ORIGINAL PAPER

Small and large number discrimination in guppies

Laura Piffer · Christian Agrillo · Daniel C. Hyde

Abstract Non-verbal numerical behavior in human infants, human adults, and non-human primates appears to be rooted in two distinct mechanisms: a precise system for tracking and comparing small numbers of items simultaneously (up to 3 or 4 items) and an approximate system for estimating numerical magnitude of a group of objects. The most striking evidence that these two mechanisms are distinct comes from the apparent inability of young human infants and non-human primates to compare quantites across the small (<3 or 4)/large (>4) number boundary. We ask whether this distinction is present in lower animal species more distantly related to humans, guppies (*Poecilia reticulata*). We found that, like human infants and non-human primates, fish succeed at comparisons between large numbers only (5 vs. 10), succeed at comparisons between small numbers only (3 vs. 4), but systematically fail at comparisons that closely span the small/large boundary (3 vs. 5). Furthermore, increasing the distance between the small and large number resulted in successful discriminations (3 vs. 6, 3 vs. 7, and 3 vs. 9). This pattern of successes and failures is similar to those observed in human infants and non-human primates to suggest that the two systems are present and functionally distinct across a wide variety of animal species.

Keywords Object file · Analog magnitude · Numerical cognition

L. Piffer (✉) · C. Agrillo
Department of General Psychology, University of Padova,
Via Venezia 8, 35131 Padova, Italy
e-mail: laura.piffer@unipd.it

D. C. Hyde
Laboratory for Developmental Studies, Department
of Psychology, Harvard University, Cambridge, MA, USA

Introduction

Humans are endowed with at least two cognitive systems that support non-verbal numerical cognition: an approximate number system (ANS) for representing the numerical magnitude of collections of objects and a parallel individuation system (PI) for representing and keeping track of a limited number of items simultaneously and distinctly (see Feigenson et al. 2004 for a review). These abilities appear to be present from human birth (Izard et al. 2009) and are shared with a wide variety of non-human animals (Feigenson et al. 2004).

The approximate number system is characterized by its systematically limited precision (e.g. Cordes et al. 2001; Dehaene 1997). When counting is not possible (or inhibited) in human adults, psychometric number discrimination functions follow Weber's Law; performance strictly depends on the ratio of the numbers to be compared (e.g. Moyer and Landauer 1967). This ratio-dependent behavior is even seen in human infants, as 6 month olds can discriminate 8 from 16 objects (ratio of 1:2), but not 8 from 12 objects (ratio of 2:3; Xu and Spelke 2000). A variety of non-human animals, including non-human primates, rats, fish, and chickens, also show a similar ratio-dependent behavior (e.g. Agrillo et al. 2008, 2010; Brannon and Terrace 2000; Buckingham et al. 2007; Cantlon and Brannon 2006; Dehaene 1997; Gallistel 1990; Gómez-Laplaza and Gerlai 2011a; Meck and Church 1983; Vallortigara et al. 2010).

Under many conditions, however, small quantities (1–3 or 4) do not appear to be represented by the approximate number system and instead are represented distinctly through the parallel individuation/object-file system (e.g. Ansari et al. 2007; Feigenson et al. 2002; Feigenson and Carey 2003, 2005; Hyde and Spelke 2009; Hyde and Wood

2011; Xu 2003). It represents individual items and their distinctness from one another (numerical identity) rather than a cardinal value of the set (see Carey 2009). In contrast to the approximate number system, the parallel individuation system is limited in capacity. In human adults, the ability to individuate, track, and maintain representations of multiple objects simultaneously is limited to around 3–5 items (Kahneman et al. 1992; Trick and Pylyshyn 1994). Attentional constraints are thought to underlie this limit (Trick and Pylyshyn 1994; Hyde and Wood 2011). Human infants also show capacity limits in parallel individuation. For instance, 12-month-old human infants reliably choose a container with more food items after watching an experimenter sequentially places 1 item in one bucket and 2 items in another bucket; they also succeed at comparisons of 1 versus 3 and 2 versus 3, but consistently fail to distinguish between the buckets in comparisons where more than 3 items are placed in any one bucket (e.g. 3 vs. 4, 2 vs. 4 and even 1 vs. 4; Feigenson et al. 2002; Feigenson and Carey 2003). Similarly, rhesus macaques are able to select the larger number of apple slices with comparisons of 1 versus 2, 2 versus 3 and 3 versus 4, but fail when more than 4 items are placed in any one bucket (e.g. 4 vs. 5; Hauser et al. 2000). Performance is not limited by the ratio comparison, but is limited by the total number of objects. Comparisons of this system, then, are more precise, as they can be made over closer ratios (e.g. 2 vs. 3) than those made by the approximate number system. The ability to make more precise comparisons in the small number range and the striking inability to make comparisons between a larger and a smaller value suggests that representations of the approximate number system are not being formed or at the least not being used productively to act over small quantities in some situations.

Whether representations through parallel individuation take precedence over representations of the approximate number system for smaller quantities or approximate representations are simply not formed over small numbers in these situations, failures in crossing the small/large number divide provide strong evidence in humans and other non-human primates that two systems are present and operate to form qualitatively distinct numerical representations. It is unclear, however, whether this distinction is present in lower animal species.

One possibility is that the parallel individuation system is a more recent evolutionary development that affords more precise comparisons of smaller quantities and therefore difficulties in making comparisons across the small/large number divide should not be seen in more distantly related animals (to primates). This possibility is supported, in part, by evidence suggesting parallel individuation requires more attentional and/or working memory resources compared to number approximation (Hyde and Wood

2011; Trick and Pylyshyn 1994). In fact, many studies that have been conducted with more distant-related species show that the approximate number system operates over the entire range of numbers and affords success across the small and large number range. For instance, studies show success across the small/large divide with parrots, songbirds, rats, and dogs (Al Aïn et al. 2009; Hunt et al. 2008; Meck and Church 1983; Ward and Smuts 2007).

Another possibility is that the two systems of non-verbal numerical cognition are more evolutionarily pervasive, not restricted to closely related species to humans. Several recent studies suggest indirectly that this may be the case. For example, salamanders succeed at comparisons of 2 versus 3 and 1 versus 2, but fail at comparisons of 4 versus 6 (Uller et al. 2003). However, given the actual "capacity limit" of salamanders is unknown, and a comparable success was not provided in the large number range, the interpretation of this failure is unclear. The numerical abilities of fish also suggest the possibility of a small/large number distinction in comparison tasks. Discrimination of larger numbers by mosquitofish and guppies shows ratio-dependent behavior where discrimination of small numbers does not (Agrillo et al. 2007, 2008, unpublished data). The crucial study with small versus small comparisons, large versus large comparison, and comparisons across the small/large number divide, however, has not been conducted. To fill this gap, we tested small from large number discriminations in fish in a quantity discrimination task requiring them to select the larger group of social companions.

Methods

Subjects

A total of 108 female guppies (*Poecilia reticulata*) were used as subjects. *P. reticulata* is an internally fertilizing species commonly studied in shoal choice preferences (Bisazza et al. 2010; Ledesma and McRobert 2008). The fish used in this experiment were descendants of wild-caught fishes collected from the Tacarigua River in Trinidad. In this species, females are known to be highly social and, in nature, form shoals of variable sizes, representing a more useful model to investigate spontaneous shoal choices compared with males. All subjects were sexually mature (approximately 4–8 month olds). Eighteen individual fish were used for each experimental condition. Fish were maintained in 150-l stock aquaria containing mixed-sex groups (20 individuals at approximately 1:1 sex ratio). Aquaria were provided with natural gravel, an air filter and live plants. Both stock aquaria and experimental tanks were maintained at a constant temperature of $25 \pm 1°C$ and a 14:10 h light/dark (L/D) photoperiod, with an 18-W

fluorescent light. Fish were fed twice daily to satiation with commercial food flakes and live Artemia nauplii before the observations.

Apparatus

The experimental apparatus was composed of three adjacent tanks and used for previous studies on fish numerical cognition (Agrillo et al. 2008, unpublished data). The central one, called "subject tank", housed the test female (36 × 60 × 35 cm). At two ends, two smaller "stimulus tanks" (36 × 10 × 35 cm) faced the subject tank (Fig. 1). Water level was equal to 10 cm. The walls were covered with green plastic to prevent subjects from seeing outside. Each tank was lit by one fluorescent lamp. A video camera was suspended about 1 m above the test tank and used to record the position of the subject during the tests.

Experimental protocol

There is substantial evidence that in social situations, individual fish in unfamiliar environments tend to join other conspecific and, if choosing between two shoals, they exhibit a preference for the larger group (Agrillo and Dadda 2007; Agrillo et al. unpublished data; Gómez-Laplaza and Gerlai 2011a; Pritchard et al. 2001). Our method took advantage of this spontaneous preference for joining the larger shoal to study quantity discrimination abilities. Subjects were used only once, while approximately eighty similar sized females (sexually mature with similar age and body size of subjects) were alternated as stimuli.

Stimulus females were introduced 10 min prior the test; then, the subject was placed into a transparent cylinder (diameter: 10 cm) in the middle of the subject tank for 2 min. This cylinder was connected to a monofilament line on a pulley, which made it possible for an observer to raise

Fig. 1 Schematic representation of the experimental apparatus: **a** subject tank **b** stimulus tanks. The time spent near the larger shoal was recorded as dependent variable

it from a remote location and allow the subject to enter the subject tank. Once released, the position of the subject was observed for 15 min, an observation period commonly adopted in shoal choice preferences in poeciliid fish (Agrillo and Dadda 2007; Agrillo et al. unpublished data; Bisazza et al. 2010). For each numerical contrast, in half of the tests, the larger group was on the left and in half it was on the right.

Previous studies using the same procedure have shown that poeciliid fish (including guppies) can distinguish between shoals differing by one individual up to 4 units, showing no ratio sensitivity within this range, suggesting that the object-file limit in poeciliid fish is 4 (Agrillo et al. 2008, unpublished data; Bisazza et al. 2010). The between-subjects design included six different experimental conditions: four small-large numerical contrasts (3 vs. 5; 3 vs. 6; 3 vs. 7; 3 vs. 9), one small–small number contrast (3 vs. 4), and one large–large number contrast (5 vs. 10).

We calculated the time spent by the subject shoaling within a distance of 10 cm from the glass facing the stimulus tanks by superimposing a line on the video. The coder was blind with respect to the aim of the experiment. A second coder has measured independently a subset of trials ($N = 40$): the Pearson correlation between the two coders was $r = 0.977$ ($P < 0.001$). The dependent variable was the proportion of time (s) spent close to the larger shoal. Subjects that spent less than the 50% of time within 10 cm from the stimulus tanks were discarded and replaced by another fish. Furthermore, to ensure that subjects were active and visited both stimuli during the tests, we counted the number of movements within the subject tank and those fish that did not visit each stimulus sector at least three times were discarded and replaced. Sixteen subjects (13%) fell in this category (3 subjects in 3 vs. 4, 3 in 3 vs. 5, 1 in 3 vs. 6, 3 in 3 vs. 7, 2 in 3 vs. 9 and 4 in 5 vs. 10). Frequencies were arcsine (square root)-transformed (Sokal and Rohlf 1995).
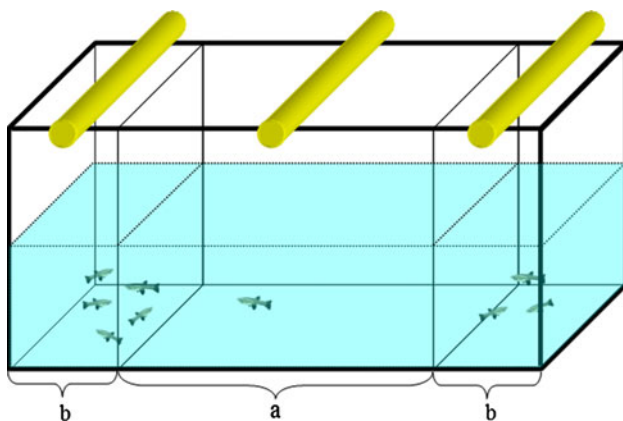
Results

Fish spent significantly more time near the larger shoal when presented with two small quantities, 3 versus 4 ($t(17) = 3.581$, $P = 0.003$), and two large quantities (5 vs. 10: $t(17) = 2.695$, $P = 0.015$; see Fig. 2). No significant difference was observed, however, when presented quantities on the small-large boundary, 3 versus 5 ($t(17) = 0.715$, $P = 0.484$). However, a significant preference for the larger shoal was found when the distance between the small and large quantities was increased, 3 versus 6 ($t(17) = 3.033$, $P = 0.008$), 3 versus 7 ($t(17) = 2.333$, $P = 0.032$), and 3 versus 9 ($t(17) = 2.186$, $P = 0.043$). A subsequent one-way ANOVA on the proportion of time
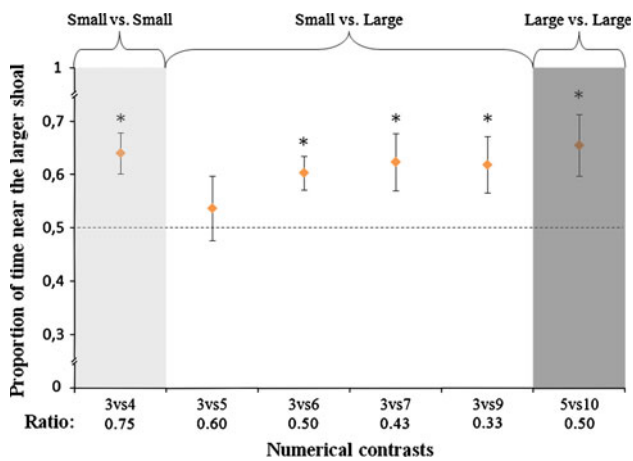
Fig. 2 Fish successfully chose the larger of two shoals in comparisons of 3 versus 4 (small number comparison) and 5 versus 10 (large number comparison). Their performance dropped to chance level when a small quantity (3) was contrasted with a large quantity (5). Increasing the numerical distance between the small and large quantity, however, afforded successful discrimination (*$P < 0.05$)

near the larger group showed no effect of the numerical ratio among the four numerical contrasts involving small versus large quantities (3 vs. 5, 3 vs. 6, 3 vs. 7 and 3 vs. 9: $F(3,71) = 0.541$, $P = 0.656$), suggesting the approximate number system may not have been used over the entire range of small-large number comparisons (see Fig. 2).

To verify the failure on 3 versus 5, we ran another independent group of subjects on the 3 versus 5 comparison and again found no significant difference in the time spent between shoals (mean ± SD: 0.472 ± 0.195, $t(17) = 0.600$, $P = 0.557$). Furthermore, there was no difference between the first and second groups on the 3 versus 5 comparison ($t(34) = 0.823$, $P = 0.416$).

To further test for differences between conditions, we compared small–small/small-large and small-large/large–large comparisons. Specifically, we compared 3 versus 4 and 3 versus 5[1] using a 2 (Number: larger/smaller shoal) × 2 (Contrast: 3 vs. 4/3 vs. 5) ANOVA. A significant main effect of Number ($F(1,52) = 4.878$, $P = 0.032$) and a significant interaction between Number and Contrast was observed ($F(1,52) = 5.434$, $P = 0.024$). The main effect of Contrast was not significant ($F(1,52) = 1.190$, $P = 0.280$). A similar analysis comparing 3 versus 5 and 5 versus 10 found a significant main effect of Number ($F(1,52) = 5.681$, $P = 0.021$) and a significant interaction between Number and Contrast ($F(1,52) = 4.967$, $P = 0.030$).

The main effect of Contrast alone was again not significant ($F(1,52) = 0.005$, $P = 0.945$).[2]

Discussion

The present study was designed to address whether two numerical systems operate distinctly in more distant-related species to primates by observing the capacity to discriminate small and large quantities in fish. Specifically, we tested number discrimination of small versus small, small versus large, and large versus large quantities. Similarities in the pattern of failures and successes were observed between fish in our study and human infants and other non-human primates in previous studies (Feigenson et al. 2002; Feigenson and Carey 2005; Xu 2003). In particular, we found that fish were able to discriminate between two small quantities (3 vs. 4) and between two large quantities (5 vs. 10). However, fish did not successfully discriminate two quantities across the small-large boundary (3 vs. 5). Like in previous studies with primates, fish were able to discriminate between two smaller quantities more precisely than between a small and a large quantity. This suggests that these comparisons (success on 3 vs. 4) were not made by the approximate number system, which is characterized by strict dependency on the ratio between the two numbers to be compared. Instead, these data fit better with the idea of a distinct mechanism operating in the small quantity range, insensitive to the numerical ratio. Another recent study is in line with this conclusion. Using the same procedure, it has been shown that guppies cannot discriminate 6 versus 8, even though the numerical ratio is the same of the small quantities successfully discriminated here (3 vs. 4), supporting the idea of a different sensitivity for numerical ratio in the small and large number range (Agrillo et al. unpublished data). Identical results were previously reported in two other studies testing a closely related species, the eastern mosquitofish (Agrillo et al. 2007, 2008).

The ability to compare small numbers of items through parallel individuation is hypothesized to be based in an

---

[1] Data from the two samples of the 3 versus 5 comparison were pooled and entered into the ANOVA, given the two groups showed no significant differences, data had a normal distribution (Kolmogorov–Smirnov one sample t test, $P > 0.1$), and no difference between groups was found in the variance (Leven test, $P > 0.05$).

[2] We also ran an ANOVA on the weighted means to account for the difference in the number of subjects in each group ($n = 36$ for 3 vs. 5, $n = 18$ for 3 vs. 4, $n = 18$ for 5 vs. 10). The analysis of the weighted means produced parallel results to those obtained on the raw scores. Specifically, when we compared 3 versus 4 and 3 versus 5, we observed a significant main effect of Number ($F(1,52) = 4.703$, $P = 0.036$) and a significant interaction between Number and Contrast ($F(1,52) = 5.504$, $P = 0.021$). The main effect of Contrast was not significant ($F(1,52) = 1.181$, $P = 0.278$). When comparing 3 versus 5 and 5 versus 10, we found a significant main effect of Number ($F(1,52) = 5.684$, $P = 0.020$) and a significant interaction between Number and Contrast ($F(1,52) = 4.902$, $P = 0.036$). Again, the main effect of Contrast alone was not significant ($F(1,52) = 0.011$, $P = 0.920$).

object-tracking system (Scholl and Pylyshyn 1999; Trick and Pylyshyn 1994). This object-tracking mechanism is not a system of numerical representation, per se, but rather, affords numerical comparison through one-to-one correspondence. To survive in their environment, fish must be able to track multiple objects such as live prey, potential predators, or social companions. Therefore, it is possible that an object-tracking mechanism—similar to that hypothesized for humans—may be displayed by fish and used for small quantity discrimination. In particular, a recent study (Bisazza et al. 2010) has demonstrated that the capacity of newborn guppies to distinguish between small quantities of social companions is inborn and displayed at birth. One-day-old fish are able to discriminate the larger shoal in 1 versus 2, 2 versus 3 and 3 versus 4, while failing to discriminate 4 versus 5 or even larger numerical ratios, such as 4 versus 8 and 4 versus 12. The ability to discriminate larger quantities (>4) emerges later, as a result of both maturation and social experience. The fact that guppies display the capacity to discriminate between small quantities at birth indirectly supports the idea that the parallel individuation or object-file system is present in comparisons of small quantities in our study.

Fish, however, were able to select the larger group when the numerical distance between the small and large quantity was increased (3 vs. 6, 3 vs. 7 and 3 vs. 9). A recent study with 7-month-old human infants observed similar results (Cordes and Brannon 2009). More specifically, using the habituation–dishabituation paradigm, infants failed to detect a twofold change in small versus large set contrasts, but successfully distinguished a fourfold change. Two hypotheses were proposed to potentially account for this performance. According to the first hypothesis—called 'noise hypothesis'—infants may initially represent small sets through parallel individuation and large sets with analog magnitudes and, subsequently, convert object files (representations through parallel individuation) into approximate magnitudes before comparing the two quantities. According to this perspective, the fact that infants require a greater ratio than that necessary to discriminate between large quantities might be explained by the potential increased noise in approximate number representations as a result of conversion from object files/parallel individuation. An alternative hypothesis—called 'threshold hypothesis'—suggests that infants may represent both small and large sets with analog magnitudes but parallel individuation representations trump approximate magnitude representations because they are discrete, precise, and more reliable. However, when the numerical ratio between small and large numbers exceeds a threshold, such as 1:4, infants may successfully compare a large and small set using solely the approximate magnitude system routinely employed in large number discriminations.

The current experimental data do not accord with either explanation of small/large number failures. The ratio at which fish succeeded in comparing across the small/large number divide was not substantially greater than the ratio-limit seen with comparisons of only large numbers in our study or in other studies of fish (Agrillo et al. 2008, unpublished data; Buckingham et al. 2007). That is, comparison precision is similar for fish whether comparing across the small-large divide or comparing just large numbers. Both accounts of the human infant data, however, would predict that precision in comparisons across the small-large divide should be worse than comparisons between large numbers only, which was not the case. In addition, we did not find ratio-dependent behavior when analyzing the successfully comparisons that spanned the small-large boundary. Presumably the approximate number system was engaged to make these successful comparisons. Although purely speculative, failure to find a ratio effect may suggest that all these comparisons were equally easy.

One interesting physical correlate of increasing the distance between a small and a large number in the infant studies cited above (Cordes and Brannon 2009) and the current fish study is that the inter-item spacing of the individual stimuli (fish in this study/dots in the infant study) decreases. A recent account of small number processing suggests that this may be the root cause of success by increasing distance between a small and large number (Hyde and Wood 2011). It may be that in comparisons close to the small/large number border (3 vs. 5 in our study; 1 vs. 4, 2 vs. 4, or 3 vs. 6 in other studies), more generous inter-item spacing encourages the attempted engagement of the parallel individuation system over the "large" number. The system's capacity limit is surpassed, and the engagement of the parallel individuation system over the large number ultimately fails. This leads to a failure in comparing the small and the large number close to the boundary. When researchers have increased the numerical distance between the small and the large number and found success, they have also inadvertently decreased the inter-item spacing between individuals. This decrease in inter-item spacing in more distance small/large comparisons may bias the system to represent the quantities through the approximate number system rather than through the parallel individuation system, leading to successes. A recent study, in fact, experimentally showed that the representation of small numbers by the parallel individuation system or the approximate number system crucially depends on whether or not items are presented (spaced) within attentional limits (Hyde and Wood 2011). When a small number of individuals is spaced beyond the resolution of attention to individuate (crowded), electrophysiological brain signatures in human adults suggest that they are represented as approximate numerical magnitudes rather than as

individuals. In contrast, when items are presented within the resolution and capacity of the attentional system to individuate, the default appears to be representation through parallel individuation and brain electrophysiology suggests that representations of approximate number are not formed. This hypothesis, that inter-item spacing differences between close and more distant small-large number comparisons differentially encourage the engagement of the parallel individuation and approximate number systems, can explain the patterns of successes and failures crossing the small-large boundary in human infants (Cordes and Brannon 2009) and in our study of fish.

It should also be noted that in our study, fish were allowed to attend both discrete (number) and continuous quantities in this study. Since numerosity often co-varies with other physical attributes such as the total area occupied by objects, one may argue that guppies were using these cues instead of numerical information to solve the task. Discriminations based on number or on continuous variables both yield ratio-dependent behavioral signatures (Cordes and Brannon 2008; Feigenson 2007) and a recent influential claim proposes that the same non-verbal magnitude system may underlie the cognitive processes of discrete and continuous quantities, such as number and space (Walsh 2003). Nevertheless, although both types of discrimination (continuous and discrete quantities) show ratio dependence in human infants, there are evidence that discriminations of continuous quantities are severely limited relative to those of number (Cordes and Brannon 2008; Barth 2008). While the present experiment was not specifically designed to disentangle the influence of continuous or discrete quantities, other studies have shown that fish can select the larger group of social companions solely on the basis of number in the large number and in the small number ranges (Bisazza et al. 2010; Dadda et al. 2009). In addition, a recent study using a training procedure has also shown no difference in the learning rate between fish trained to use numerical information only and fish trained to use continuous quantities only, suggesting that number per se is not more cognitively demanding than continuous quantities (Agrillo et al. 2011). Lastly, the application of a generalized magnitude system across all quantities would not predict the failure we see at the small-large number boundary, and therefore, reliance on other non-numerical continuous parameters cannot entirely explain our results.

Unfortunately, we can only speculate on the exact mechanisms underlying small and large number discrimination in guppies, and the functional range of these systems is less clear across fish species. For example, angelfish seem to have object-file limit of 3, fail at the comparison of 3 versus 4 where we see success in guppies, and succeed when comparing larger quantities to a single individual

(e.g. 1 vs. 4; Gómez-Laplaza and Gerlai 2011b). Similarly, failures to discriminate 3 versus 4 under some conditions (Bradner and McRobert 2001) suggest a limit of 3 in mollies. An object file limit of 3 has also been reported in goldbelly topminnows (Agrillo and Dadda 2007), while a limit of 4 has been observed in guppies (the present study), in mosquitofish (Agrillo et al. 2008), and in the peacock blenny (Hennig 1977). These differences raise the question of why different results are observed across the species. One possibility is that the differences observed between species may have been shaped by evolution on the basis on different pressure selections (i.e., high/low predator density, different shoal composition, etc.). Another possibility is that different results may depend on the different methodologies adopted between different studies. A previous work has indeed shown that the limit exhibited by topminnows in the ability to select the larger shoal is influenced by the type of procedure, with fish able to discriminate 3 versus 2 only in one of two different procedures (Agrillo and Dadda 2007). When the same apparatus and methodology has been adopted to test different species—guppies and mosquitofish—identical results were reported, both for small and large number discrimination (Agrillo et al. 2008, unpublished data), reinforcing the idea that differences in procedures may underlie many of the differences observed between species.

Despite the differences observed between species, the previous literature and the results reported here support the idea previously advanced in literature—distinct representations are often formed over small and large numbers to perform quantitative comparisons. In addition, the similarities reported in fish to those reported previously in human infants and non-human primates (see Feigenson et al. 2004) suggest that the two systems are present and functional across a wide range of animal species.

References

Agrillo C, Dadda M (2007) Discrimination of the larger shoal in the poeciliid fish *Girardinus falcatus*. Ethol Ecol Evol 19:145–157

Agrillo C, Dadda M, Bisazza A (2007) Quantity discrimination in female mosquitofish. Anim Cogn 10:63–70

Agrillo C, Dadda M, Serena G, Bisazza A (2008) Do fish count? Spontaneous discrimination of quantity in female mosquitofish. Anim Cogn 11(3):495–503

Agrillo C, Piffer L, Bisazza A (2010) Large number discrimination by fish. PLoS ONE 5(12):e15232. doi:10.1371/journal.pone.0015232

Agrillo C, Piffer L, Bisazza A (2011) Number versus continuous quantity in numerosity judgments by fish. Cognition 119:281–287

Al Aïn S, Giret N, Grand M, Kreutzer M, Bovet D (2009) The discrimination of discrete and continuous amounts in African grey parrots (Psittacus erithacus). Anim Cogn 12:145–154

Ansari D, Lyons I, van Eimeren L, Xu F (2007) Linking visual attention and number processing in the brain: the role of the temporo-parietal junction in small and large non-symbolic number comparison. J Cogn Neurosci 19:1845–1853

Barth H (2008) Judgments of discrete and continuous quantity: an illusory Stroop effect. Cognition 109(2):251–266

Bisazza A, Piffer L, Serena G, Agrillo C (2010) Ontogeny of numerical abilities in fish. PLoS ONE 5(11):e15516. doi: 10.1371/journal.pone.0015516

Bradner J, McRobert SP (2001) The effect of shoal size on patterns of body colour segregation in mollies. J Fish Biol 59(4):960–967

Brannon EM, Terrace HS (2000) Representation of the numerosities 1–9 by rhesus macaques (Macaca mulatta). J Exp Psych Anim Behav Proc 26(1):31–49

Buckingham JN, Wong BBM, Rosenthal GG (2007) Shoaling decisions in female swordtails: how do fish gauge group size? Behaviour 144:1333–1346

Cantlon JF, Brannon EM (2006) Shared system for ordering small and large numbers in monkeys and humans. Psychol Sci 17(5):401–406

Carey S (2009) The origin of concepts. Oxford University Press, New York

Cordes S, Brannon EM (2008) Quantitative competencies in infancy. Dev Sci 11:803–808

Cordes S, Brannon EM (2009) Crossing the divide: infants discriminate small from large numerosities. Dev Psych 45:1583–1594

Cordes S, Gelman R, Gallistel CR, Whalen J (2001) Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. Psych Bull Rev 8:698–707

Dadda M, Piffer L, Agrillo C, Bisazza A (2009) Spontaneous number representation in mosquitofish. Cognition 112:343–348

Dehaene S (1997) The number sense. Oxford University Press, Cambridge

Feigenson L (2007) The equality of quantity. Trends Cogn Sci 11(5):185–187

Feigenson L, Carey S (2003) Tracking individuals via object-files: evidence from infants' manual search. Dev Sci 6:568–584

Feigenson L, Carey S (2005) On the limits of infants' quantification of small object arrays. Cognition 97:295–313

Feigenson L, Carey S, Hauser MD (2002) The representations underlying infants' choice of more: object files versus analog magnitudes. Psychol Sci 13:150–156

Feigenson L, Dehaene S, Spelke ES (2004) Core systems of number. Trends Cogn Sci 8:307–314

Gallistel CR (1990) Representations in animal cognition: an introduction. Cognition 37:1–22

Gómez-Laplaza LM, Gerlai R (2011a) Can angelfish (Pterophyllum scalare) count? Discrimination between different shoal sizes follows Weber's law. Anim Cogn 14(1):1–9

Gómez-Laplaza LM, Gerlai R (2011b) Spontaneous discrimination of small quantities: shoaling preferences in angelfish (Pterophyllum scalare). Anim Cogn 14(4):565–574

Hauser MD, Carey S, Hauser LB (2000) Spontaneous number representation in semi-free-ranging rhesus monkeys. Proc R Soc Lond B 267:829–833

Hennig M (1977) Counting ability in Blennius-pavo Risso (Blenniidae, Perciformes). Zool Anz 199:1–18

Hunt S, Low J, Burns KC (2008) Adaptive numerical competency in a food-hoarding songbird. Proc R Soc Lond B 275:2373–2379

Hyde DC, Spelke ES (2009) All numbers are not equal: an electrophysiological investigation of small and large number representations. J Cogn Neurosci 21:1039–1053

Hyde DC, Wood JN (2011) Spatial attention determines the nature of non-verbal numerical cognition. J Cogn Neurosci 23:2336–2351

Izard V, Sann C, Spelke ES, Streri A (2009) Newborn infants perceive abstract numbers. Proc Nat Acad Sci USA 106:10382–10385

Kahneman D, Treisman A, Gibbs BJ (1992) The reviewing of object files: object-specific integration of information. Cogn Psych 24:175–219

Ledesma JM, McRobert SP (2008) Shoaling in juvenile guppies: the effects of body size and shoal size. Behav Process 77(3):384–388

Meck WH, Church RM (1983) A mode control model of counting and timing processes. J Exp Psych Anim Behav Proc 9:320–334

Moyer RS, Landauer TK (1967) The time required for judgments of numerical inequality. Nature 215:1519–1520

Pritchard VL, Lawrence J, Butlin RK, Krause J (2001) Shoal choice in zebrafish, Danio rerio: the influence of shoal size and activity. Anim Behav 62:1085–1088

Scholl BJ, Pylyshyn ZW (1999) Tracking multiple items through occlusion: clues to visual objecthood. Cogn Psych 38:259–290

Sokal RR, Rohlf FJ (1995) Biometry. Freeman and Company, New York

Trick LM, Pylyshyn ZW (1994) Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. Psych Rev 101:80–102

Uller C, Jaeger R, Guidry G, Martin C (2003) Salamanders (Plethodon cinereus) go for more: rudiments of number in an amphibian. Anim Cogn 6:105–112

Vallortigara G, Regolin L, Chiandetti C, Rugani R (2010) Rudiments of mind: insights through the chick model on number and space cognition in animals. Comp Cogn Behav Rev 5:78–99

Walsh V (2003) A theory of magnitude: common cortical metrics of time, space and quantity. Trends Cogn Sci 7:483–488

Ward C, Smuts BB (2007) Quantity-based judgments in the domestic dog (Canis lupus familiaris). Anim Cogn 10:71–80

Xu F (2003) Numerosity discrimination in infants: evidence for two systems of representations. Cognition 89:B15–B25

Xu F, Spelke ES (2000) Large number discrimination in 6-month-old infants. Cognition 74:B1–B11