation system operates over small numbers (Feigenson et al. 2002).

Intriguingly, some recent data seem to suggest a similar phenomenon exists in fish. Piffer et al. (2012) found that, like human infants, guppies succeed at comparisons between large numbers (5 vs. 10) and at comparisons between small numbers (3 vs. 4), but systematically fail at comparisons that cross the small/large boundary (3 vs. 5).

However, contrasting data have been reported by Gómez-Laplaza and Gerlai (2011) on a different species of fish. Angelfish seem to have an object-file limit of 3 (similar to that of infants) and thus fail at the comparison of 3 versus 4. However, unlike infants, they succeed when comparing larger quantities to a single individual (1 vs. 4).

There are, however, some differences between these studies and those conducted on infants. First, fish were requested to choose between groups of conspecifics of different numerosness (as a result of their spontaneous tendency to show shoaling behavior). Thus, stimuli were always fully visible to the animals making possible that continuous physical variables (area, boundary length, density, motion signals) that co-vary with number would have played a crucial role. In fact, most of the research with fish could be better characterized in terms of relative quantity judgements rather than relative number judgements. Nonetheless, the use of continuous physical variables also occurred in the aforementioned research with infants searching for different quantities of crackers (Feigenson et al. 2002), though in this case responses were based on memory rather than on direct perception. Second, the discrimination between 1 and 4 may represent a special condition because of the use of a single item (1). There is evidence that a (non-verbal) distinction between singular and plural is available to animals. In rhesus monkeys Barner et al. (2008) reported discrimination of numerical values, when singular and plural sets (1 vs. 2 and 1 vs. 5) were compared and not when two plural sets (2 vs. 3, 2 vs. 4 and 2 vs. 5) were compared.

Here, we developed a novel procedure to study numerosness discrimination in fish in an attempt to disentangle some of these contradictory results. The procedure makes use of social stimuli as attractors, as in studies of Piffer et al. (2012) and Gómez-Laplaza and Gerlai (2011). However, unlike these studies and similarly to experiments with infants, the stimuli were not visible to the fish at test. The task involved having the fish compare what they see at the moment of choice (equal numbers of conspecifics) with memory of where some extra conspecifics would be. Using the novel method, we first established a size-set limit for discrimination (using 1 vs. 2, 2 vs. 3, and 3 vs. 4 discriminations). We then tested fish for performance at discriminations between two numerosness spanning outside the boundary of the two presumed numerical systems, both with singular/plural (1 vs. 4) and plural (2 vs. 4) comparisons, as in experiments with infants.

## Materials and methods

### Subjects and rearing conditions

The Redtail Splitfin (*Xenotoca eiseni*) is a species belonging to the family Goodeidae; its natural habitat are

rivers in the highland of Mexico. Being a livebearer, *X. eiseni* is characterized by a high degree of sexual dimorphism, except for the size of sexes. Sexually adult males have a bump behind the head and their caudal fin and peduncular area color are orange. Females are more plainly colored, lacking the color on the tail, and are generally slightly larger than males. The low degree of sexual-size dimorphism compared with other livebearer families is supposed to be a result of a sexual selection related to the fact that both males and females strongly prefer mates of their own size, linked to the lack, in males, of a specialized copulatory organ and to the need for the partner to be exactly synchronized during sperm transfer. Competition for access to females is intense in males (Ritchie et al. 2007). We took advantage of this to investigate males approach to the presence of different quantities of females.

Subjects were reared in a 150-l glass aquarium, in mixed sex-groups of about 10–15 fish with a males/females ratio of 3:2. Testing fish were taken from the aquarium at the start of the experiments and reintroduced in it at the end. The ground was covered with gravel and vegetation mimicking a natural environment. The water temperature was maintained at 25 °C. Fish were fed once a day with dry food (GVG-Mix SERA®).

In all the experiments, males were used as test subjects, whereas females as target (sexual) stimuli (we selected females of the same size). The range of fish total lengths was between 2 and 3 cm.

### Apparatus

The experimental apparatus (see Fig. 1) was a plastic rectangular test tank (33 × 23 × 20 cm), whose walls were white colored. Two isolated and sealed sectors (20 × 5 × 17 cm) were located on the shorter sides, each housing one of the groups of female fish of different numerosness used as target stimuli. One half of the inner part of the two sectors was transparent so as females were fully visible from the center of the test tank to the test fish, and the other half was opaque (see Fig. 1). A fluorescent 60-W lamp lit the box, and a video-camera (SONY “Handycam DCR-SR58”) recorded fish behavior from above (80 cm) the set up.

Female was first introduced into the transparent part of the sectors (for example, two females into the sector to the right and one female into the sector to the left (in the case of a comparison 1 vs. 2); subsequently, the test male was introduced in the middle of the tank into a plastic, transparent cylinder (6.5 cm in diameter and 14.5 cm in height). At the end of this “observation phase,” which lasted 5 min, one or more of the females (depending on the experiment, in the case of 1 vs. 2 discrimination, one female) of the sector housing the larger females group were gently moved, using a transparent plastic stick (without touching



**Fig. 1** A photograph of the apparatus used for the experiments. In this case, a discrimination 1 versus 2 is shown. Note that an identical number of fish (1) is visible to the test fish at the opposite ends of the set up through the transparent sectors

the animals) into the opaque part of the sector so that they were no longer visible to the test male, leaving visible into the transparent parts of each of the two sectors exactly the same number of females (one female in each sector in this case, see Fig. 1). After a delay of 5 or 30 s, the cylinder housing the test male was gently lifted up allowing the test fish to approach one or other of the two sectors. Male fish were tested in two daily blocks of 15 trials, one half of the animals first with a delay of 5 s and then with a delay of 30 s after disappearance of part of individuals females, the other half vice versa. The interval between trials was 2 min, during which the testing fish was confined within the cylinder and located in correspondence to the opaque sectors of the tank.

Water was changed across fish, and a filter was located in the set up during the night that moved the water and mixed any olfactory cues.

The first choices of the test males when entering with its entire body one or other of the two end areas (8 cm in length) close to the two sectors (identified by the black rows drawn on the floor, see Fig. 1) were computed from videorecording. Three different observers scored the videos and scoring appeared to be fully consistent among the different observers.

The position (to the left or to the right) of the larger group of females was changed at every test trial, following a semi-random sequence (Fellows 1967) and the members of each group also changed across test fish. Moreover, we paid particular attention in choosing females of the same size and as close as possible to the size of the test male.

### Experiment I: 1 versus 2

Eight males and 3 females of *X. eiseni* were used in this experiment. One female was placed in a sector, two females in the other sector. At the end of the “observation

phase,” one of the female of the larger group was moved into the opaque part of the sector, so that at test, after a delay of 5 or 30 s, exactly the same number of females (1) were visible to the test male subject in each of the two sectors.

#### Experiment II: 2 versus 3

Eight males and 5 females of *X. eiseni* were used in this experiment. Two females were placed in a sector, three females in the other sector. At the end of the “observation phase,” one of the female of the larger group was moved into the opaque part of the sector, so that at test, after a delay of 5 or 30 s, exactly the same number of females (2) were visible to the test male subject in each of the two sectors.

#### Experiment III: 3 versus 4

Eight males and 7 females of *X. eiseni* were used in this experiment. Three females were placed in a sector, four females in the other sector. At the end of the “observation phase,” one of the female of the larger group was moved into the opaque part of the sector, so that at test, after a delay of 5 or 30 s, exactly the same number of females (3) were visible to the test male subject in each of the two sectors.

#### Experiment IV: 1 versus 4

Eight males and 5 females of *X. eiseni* were used in this experiment. One female was placed in a sector, four females in the other sector. At the end of the “observation phase,” three of the females of the bigger group were moved into the opaque part of the sector, so that at test, after a delay of 5 or 30 s, exactly the same number of females (1) were visible to the test male subject in each of the two sectors. (Note that no consistent differences in time were associated with moving multiple or single fish because of their affiliative tendencies.)

#### Experiment V: 2 versus 4

Eight males and 6 females of *X. eiseni* were used in this experiment. Two females were placed in a sector, four females in the other sector. At the end of the “observation phase,” two of the females of the bigger group were moved into the opaque part of the sector, so that at test, after a delay of 5 or 30 s, exactly the same number of females (2) were visible to the test male subject in each of the two sectors.

From the videorecordings, the first choices made by the test fish in either of the two end areas of the tank, close to one or other of the two groups, were computed.

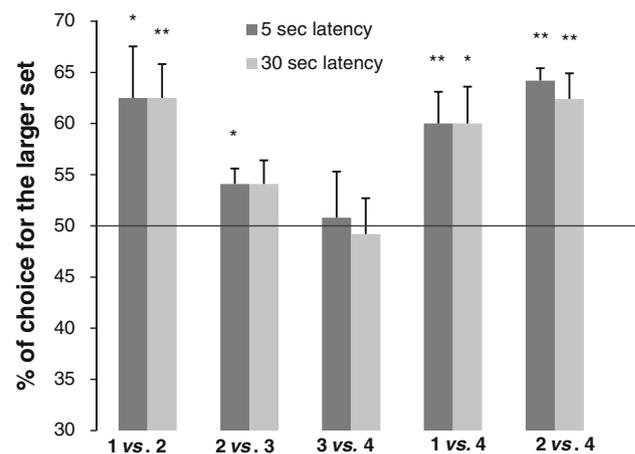
Percentages of choices for the sector with the group with large numerosness were computed for each fish (for each of the two latency times) and entered an analysis of variance with Type of test (e.g. 1 vs. 2, 2 vs. 3, 3 vs. 4...) and latency times (time elapsed after disappearance of some of the female fish, i.e. 5 s or 30 s). One-sample *t* tests (two-tailed) were then used to estimate significant departures from chance level (50 %) in percentages of choices.

## Results and discussion

We first considered the series of numerosness discrimination (Exps. I to III) to establish the set-size limit in this species (Fig. 2). An ANOVA was performed with Type of test (1 vs. 2, 2 vs. 3, 3 vs. 4) as a between subjects factor and latency (5, 30 s) as a within subjects factor. The ANOVA revealed only a significant main effect of the Type of test [ $F(2,21) = 5.235$   $p = 0.014$ ; Latency:  $F(1,21) = 0.045$   $p = 0.834$ ; Type of test  $\times$  Latency:  $F(2,21) = 0.045$   $p = 0.956$ ]. Separate comparisons revealed significant differences between (1 vs. 2) and (2 vs. 3) and (1 vs. 2) and (3 vs. 4) conditions [respectively,  $t(14) = 2.132$   $p = 0.051$  and  $t(14) = 2.707$   $p = 0.017$ ], but not between (2 vs. 3) and (3 vs. 4) conditions [ $t(14) = 1.330$   $p = 0.205$ ].

One-sample two-tailed *t* tests revealed significant preferences for the larger numerosness in the 1 versus 2 and 2 versus 3 conditions [respectively,  $t(7) = 3.416$   $p = 0.011$  and  $t(7) = 3.035$   $p = 0.019$ ], but not in the 3 versus 4 condition [ $t(7) = 0.0001$ ]. Fish thus showed the same set-size limit shown by infants (see Introduction).

The ANOVA performed for the 1 versus 4 and 2 versus 4 test conditions did not reveal any statistically significant



**Fig. 2** Percentages of choice for the larger set in discriminations with different numerosness (group means with SEM are shown). Significant departures from chance level (50 %) are shown by asterisks (two-tailed one-sample *t* tests, \*\* $p < 0.01$ , \* $p < 0.05$ )

effect [Type of test:  $F(1,14) = 0.009$   $p = 0.207$ ; Latency:  $F(1,14) = 0.08$   $p = 0.781$ ; interaction Type of test  $\times$  Latency:  $F(1,14) = 0.08$   $p = 0.781$ ).

One-sample two-tailed *t* tests revealed significant preferences for the larger numerosness in both the 1 versus 4 and 2 versus 4 conditions [respectively,  $t(7) = 4.583$   $p = 0.003$  and  $t(7) = 10.583$   $p < 0.0001$ ]. Thus, unlike human infants, fish appeared able to discriminate between numerosness that cross the divide between the small and the large numerosness systems.

## General discussion

Fish were tested with a novel procedure that involves comparison of what they could see at the moment of choice (i.e. equal number of females) with memory of where the extra females were located during initial stimuli presentation. Thus, other than a test for quantity discrimination, the procedure was a test of how much information can be kept in memory. The results showed that fish performed very well in sets of 1 versus 2 and 2 versus 3 items, but failed at 3 versus 4 items, thus showing the same set-size limit as infants for discrimination of small quantities in similar tests (Feigenson et al. 2002). However, unlike infants tested in the crackers discrimination test, fish succeeded when tested with quantities that spanned the boundary of the two systems, that is, 1 versus 4 and 2 versus 4.

Interestingly, fish performed as well with a 5-s delay as with a 30-s delay, revealing surprisingly good short-term memory of quantities. It is important to stress that fish exhibited their behavior in the absence of any specific learning associated with any real reward, and thus what they showed appears to be a truly core ability, based on the ethology/ecology of the species.

There are different views in the literature concerning the non-symbolic representational systems that would be available for relative number/quantity discrimination (see for a review Hyde 2011). One view is that the OFS is specialized to represent small numbers and the AMS to represent large numbers. In contrast to the idea that numerical range determines when each system will be engaged, several authors argued that the AMS operates over both large and small numbers (Meck and Church 1983; Brannon and Terrace 1998; Cantlon and Brannon 2006). It should be noted, however, that the role of continuous stimulus variables has not been always ruled out in these studies, both in infants and animals studies. Thus, rather than talking of relative number discrimination, it seems better to use the term relative quantity judgements in those cases where area, boundaries length, or (as in this case and other fish experiments) amount of movement could co-vary with number, thus making it unclear,

whether number is the controlling dimension in the behavior of animals. Indeed, research on human infants does not equate the use of OFS with true use of number. Feigenson et al. (2002) argued that in crackers test, infants “relied on object-file representations, comparing mental models via total volume or surface area rather than via one-to-one correspondence between object-files” (p. 150).

Unlike 12–14-month-old infants (Feigenson et al. 2002) and monkeys (Hauser et al. 2000; Barner et al. 2008) that failed to discriminate between 1 versus 4 pieces of food; fish could distinguish between collections of 1 versus 4 and 2 versus 4 groups of conspecifics. Thus, irrespective of whether the fish discrimination was based on quantity or number (as noted above the same ambiguity is apparent in studies with human infants), our results suggest a continuity in processing small and large numbers. Our results are also at odds with those reported by Piffer et al. (2012) in guppies but in agreement with those reported by Gómez-Laplaza and Gerlai (2011) in angelfish, both with respect to the set-size limit (3 in both redtail splitfins and angelfish) and with respect to the ability to discriminate between two numerosness that cross the boundaries between the two systems (which again seems to be present in both redtail splitfins and angelfish but not in guppies).

The different performance of guppies could not be explained by motivational factors, related to the kind of attractors used, since we used social attractors as well. Interestingly, recent evidence suggests similar abilities to discriminate numerosness that cross the boundaries of the small and large numerosity systems in chicks as well, using both social and non-social (food) attractors (Rugani et al. 2012). Interestingly, the method used in chicks allowed for control of continuous physical variables, thus providing strong evidence for continuity of the use of the AMS system.

Of course, the fact that the AMS in some cases could process small numbers is not evidence that an OFS does not exist in non-human animals. Caution, however, seems necessary concerning evidence in fish, and for the role of continuous physical variables has not been properly addressed in most of the studies (e.g. Agrillo et al. 2012). It can be argued that in our study at test, the same amount of physical stimulation was available. Yet, the possibility that fish would maintain in memory continuous physical variables available during the exposure phase cannot be ruled out (in spite of the relatively long delay period). As already mentioned, infants do encode continuous stimulus variables in crackers studies (Feigenson et al. 2002). Moreover, recent evidence has shown that continuous variables are computed by animals for sets of objects that are not present at the same time and that are no longer visible at the time of choice, also for large numerosness (Rugani et al. 2011). What is probably urgent is to understand more precisely what is the role of continuous physical variables in

numerousness estimation in the different species and what conditions would favor the engagement of either OFS or AMS system.

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