

## Quantity Discrimination by Zebrafish (*Danio rerio*)

Davide Potrich and Valeria Anna Sovrano  
University of Trento

Gionata Stancher  
University of Trento and Fondazione Museo Civico  
di Rovereto, Rovereto, Italy

Giorgio Vallortigara  
University of Trento

Discrimination of quantity (magnitude) was investigated in zebrafish (*Danio rerio*). Male zebrafish chose to approach the location previously occupied by the larger in number between 2 groups of female conspecifics (no longer visible at test) in sets of 1 versus 2 items, and 2 versus 3 items, but failed at 3 versus 4 items; similarly, when tested with larger numbers, zebrafish succeeded with 2 versus 4, 4 versus 6, and 4 versus 8 items, but failed with 6 versus 8 items. The results suggest that zebrafish rely on an approximate number system to discriminate memorized sets of conspecifics of different magnitudes, the degree of precision in recall being mainly dependent on the ratio between the sets to be discriminated.

*Keywords:* quantity discrimination, number, numerical cognition, approximate number system, zebrafish

It has been suggested that nonsymbolic discrimination of numerical magnitudes (quantities) is based on an approximate number system (ANS). The ANS provides approximate estimates of the numerical magnitude, or numerosity, of a set of objects (for reviews, see Butterworth, 1999; Hyde, 2011; Nieder & Dehaene, 2009). The imprecision of ANS increases as a function of numerical magnitudes, and, as a result, discrimination of any two numerical magnitudes depends on the ratio between them, following Weber's Law (Gallistel, 1990). There is now evidence for the existence of ANS in a variety of nonhuman species (for a review, see Vallortigara, 2014), and its neural bases have begun to be investigated in both primates (Nieder, 2013; Roitman, Brannon, & Platt, 2007; Viswanathan & Nieder, 2013, 2015) and birds (Ditz & Nieder, 2015). In humans, however, an ability to simultaneously represent and track objects through parallel individuation on the basis of working memory has been described. This system is dubbed *object file system* (OFS) because, unlike the ANS, which

encodes one mental symbol to summarize the set, the OFS encodes a distinct mental/neural symbol for each item (see Carey, 2009, for a review).

Representations through parallel individuation would afford more fine-grained numerical discriminations than those of the ANS, but it is limited to only a few items (usually about three). It has been found, for example, that 12- to 14-month-old infants are able to choose the larger set with one versus two, one versus three, and two versus three elements, but fail in the one versus four, or two versus four, comparison in quantity discrimination tasks (Feigenson, Carey, & Hauser, 2002). This suggests an impairment in numerical discrimination when the items to be discriminated may be represented in different systems, that is, the small (parallel individuation system; e.g., two) and the large (ANS, e.g., four) numerical systems. Conflicting results have, however, been recently reported regarding the existence of the OFS in human infants (see, e.g., Cordes & Brannon, 2009; Coubart, Izard, Spelke, Marie, & Streri, 2014).

Research using phylogenetically distant species may provide insights about the origins and the mechanisms for quantity discrimination.

It should be noted that for many mammals and birds, and certainly for nearly all primate species tested, the ANS has been shown to account for the observed performance patterns (e.g., Beran, 2007; Cantlon & Brannon, 2006; Jones & Brannon, 2012; Rugani, Vallortigara, & Regolin, 2014; and see reviews in Brannon, 2006, and Brannon & Merritt, 2011), whereas the OFS has only received limited support (e.g., Hauser, Carey, & Hauser, 2000). Surprisingly, however, some evidence for a two-system mechanism has been reported recently for fish. Piffer, Agrillo, and Hyde (2012) confined *Poecilia reticulata* fish singly in the center of a tank, where, on the two opposite sides, two numerically different groups of conspecifics were located. After an observation period, the test fish were left free to move toward one or the other of the two groups, choosing the larger one. The results showed

---

This article was published Online First September 7, 2015.

Davide Potrich, Center for Mind/Brain Sciences, University of Trento; Valeria Anna Sovrano, Center for Mind/Brain Sciences and Department of Psychology and Cognitive Sciences, University of Trento; Gionata Stancher, Center for Mind/Brain Sciences, University of Trento, and Fondazione Museo Civico di Rovereto, Rovereto, Italy; Giorgio Vallortigara, Center for Mind/Brain Sciences, and Department of Psychology and Cognitive Sciences, University of Trento.

This study was supported by a research grant from by the Cassa di Risparmio of Trento e Rovereto. We thank Elena Baruzzo and Corinna Manzardo for their help with the experiments, and the Fondazione Museo Civico of Rovereto for the facilities made available in the field station of "SperimentArea."

Correspondence concerning this article should be addressed to Davide Potrich or Giorgio Vallortigara, Center for Mind/Brain Sciences, University of Trento, Piazza della Manifattura 1, 38068 Rovereto (Trento), Italy. E-mail: [davide.potrich@unitn.it](mailto:davide.potrich@unitn.it) or [giorgio.vallortigara@unitn.it](mailto:giorgio.vallortigara@unitn.it)

that, like human infants, fish were able to discriminate between two large numerosities (more than three) as well as two small numerosities (less than three), but they failed in the comparison between two groups with different numerosities that crossed the boundary of the two systems (e.g., three vs. five). However, these results were not confirmed in a different species of fish (angel fish, *Pterophyllum scalare*) by Gómez-Laplaza and Gerlai (2011). These authors found that angel fish were not able to discriminate between three versus four items, thus apparently showing a set size limit of about three elements in accordance with the existence of an OFS. However, unlike 12-month-old infants, they succeeded when they had to compare groups with two numerosities that belonged, respectively, one to the large system and one to the small system (such as, e.g., a discrimination between one vs. four elements). This suggests that failure to discriminate three versus four items would not mark the transition between a small and a large number system, but would simply reflect a limit ratio that, in accordance with Weber's law, would prove impossible to discriminate by fish using the ANS.

In all these studies, the elements to be discriminated (conspecifics) were fully visible to the test animals, making the role of continuous physical variables that covary with number (area, contour length, amount of motion, etc.) very prominent. Stancher, Sovrano, Potrich, and Vallortigara (2013) developed a novel procedure that made use of social stimuli as attractors, as in studies of Piffer et al. (2012) and Gómez-Laplaza and Gerlai (2011), that were, however, not visible to the fish during the test, similar to experiments with infants. In this task, fish should compare what they see at the moment of choice (an equal number of conspecifics in two different locations) with memory of the location previously occupied by the larger in number between two groups of conspecifics.

Clearly, this did not rule out the possible use of continuous variables in guiding fish decisions; however, decisions should be based on memory rather than on direct perception of continuous physical variables, thus making the new procedure more similar to that used in human infants to support the existence of the OFS (e.g., Feigenson et al., 2002). The results with redbtail splitfin fish (*Xenotoca eiseni*) showed that they chose the location previously occupied by the larger in number between two groups of conspecifics in sets of one versus two items, and two versus three items, but failed at three versus four items, showing the same set-size limit as infants and other species of fish for discrimination of small quantities. However, unlike infants, fish succeeded when they were tested for performance at discriminations between two numerosities that spanned outside the boundary of the two presumed numerical systems (one vs. four and two vs. four). This, again, would suggest that the set-size limit at around three items would reflect a ratio limit (i.e., discrimination of three vs. four) rather than the signature of a different system (the OFS). Unfortunately, larger numerosities with the same ratio of 3:4 (e.g., six vs. eight), or with an easier ratio such as 2:3 (e.g., four vs. six), were not tested.

In the present article, we used the same method but in a different fish species, namely, zebrafish (*Danio rerio* [*D. rerio*]), and compared discriminations of one versus two, two versus three, three versus four, two versus four, four versus six, four versus eight, and six versus eight. Besides providing an extension to the range of number ratios and fish species studied, testing of zebrafish appears

important because, given its widespread use in the field of genomics, it may provide a useful model organism linking research from behavior and genetics to the study of quantity representations.

## Experiment 1

### Method

**Subjects and rearing conditions.** The zebrafish (*D. rerio*) is a species belonging to the family Cyprinidae. It is fish that lives in shoals, is very active, and is constantly in movement. Zebrafish feed on insect larvae, small crustaceans, and worms.

*D. rerio* shows only a small degree of sexual dimorphism. Competition for access to females is intense in males; we took advantage of this to investigate males approach to the presence of different quantities of females.

Subjects were reared in a 20-L plastic aquarium (23 × 38 × 25 cm) in isolated sex groups, in order to make the discrimination of sex easy. The ground was covered with gravel and vegetation mimicking a natural environment. The water temperature was maintained at 25 °C and each aquarium contained a pump and filter system (Micro Jet Filter MCF 40). The aquariums were illuminated by an 18-W white fluorescent lamp following a light cycle of 12 hr. Fish were fed once a day with dry food (GVG). In all the experiments, males were used as test subjects, whereas females were used as target (sexual) stimuli (we selected females of the same size). The range of fish total lengths was between 4 cm and 5 cm for both males and females.

**Apparatus.** The experimental apparatus (see Figure 1) was located in a darkened room and consisted of a plastic rectangular test tank (33 × 23 × 20 cm) with white-colored walls. Two

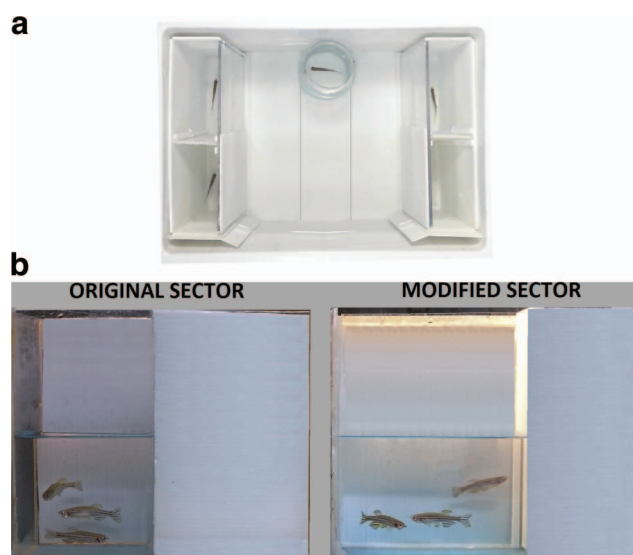


Figure 1. (a) A photograph of the apparatus used for the experiments. In this case, Discrimination 1 versus 2 is shown. Note that an identical number of fish ( $n = 1$ ) is visible to the test fish at the opposite ends of the setup through the transparent sectors. (b) Details of the sector parts (transparent and opaque), visible from the experimental fish, in the original (Experiment 1) and modified (Experiment 2) apparatus. See the online article for the color version of this figure.

isolated sectors ( $20 \times 5 \times 17$  cm) were located on the shorter sides, each housing one of the groups of female fish of different numerical size used as target stimuli. One part of the two sectors was transparent (9.5 cm) so that females were fully visible from the center of the test tank to the test fish; the other part was opaque (10.5 cm; see Figure 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 setup.

**Procedure.** Female were first introduced into the transparent part of the sectors (e.g., in the case of a comparison of one vs. two, two females were introduced into the sector to the right, and one female into the sector to the left); subsequently, the test male was introduced in the middle of the tank in a transparent plastic cylinder (6.5 cm in diameter and 14.5 cm in height). At the end of this "observation phase," one or more of the females, depending on the discrimination to be carried out (in the example of one vs. two discrimination, one female), of the sector housing the larger females group were gently moved, using a transparent plastic stick (without touching the animals), into the opaque part of the sector so that they were no longer visible to the test male, leaving exactly the same number of females visible in the transparent parts of each of the two sectors (one female in each sector in the example; see Figure 1, a and b). After a delay of 5 s or 30 s, the cylinder housing the test male was gently lifted up, allowing the test fish to approach one or the 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 some of the females, and vice versa for the other half. The interval between trials was 2 min.

The first choices of the test males, when entering 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 Figure 1a) with its entire body, were computed from the video recording.

The position (to the left or to the right) of the larger group of females was changed at every test trial, following a semirandom sequence (Fellows, 1967). We paid particular attention to choosing females of the same size and as close as possible to the size of the test male.

**Discrimination 1 versus 2.** Eight males (experimental subjects) and three females (sexual attractors) of *D. rerio* were used in this experiment. One female was placed in one sector, and two females in the other sector. At the end of the observation phase, one of the females of the larger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 1$ ) were visible to the test male subject in each of the two sectors.

**Discrimination 2 versus 3.** Eight males and five females of *D. rerio* were used in this experiment. Two females were placed in one sector, and three females in the other sector. At the end of the observation phase, one of the females of the larger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 2$ ) were visible to the test male subject in each of the two sectors.

**Discrimination 3 versus 4.** Eight males and seven females of *D. rerio* were used in this experiment. Three females were placed in one sector, and four females in the other sector. At the end of the observation phase, one of the females of the larger group was moved into the opaque part of the sector, so that at test, after a

delay of 5 s or 30 s, exactly the same number of females ( $n = 3$ ) were visible to the test male subject in each of the two sectors.

**Discrimination 2 versus 4.** Eight males and six females of *D. rerio* were used in this experiment. Two females were placed in one sector, and four females in the other sector. At the end of the observation phase, two of the females of the bigger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 2$ ) were visible to the test male subject in each of the two sectors.

**Discrimination 4 versus 6.** Eight males and 10 females of *D. rerio* were used in this experiment. Four females were placed in one sector, and six females in the other sector. At the end of the observation phase, two of the females of the bigger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 4$ ) were visible to the test male subject in each of the two sectors.

**Data analysis.** The first choice made by the test fish in either of the two end areas of the tank, close to one or the other of the two groups, was computed from the video recordings. Percentages of choices for the sector with the group with large numerosities were computed for each fish (for each of the two latency times) and entered an analysis of variance with type of test (e.g., one vs. two, two vs. three, three vs. four, and so on) and latency (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 for each type of test.

To estimate the effect sizes, we used partial eta-squared ( $\eta_p^2$ ) as the index for ANOVA, and Cohen's *d* as the index for *t* tests. Cohen's kappa ( $\kappa$ ) was used to evaluate the interobserver reliability based on 20% of the trials, which revealed a strong interobserver agreement ( $\kappa = 0.99$ ).

## Results

An ANOVA was performed with Discrimination (one vs. two, two vs. three, three vs. four, two vs. four, four vs. six) as a between-subjects factor, and Latency (5 s, 30 s) as a within-subjects factor. The ANOVA revealed only a significant main effect of Discrimination,  $F(4, 35) = 4.501, p = .005, \eta_p^2 = 0.34$ . There were no other statistically significant effects (Latency,  $F[1, 35] = 0.268, p = .608$ ; Discrimination  $\times$  Latency,  $F[4, 35] = 0.489, p = .744$ ). The results are shown in Figure 2.

The Least Significant Difference (LSD) post hoc test revealed significant differences between Conditions 1 versus 2 and 3 versus 4 ( $p = .001$ , Cohen's  $d = 1.53$ ), Conditions 2 versus 3 and 3 versus 4 ( $p = .012$ , Cohen's  $d = 1.21$ ), but not between Conditions 1 versus 2 and 2 versus 3 ( $p = .357$ ), or Conditions 2 versus 4 and 4 versus 6 ( $p = .156$ ). There were other significant differences between Conditions 1 versus 2 and 4 versus 6 ( $p = .003$ , Cohen's  $d = 1.70$ ), and Conditions 2 versus 3 and 4 versus 6 ( $p = .031$ , Cohen's  $d = 1.33$ ).

One-sample two-tailed *t* tests revealed significant choices for the larger numerosity in Discriminations 1 versus 2,  $t(7) = 5.974, p = .001$ , 2 versus 3,  $t(7) = 5.916, p = .001$ , and 2 versus 4,  $t(7) = 2.816, p = .026$ , but not Discriminations 3 versus 4,  $t(7) = 0.007, p = .995$ , and 4 versus 6,  $t(7) = 0.552, p = .598$ .

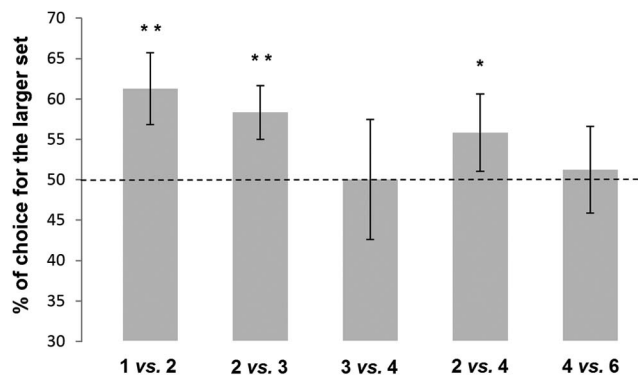


Figure 2. The graph shows the percentages of choice for the larger set in discriminations with different numerosness (group means with 95% confidence intervals are shown). Significant departures from chance level (50%) are shown by asterisks (two-tailed one-sample *t* tests; \*  $p < .05$ , \*\*  $p < .01$ ).

Discussion

The results apparently confirmed those obtained with redbtail splitfin (Stancher et al., 2013) and angel fish (Gómez-Laplaza & Gerlai, 2011), with a drop-off of discrimination with a ratio of 3:4, which seemed to occur irrespective of the largeness of numerical magnitudes, because significant discrimination was apparent with two versus four items (i.e., with a 1:2 ratio, and one number set exceeding any alleged small number system). One problem with this interpretation, however, is that zebrafish failed the four-versus-six discrimination, which has the same ratio (2:3) as the two-versus-three discrimination that zebrafish succeeded to perform. We wondered whether this unusual outcome, which would be incompatible with either the ANS and OFS, can be accounted for by a simple hypothesis, namely, that when the number of females is very large, their visibility by the test fish would be difficult in the small tank because of mutual visual occlusion among females. This hypothesis was tested in Experiment 2.

Experiment 2

Four discriminations were investigated, two aimed at verifying the lack of discrimination with a 3:4 ratio in the range of both small (three vs. four) and large (six vs. eight) numerosity, and two aimed at verifying the presence of discrimination with higher ratios (1:2 and 2:3), even with large numerosity (four vs. eight, four vs. six).

Method

**Subjects, apparatus, and rearing conditions.** Rearing conditions were the same as in Experiment 1. Naïve zebrafish were used. A slightly different version of the apparatus was used, in which only the sizes of the parts of the two sectors housing the females were changed, the transparent part now being 13 cm and the opaque part being 7 cm (see Figure 1). This change was made in order to accommodate a greater number of females in the transparent sector, allowing best visibility of them by the test fish.

Procedure.

**Discrimination 3 versus 4.** Six males and seven females of *D. rerio* were used in this experiment. Three females were placed

in one sector, and four females in the other sector. At the end of the observation phase, one of the females of the larger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 3$ ) were visible to the test male subject in each of the two sectors.

**Discrimination 4 versus 6.** Eight males and 10 females of *D. rerio* were used in this experiment. Four females were placed in one sector, and six females in the other sector. At the end of the observation phase, two of the females of the bigger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 4$ ) were visible to the test male subject in each of the two sectors.

**Discrimination 4 versus 8.** Eight males and 12 females of *D. rerio* were used in this experiment. Four females were placed in one sector, and eight females in the other sector. At the end of the observation phase, four of the females of the bigger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 4$ ) were visible to the test male subject in each of the two sectors.

**Discrimination 6 versus 8.** Seven males and 14 females of *D. rerio* were used in this experiment. Six females were placed in one sector, and eight females in the other sector. At the end of the observation phase, two of the females of the bigger group was moved into the opaque part of the sector, so that at test, after a delay of 5 s or 30 s, exactly the same number of females ( $n = 6$ ) were visible to the test male subject in each of the two sectors.

**Data analysis.** Data were analyzed in the same way as in Experiment 1.

Results

Results are shown in Figure 3. The ANOVA revealed only a significant main effect of Discrimination,  $F(3, 25) = 6.142$ ,  $p = .003$ ,  $\eta_p^2 = 0.424$ . Latency,  $F(1, 25) = 0.073$ ,  $p = .790$ , and Discrimination  $\times$  Latency,  $F(3, 25) = 1.170$ ,  $p = .341$ , were not significant.

The LSD post hoc test revealed significant differences between Conditions 3 versus 4 and 4 versus 6 ( $p = .003$ , Cohen's  $d = 1.60$ ), Conditions 3 versus 4 and 4 versus 8 ( $p = .001$ , Cohen's

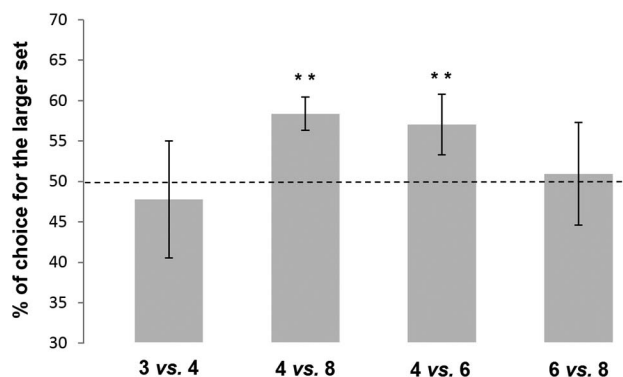


Figure 3. The graph shows the percentages of choice for the larger set in discriminations with different numerosness (group means with 95% confidence intervals are shown). Significant departures from chance level (50%) are shown by asterisks (two-tailed one-sample *t* tests; \*  $p < .05$ , \*\*  $p < .01$ ).

$d = 2.05$ ), but not between Conditions 3 versus 4 and 6 versus 8 ( $p = .294$ ). There were other significant differences between Conditions 4 versus 8 and 6 versus 8 ( $p = .013$ , Cohen's  $d = 1.44$ ), and Conditions 4 versus 6 and 6 versus 8 ( $p = .035$ , Cohen's  $d = 1.05$ ).

One sample two-tailed  $t$  tests revealed significant choices for the larger numerosity in discriminations of four versus six,  $t(7) = 4.470$ ,  $p = .003$ , and four versus eight,  $t(7) = 9.510$ ,  $p \leq .0001$ , but not three versus four,  $t(5) = -0.791$ ,  $p = .465$ , and six versus eight,  $t(6) = 0.367$ ,  $p = .726$ .

## Discussion

Results using a larger tank, which prevented too much overlap in the fish so that all individuals could be seen clearly, showed that quantity discrimination fitted nicely with the prediction from the ANS mechanism, that is, the ratio between the sets to be discriminated was the main determinant of fish performance.

## General Discussion

The results reported here with zebrafish appear to be in agreement with the idea of a single mechanism for dealing with approximate estimation of the magnitude of numerosity of sets of social objects, both small and large, that is, the ANS or some equivalent. Results of Experiment 2 in particular revealed that when visibility of relatively large numbers of conspecifics is guaranteed via a large tank in the exposure phase, zebrafish could deal with discrimination of large numbers, and the degree of imprecision depends mainly on the ratio of the numbers, not the fact that the two items are above or below a threshold of about three elements.

It should be noted, however, that although most of the evidence available suggest continuity in the processing of small and large numerosity (e.g., nonhuman primates, see Brannon & Terrace, 1998, Cantlon & Brannon, 2007, Judge, Evans, & Vyas, 2005, and Smith, Piel, & Candland, 2003; birds, see Rugani, Fontanari, Simoni, Regolin, & Vallortigara (2009); Rugani, Regolin & Vallortigara, (2011); Rugani, Cavazzana, Vallortigara, & Regolin (2013); fish, see Gómez-Laplaza & Gerlai, 2011), there are also reports suggesting that the existence of some equivalent of an OFS with a set-size limit at around three to four items (e.g., chimpanzees, see Tomonaga & Matsuzawa, 2002; birds, see Rugani, Regolin, & Vallortigara, 2008, and Rugani, Regolin, & Vallortigara 2010; honeybees, see Dacke & Srinivasan, 2008). It is also important to emphasize that in at least one case, a nonhuman species, an African grey parrot (*Psittacus erithacus*) named Alex, has shown an ability to use exact, and not approximate, number representations (Pepperberg, 2012; Pepperberg & Carey, 2012).

There are also different views concerning the role of the two systems (for a review, see Hyde, 2011). According to one view, the OFS would represent small numbers, and the ANS would represent large numbers. According to another, the ANS operates over both large and small numbers, and OFS only over small numbers (Brannon & Terrace, 1998; Cantlon & Brannon, 2006; Meck & Church, 1983). It is likely that differences in task demands may explain some of the discrepancy in the literature. For instance, it has been suggested that stimuli presentation and consequent attentional mechanisms rather than the numerosity per se can elicit processing by either system: When attention is focused on a single

item of a set, the representation would be supported by the OFS, whereas when the attention would be focused on the overall set (as in the case of the present experiments), the representation would be supported by the ANS (Hyde, 2011; Rugani, Cavazzana, Vallortigara, & Regolin, 2013).

It should also be stressed that although fish in these experiments make their judgments on the basis of memory, rather than by direct sensory stimulation with different number of conspecifics, the issue of the control of continuous physical variables remains unaddressed (in principle, fish could have memorized continuous physical variables, as in most animals studies, rather than number per se). Thus, quantity discrimination rather than number discrimination appears to be the most appropriate labeling for these sorts of studies.

We believe that an interesting aspect of our results is the possibility of using zebrafish for investigation of the representation of quantity. The zebrafish is a very successful model for investigation of a range of topics in the biology of development and genetics. And the huge development of the field of genomics holds promise for making major advances in our understanding of animal cognition. Yet behavioral analyses with organism models like zebrafish focus on simple perceptual, motivational, or learning processes. To leverage research on such models for purposes of investigating the genetic bases of basic cognitive capacities, it is crucial to investigate and develop behavioral assays of cognitive mechanisms that may be shared between humans and nonhuman animals. Interesting steps forward have been recently provided by studies on social (Oliveira, 2013) and spatial (Lee, Vallortigara, Flore, Spelke, & Sovrano, 2013) cognition of zebrafish; it may be that studies on numerical/quantity cognition could prove relevant as well.

## References

- Beran, M. J. (2007). Rhesus monkeys (*Macaca mulatta*) succeed on a computerized test designed to assess conservation of discrete quantity. *Animal Cognition*, *10*, 37–45. <http://dx.doi.org/10.1007/s10071-006-0028-5>
- Brannon, E. M. (2006). The representation of numerical magnitude. *Current Opinion in Neurobiology*, *16*, 222–229. <http://dx.doi.org/10.1016/j.conb.2006.03.002>
- Brannon, E. M., & Merritt, D. (2011). Evolutionary foundations of the approximate number system. In S. Dehaene & E. M. Brannon (Eds.), *Space, time, and number in the brain: Searching for the foundations of mathematical thought* (pp. 207–224). London, Elsevier. <http://dx.doi.org/10.1016/B978-0-12-385948-8.00014-1>
- Brannon, E. M., & Terrace, H. S. (1998). Ordering of the numerosities 1 to 9 by monkeys. *Science*, *282*, 746–749. <http://dx.doi.org/10.1126/science.282.5389.746>
- Butterworth, B. (1999). *The mathematical brain*. London, UK: Macmillan.
- Cantlon, J. F., & Brannon, E. M. (2006). Shared system for ordering small and large numbers in monkeys and humans. *Psychological Science*, *17*, 401–406. <http://dx.doi.org/10.1111/j.1467-9280.2006.01719.x>
- Cantlon, J. F., & Brannon, E. M. (2007). Basic math in monkeys and college students. *PLoS Biology*, *5*, e328. <http://dx.doi.org/10.1371/journal.pbio.0050328>
- Carey, S. (2009). *The origin of concepts*. New York, NY: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780195367638.001.0001>
- Cordes, S., & Brannon, E. M. (2009). Crossing the divide: Infants discriminate small from large numerosities. *Developmental Psychology*, *45*, 1583–1594. <http://dx.doi.org/10.1037/a0015666>

- Coubart, A., Izard, V., Spelke, E. S., Marie, J., & Streri, A. (2014). Dissociation between small and large numerosities in newborn infants. *Developmental Science, 17*, 11–22. <http://dx.doi.org/10.1111/desc.12108>
- Dacke, M., & Srinivasan, M. V. (2008). Evidence for counting in insects. *Animal Cognition, 11*, 683–689. <http://dx.doi.org/10.1007/s10071-008-0159-y>
- Ditz, H. M., & Nieder, A. (2015). Neurons selective to the number of visual items in the corvid songbird endbrain. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 112*, 7827–7832. <http://dx.doi.org/10.1073/pnas.1504245112>
- Feigenson, L., Carey, S., & Hauser, M. (2002). The representations underlying infants' choice of more: Object files versus analog magnitudes. *Psychological Science, 13*, 150–156. <http://dx.doi.org/10.1111/1467-9280.00427>
- Fellows, B. J. (1967). Chance stimulus sequences for discrimination tasks. *Psychological Bulletin, 67*, 87–92. <http://dx.doi.org/10.1037/h0024098>
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: Bradford Books/MIT Press.
- Gómez-Laplaza, L. M., & Gerlai, R. (2011). Spontaneous discrimination of small quantities: Shoaling preferences in angelfish (*Pterophyllum scalare*). *Animal Cognition, 14*, 565–574. <http://dx.doi.org/10.1007/s10071-011-0392-7>
- Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings. Biological Sciences/The Royal Society, 267*, 829–833. <http://dx.doi.org/10.1098/rspb.2000.1078>
- Hyde, D. C. (2011). Two systems of non-symbolic numerical cognition. *Frontiers in Human Neuroscience, 5*, 150. <http://dx.doi.org/10.3389/fnhum.2011.00150>
- Jones, S. M., & Brannon, E. M. (2012). Prosimian primates show ratio dependence in spontaneous quantity discriminations. *Frontiers in Comparative Psychology, 3*, 550.
- Judge, P. G., Evans, T. A., & Vyas, D. K. (2005). Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes, 31*, 79–94. <http://dx.doi.org/10.1037/0097-7403.31.1.79>
- Lee, S. A., Vallortigara, G., Flore, M., Spelke, E. S., & Sovrano, V. A. (2013). Navigation by environmental geometry: The use of zebrafish as a model. *The Journal of Experimental Biology, 216*, 3693–3699. <http://dx.doi.org/10.1242/jeb.088625>
- Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. *Journal of Experimental Psychology: Animal Behavior Processes, 9*, 320–334. <http://dx.doi.org/10.1037/0097-7403.9.3.320>
- Nieder, A. (2013). Coding of abstract quantity by “number neurons” of the primate brain. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology, 199*, 1–16. <http://dx.doi.org/10.1007/s00359-012-0763-9>
- Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annual Review of Neuroscience, 32*, 185–208. <http://dx.doi.org/10.1146/annurev.neuro.051508.135550>
- Oliveira, R. F. (2013). Mind the fish: Zebrafish as a model in cognitive social neuroscience. *Frontiers in Neural Circuits, 7*, 131. <http://dx.doi.org/10.3389/fncir.2013.00131>
- Pepperberg, I. M. (2012). Further evidence for addition and numerical competence by a Grey parrot (*Psittacus erithacus*). *Animal Cognition, 15*, 711–717. <http://dx.doi.org/10.1007/s10071-012-0470-5>
- Pepperberg, I. M., & Carey, S. (2012). Grey parrot number acquisition: The inference of cardinal value from ordinal position on the numeral list. *Cognition, 125*, 219–232. <http://dx.doi.org/10.1016/j.cognition.2012.07.003>
- Piffer, L., Agrillo, C., & Hyde, D. C. (2012). Small and large number discrimination in guppies. *Animal Cognition, 15*, 215–221. <http://dx.doi.org/10.1007/s10071-011-0447-9>
- Roitman, J. D., Brannon, E. M., & Platt, M. L. (2007). Monotonic coding of numerosity in macaque lateral intraparietal area. *PLoS Biology, 5*(8), e208. <http://dx.doi.org/10.1371/journal.pbio.0050208>
- Rugani, R., Cavazzana, A., Vallortigara, G., & Regolin, L. (2013). One, two, three, four, or is there something more? Numerical discrimination in day-old domestic chicks. *Animal Cognition, 16*, 557–564. <http://dx.doi.org/10.1007/s10071-012-0593-8>
- Rugani, R., Fontanari, L., Simoni, E., Regolin, L., & Vallortigara, G. (2009). Arithmetic in newborn chicks. *Proceedings. Biological Sciences/The Royal Society, 276*, 2451–2460. <http://dx.doi.org/10.1098/rspb.2009.0044>
- Rugani, R., Regolin, L., & Vallortigara, G. (2008). Discrimination of small numerosities in young chicks. *Journal of Experimental Psychology: Animal Behavior Processes, 34*, 388–399. <http://dx.doi.org/10.1037/0097-7403.34.3.388>
- Rugani, R., Regolin, L., & Vallortigara, G. (2010). Imprinted numbers: Newborn chicks' sensitivity to number vs. continuous extent of objects they have been reared with. *Developmental Science, 13*, 790–797. <http://dx.doi.org/10.1111/j.1467-7687.2009.00936.x>
- Rugani, R., Regolin, L., & Vallortigara, G. (2011). Summation of large numerosity by newborn chicks. *Frontiers in Psychology, 2*, 179. <http://dx.doi.org/10.3389/fpsyg.2011.00179>
- Rugani, R., Vallortigara, G., & Regolin, L. (2013). Numerical abstraction in young domestic chicks (*Gallus gallus*). *PLoS ONE, 8*, e65262. <http://dx.doi.org/10.1371/journal.pone.0065262>
- Rugani, R., Vallortigara, G., & Regolin, L. (2014). From small to large: Numerical discrimination by young domestic chicks (*Gallus gallus*). *Journal of Comparative Psychology, 128*, 163–171. <http://dx.doi.org/10.1037/a0034513>
- Smith, B. R., Piel, A. K., & Candland, D. K. (2003). Numeracy of a socially housed hamadryas baboon (*Papio hamadryas*) and a socially housed squirrel monkey (*Saimiri sciureus*). *Journal of Comparative Psychology, 117*, 217–225. <http://dx.doi.org/10.1037/0735-7036.117.2.217>
- Stancher, G., Sovrano, V. A., Potrich, D., & Vallortigara, G. (2013). Discrimination of small quantities by fish (redtail splitfin, *Xenotoca eiseni*). *Animal Cognition, 16*, 307–312. <http://dx.doi.org/10.1007/s10071-012-0590-y>
- Tomonaga, M., & Matsuzawa, T. (2002). Enumeration of briefly presented items by the chimpanzee (*Pan troglodytes*) and humans (*Homo sapiens*). *Animal Learning & Behavior, 30*, 143–157. <http://dx.doi.org/10.3758/BF03192916>
- Vallortigara, G. (2014). Foundations of number and space representations in precocial species. In D. C. Geary, D. B. Beach, & K. Mann Koepke (Eds.), *Evolutionary origins and early development of number processing* (pp. 35–66). New York, NY: Elsevier.
- Viswanathan, P., & Nieder, A. (2013). Neuronal correlates of a visual “sense of number” in primate parietal and prefrontal cortices. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 110*, 11187–11192. <http://dx.doi.org/10.1073/pnas.1308141110>
- Viswanathan, P., & Nieder, A. (2015). Differential impact of behavioral relevance on quantity coding in primate frontal and parietal neurons. *Current Biology, 25*, 1259–1269. <http://dx.doi.org/10.1016/j.cub.2015.03.025>

Received May 6, 2015

Revision received June 24, 2015

Accepted June 26, 2015 ■