

Fish can use numerical information when discriminating between small discrete quantities

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Abstract

Research on human infants and non-human animals has demonstrated that rudimentary numerical abilities pre-date the evolution of human language. Nonetheless animals can base their quantity judgments on continuous perceptual cues that correlate with number and it is unclear whether animals other than mammals and birds can use number. In the present work we adopted two different approaches to investigate whether basal vertebrates, such as fish, can discriminate between small quantities by using numerical information only. In experiment 1 we investigated the non numerical perceptual cues preferentially used by fish to discriminate between two and three elements; in experiment 2 fish were then trained to distinguish between the two quantities when continuous variables were controlled for. Lastly (experiment 3) we observed the spontaneous choice between a group of two and a group of three social companions using a method similar to 'item by item' presentation of the stimuli to prevent the access to non-numerical information. On the whole, our results suggest that fish can represent and use numerical information for discriminating small quantities.

Keywords: Numerical competence; Continuous variables; Comparative cognition.

Introduction

The ability to count objects or discriminate among sets containing different number of items can affect survival and reproduction in many natural contexts. Laboratory studies have shown that mammals (Beran, 2008; Kilian et al., 2003; West & Young, 2002), birds (Brannon et al., 2001) amphibians (Uller et al., 2003) and fishes (Agrillo et al., 2007) are able to discriminate between two quantities of objects.

However, since stimulus numerosness co-varies with non-numerical extent, such as the total area occupied by objects, the sum of their contour, their density and luminance, organisms can provide quantity judgments without necessarily being capable of abstract numerical

representation (Feigenson et al., 2002b; Pisa & Agrillo, 2009).

In a recent study (Agrillo et al., 2008) we systematically investigated the ability to discriminate between two quantities in a small freshwater fish, the mosquitofish (*Gambusia holbrooki*). As many other fish, mosquitofish placed in an unknown, potentially dangerous environment, select the larger of two simultaneously presented shoal, probably because larger groups offer better protection from predators (Agrillo & Dadda, 2007; Hager & Helfman, 1991). In choice tests mosquitofish were found to discriminate between two shoals that differed by one element when the paired numbers were 1vs2, 2vs3 and 3vs4, but not 4vs5 or larger group sizes, a limit that coincides with that observed in monkeys and apes when using a spontaneous preference paradigm. Using larger shoals as stimulus, a discrimination was still possible provided the number ratio was 1:2 or smaller (e.g. 4vs8, or 8vs16 fish but not 4vs6 or 8vs12 fish). Within the large number range (> 4 elements), preference for the large shoal significantly increased with decreasing numerosity ratio in accordance with Weber's Law while such relationship was not observed within the small number range, suggesting the possible existence in fish of two numerical systems as evidenced in primates (Flombaum et al., 2005; Hauser et al., 2000) and human infants (Feigenson et al., 2002a). However we found that, when we controlled for continuous variables (the cumulative area occupied by fish and the overall quantity of movements of the fish within a shoal), fish failed to discriminate, suggesting that they attend more to non-numerical extent than to numerosity itself.

The fact that mosquitofish spontaneously compare different quantities by using non numerical perceptual cues that correlate with number does not necessarily imply that fish are unable to discriminate two groups on the basis of the numerosity of the items alone. Overall perceptual cues may simply be the easiest indicators of numerosity in this task, and indeed both adult humans and non-human mammals, in many circumstances, base number estimation primarily on

proxy measures such as density or the cumulative surface area occupied by items (Durgin, 1995; Vos et al., 1988; Kilian et al., 2003).

The present work aims at investigating fish ability to discriminate between small quantities (2 and 3 elements) by using numerical information only. We adopted two different approaches: in the first two experiments we set up a training procedure similar to that used with mammals, consisting in training animals to discriminate between sets containing different numbers of geometric figures while controlling for the perceptual non-numerical variables (Brannon & Terrace, 1998; Judge et al., 2005).

In detail, the first experiment aimed to determine which cues mosquitofish used spontaneously when both numerical information and continuous physical attributes were available. Subjects learned a discrimination between 2 and 3 objects in the absence of any manipulation of the stimuli; after animals had achieved learning criterion they were tested without reward while controlling for one perceptual non-numerical variable at a time.

In the second experiment we trained fish to discriminate between 2 and 3 objects while we simultaneously controlled for non-numerical variables, in order to determine whether fish could discriminate by using only numerical information.

In the third experiment we adapted the procedure of 'item by item' presentation (Beran, 2004; Beran & Beran, 2004; Hauser et al., 2000) to spontaneous choice of social groups. Fish were placed in a new environment where they could choose between a group of two and a group of three social companions. During the test the subject could only see the members of each stimulus shoal one at a time, thus preventing the possibility that they could use non-numerical cues, such as the cumulative surface area occupied by stimulus fish, to estimate the larger set.

Experiment 1

Cues spontaneously used by fish to discriminate between quantities. The first experiment investigated which cues fish tend to use when distinguishing between two and three figures. Ten female mosquitofish were subjected to a pre-training phase of 7 days in which they accustomed to doors and stimuli similar to those they encountered in the training phase. Each female was then singly placed in an unfamiliar and uncomfortable place (Fig. 1) and were trained to discriminate between two doors in order to re-join their social group. Doors were associated with a pair of stimuli consisting of two or three small figures (Fig. 2). These figures were randomly selected with replacement from a pool of approximately 100, and no control for non-numerical variables was operated in the training phase. Subjects were given six trials per day for a maximum of ten days; after each trial, a new set of two and three figures was presented. Once a subject had reached the learning criterion, it was admitted to the test phase and was examined in the

same apparatus without reward while controlling for one perceptual non-numerical variable at time. We controlled those variables that were shown to be relevant in previous studies with vertebrates, namely the total luminance of the two stimuli, the sum of perimeter of the figures, the cumulative surface area, and the overall space occupied by the sets.

Results. All ten subjects reached the learning criterion in the training phase (chi square test, $p < 0.05$), but one was excluded from the subsequent phase due to poor health, and hence nine started the test phase. We found no difference in proportion of correct choices between fish trained with the three figures as positive (mean \pm std. dev.: 0.753 ± 0.065) and those trained with two figures as positive (0.678 ± 0.028 ; $t(7) = 2.337$, $p = 0.052$). A significant discrimination was observed when no perceptual cue was controlled for ($t(8) = 2.449$, $p = 0.020$) and when the total luminance was controlled for ($t(8) = 2.310$, $p = 0.025$); no significant choice toward the trained quantity was found when the sum of perimeter of the figures ($t(8) = 1.316$, $p = 0.225$), the cumulative surface area ($t(8) = -1.512$, $p = 0.169$), and the overall space occupied by the sets ($t(8) = -0.373$, $p = 0.719$) were controlled for.

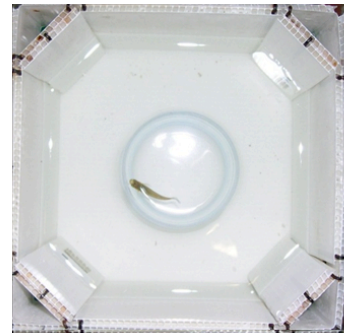


Figure 1: Apparatus used in Experiment 1. Subjects are singly placed in the middle of a white cubic tank and two doors (one associated to three and the other associated to two elements) were available at two opposite corners. Only the door associated to the reinforced quantity permits fish to re-join shoal mates in the outer tank (not shown).

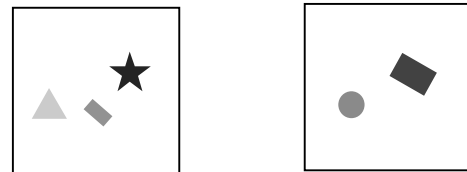


Figure 2: Example of stimuli used in Experiment 1.

However, since area and perimeter of the figures are strictly related to each other, in this experiment by controlling one variable we inevitably affected the other, so that it was not possible to conclude whether one or both variables were

important in the discrimination. We thereby set up a control test with ten new subjects, using the same procedure as before in training phases, whereas in the test phase fish were presented with only two different sets of stimuli: one in which the cumulative surface area of the stimuli was paired whereas the sum of perimeter was not (i.e. the perimeter could suggest the exact ratio between the quantities), and one in which the sum of the perimeter was paired whereas the cumulative surface area was not (i.e. the area could suggest the exact ratio between the quantities).

When the relative ratio of the areas (but not the perimeter) was predictive of the numerical ratio, we observed a significant choice toward the trained quantity ($t(9) = 3.786$, $p = 0.004$) whereas no significant choice was observed in the condition in which the perimeter, but not the area, could be used to distinguish between two quantities ($t(9) = -0.653$, $p = 0.530$). The difference between the two conditions was significant (paired t-test, $t(9) = 2.865$, $p = 0.019$).

On the whole results showed that fish seemed to attend the cumulative surface area and the overall space occupied by the sets: interestingly we observed a negative correlation between the proportion of correct choices when the cumulative surface area was controlled and when the overall space of the sets was paired (Spearman test, $\rho_s = -0.734$, $p = 0.024$). This seems to suggest an individual variability in the strategy used, since some subjects tended to rely on the cumulative surface area for discriminating, while other fish attended the overall space to solve the task.

Experiment 2

Discrimination of small quantities using only numerical information. In the second experiment we trained fourteen fish to discriminate between 2 and 3 figures while we simultaneously controlled stimuli for non-numerical variables in both the pre-training and the training phase, with the aim of determining whether fish could learn the discrimination using only numerical information. Using the same geometric figures as the previous experiment, we designed pairs of stimuli in which the total luminance, the cumulative surface area and the overall space occupied by the sets were paired between the groups with two and three elements.

Results. We found no difference in the proportion of correct choices between fish trained with the three figures as positive (mean \pm std. dev.: 0.690 ± 0.037) and those trained with two figures as positive (0.651 ± 0.070 ; $t(12) = 1.328$, $p = 0.209$). All 14 fish reached the learning criterion (chi square test, $p < 0.05$), proving thus able to select the trained numerosity. Overall the choice for the trained stimuli is highly significant ($t(13) = 11.103$, $p < 0.001$).

As a by-product of controlling for three perceptual variables, stimuli differed for two other non-numerical variables that fish could have used instead of number to learn the discrimination. The by-product of pairing the cumulative surface area between sets with two and three

elements was that in the latter sets smaller-than-average figures were more frequent. The by-product of pairing the overall space occupied by configuration was that figures were more spaced out in the sets containing two figures. After reaching the criterion, fish were thereby subjected to a test phase without reinforcement using pairs of stimuli composed of figures of identical size and similarly spaced. Results showed that fish significantly selected the trained numerosity even in this case ($t(13) = 4.397$, $p = 0.001$).

When we compared the number of trials necessary to reach criterion in experiment 1 (when all numerical and non-numerical cues were available) and experiment 2 (where only numerical cues were available), we found no significant difference (trials in experiment 1: 25.2 ± 11.7 ; trials in experiment 2: 29.14 ± 9.7 ; $F(1,33) = 1.064$, $p = 0.170$).

Experiment 3

Spontaneous use of number in a shoal choice test. There is a substantial evidence that single mosquitofish, that happen to be in a unknown environment, tend to join other conspecifics and, if choosing between two shoals, they exhibit a preference for the large one (Agrillo et al., 2008). We then used this spontaneous tendency to join the larger shoal to study the ability to distinguish between 3 and 2 social companions by calculating the time spent near the shoals.

The experimental apparatus was composed by three separate sectors built within a large aquarium (Fig. 3). The central hourglass-shaped sector housing the subject consisted of a corridor interconnecting two identical choice areas provided with a glass front allowing seeing the stimuli. Each stimulus sector consisted of a rectangular area, subdivided longitudinally by glass panes in four identical compartments housing the stimulus fishes. In the area facing the stimuli we placed 9 artificial vertical green plastic screens aligned a grid of 3 by 3, so that the subject could only see one stimulus fish at time from any position of its sector.

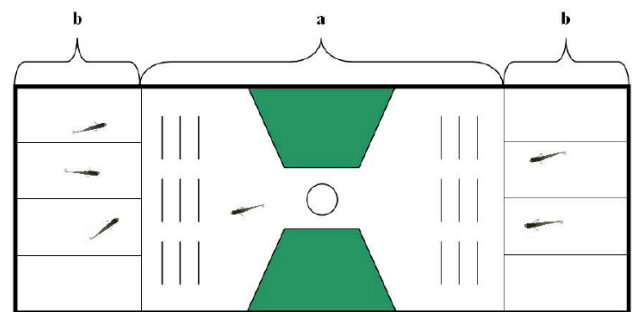


Figure 3: Schematic representation of the apparatus. Subjects are singly inserted in the central sector (a) and two groups of conspecifics differing in numerosity were visible in the 'stimulus sectors' (b). Subjects could not see more than one stimulus fish at time.

Stimulus females were introduced in the apparatus, one female per compartment, the afternoon before the test and allowed to settle overnight. At the beginning of the test, the subject was introduced in the corridor and allowed to explore the apparatus for one hour. Hence the position of the subject was recorded for 60 minutes with a digital cam.

Eighteen subjects were observed choosing between 3 and 2 stimulus fishes. Half of the trials started with the larger group on the left whereas half of the trials started with the larger group on the right. Furthermore in half of the trials we matched the distance between each stimulus fish and in the other half we matched the proportion of space occupied by the group (i.e. the distance between the two most lateral fish).

Results. Shoal preference was calculated as the time spent by the subject female shoaling within a distance of 5 cm from the glass facing the stimulus sector. The observer of the video was blind with respect to the aim of the experiment. A repeated measure ANOVA was performed, with the numerosity (larger or smaller shoal) as within-subject factor, while the position of the larger shoal (right or left) and the composition of the stimulus shoals (same distance among the fish or same proportion of space of the shoals) as between-subject factors. Subjects spent more time near the larger shoal ($F(1,14) = 7.420$, $p = 0.016$). We found no effect of left-right position of the stimuli ($F(1,14) = 0.180$, $p = 0.677$) and no difference between trials in which we matched the distance between fish in the two shoals and trials in which we matched the proportion of space occupied by the shoals ($F(1,14) = 1.363$, $p = 0.263$). No interaction was significant (all $ps > 0.05$).

There is a simple explanation for these results based on the possibility that fish do not represent number but simply are attracted by a companion when they could see one and leave that side of the apparatus when they could not see another fish. Because two out of four places are empty by the smaller shoal and only one out of four is so by the larger one, this would imply a larger probability of leaving the former. To test this possibility, we measured the number of times subjects moved away from each of the eight compartments and calculated the average departure rate when subjects could see a companion (total departures from occupied compartments/5) and when subjects could not see another fish (total departures from empty compartments/3).

The proportion of departures from an occupied compartment was slightly greater (0.561 ± 0.238) than the proportion of departures from an empty one (0.439 ± 0.238) but the difference was not statistically significant (one sample t-test, $t(11) = 1.092$; $p = 0.290$).

Discussion

The present work aimed at assessing whether fish can use numerical information in order to discriminate between small quantities. We have tackled the problem using two

complementary approaches. In the second experiment fish were trained to distinguish between two sets of figures that differed in numerosity but were paired for non-numerical variables. In the third experiment, fish were observed in a free choice test between two shoals differing in numerosity using a procedure similar to 'item by item' presentation that prevented them to use non-numerical information. The results of experiment 2 and 3 support the conclusion that mosquitofish can discriminate small discrete quantities using numerical information only. Fish should thus likely be added to the list of organisms, six month old infants, non-human primates, dolphins, dogs and birds that have been shown up to now to be capable of mentally representing number and comparing numerosities (Brannon et al., 2001; Hauser et al., 2000; Kilian et al., 2003; West & Young, 2000; Xu & Spelke, 2000).

In detail, the results of the first experiment show that the ability of mosquitofish to discriminate among sets containing a different amount of elements is not limited to the socio-sexual context (Agrillo et al., 2007, 2008), but also applies to sets of abstract elements. Indeed, experiment 1 provides evidence that fish trained to discriminate between small sets of figures spontaneously base their discrimination on non-numerical features of the stimuli, namely the cumulative surface area occupied by figures and the overall space occupied by the sets, while they apparently ignored the numerical information and other available cues such as the sum of perimeters or the total luminance of the stimuli. We found a negative correlation between the proportion of correct choices when the cumulative surface area was controlled and when the overall space of the sets was paired, thus indicating that there was an individual variability in the strategy used, with some subjects relying on the cumulative surface area for discriminating and not being affected by the overall space, while others used the overall space but not area to solve the task.

The results of experiment 2 clearly show that, when the access to the non-numerical information was prevented by matching them between the stimuli, mosquitofish could still learn the discrimination and indeed they required approximately the same number of trials suggesting that the priority of perceptual over numerical information is probably not related to a greater cognitive load imposed by direct numerical computation.

Why do mosquitofish preferentially use continuous extent over numerical information given that the two alternatives are similar in cognitive demand? One possibility is that quantity information is ecologically more relevant for this species. For example, in foraging contexts animals often tend to maximise the amount of resources acquired with a minimum of energy expenditure. Even though number of items and total amount of resources gained frequently correlate, sometimes this does not occur, for example when there is a large variation in the size of food items. Selection for optimising food intake could have favoured mechanisms based on continuous extent, such as area, as they are more reliable indicators of the resource potentially gained.

Alternatively, perceptual cues of the stimuli may simply be the quickest indicator of the numerosity, for example because they involve earlier stages in neural visual or auditory processing (Beran et al., 2008; Breukelaar & Dalrymple-Alford, 1998; Stevens et al., 2007).

The third experiment, using a method similar to 'item by item' presentation, provided the indication that fish are capable of spontaneously selecting the larger set relying exclusively on numerical information and without the need of an extensive training procedure. In fact in our test fish were able to choose between shoals containing different numbers of fish even if they could only see one fish at time by swimming along the glass divider beyond which the group of fish was located. However a simpler possibility to explain these results is that the focal fish did not represent the numerosity of the shoals, but simply tended to stay in places where they could see another fish and leave when they could not see companions. Because there are two empty places by the smaller shoal and only one by the larger shoal, this would imply a smaller probability of leaving the larger shoal and hence longer time spent near it. Nonetheless an analysis of the frequency of departures from each compartment revealed that fish were equally likely to leave a sector occupied by a stimulus fish or an empty one and thus apparently ruled out an explanation based on non cognitive processes.

In a previous study (Agrillo et al., 2008) we found that mosquitofish confronted with two fully visible shoals were influenced by the total areas covered by fishes when discriminating between small numbers; here we report that in different conditions they can spontaneously use number to discriminate the same quantities. The comparison of these studies hence suggests that mosquitofish can rely on multiple cues to estimate numerosity and that the access to the numerical information over the non numerical one may be task- and context-depend. To discriminate which of two mosquitofish shoals is more numerous is likely to be a complex endeavor. Shoals may be spaced out and often not simultaneously visible, fishes frequently move within the shoal, can change orientation and occlude each other. In this condition it may be advantageous to encode multiple attributes of the stimulus (number, area, movement, etc) and base number estimation on different combinations of cues depending on contextual variables such as the structure of environment, the time available for the choice, the numerosity and numerical ratio of items. Recent studies on humans and non-human primates suggest that this may be a common situation. Hurewitz and colleagues (2006) showed that adult humans asked to order two arrays of dots, spontaneously and automatically encoded information about size, area and number of dots. This study has provided evidence that the extraction of the representation of discrete quantity proceeds more rapidly than the extraction of a representation of continuous extent (the overall area occupied by stimuli) when there is a large numerical distance, while the reverse occurs when the numerical ratio comes close to 1. Experiments on pre-verbal infants using a

habituation paradigm also suggest that they attend to continuous extent and numerosity simultaneously. The relative salience of these two dimensions depends on the type of task, with infant preferentially attending to number over continuous extent when tested with large sets of objects (reviewed in Cordes & Brannon, 2008). Similarly Cantlon and Brannon (2007) showed that macaques spontaneously encode information about number, despite the fact that continuous dimensions are available to discriminate quantities. When number and continuous extent were contrasted, monkeys were more likely to use number if the numerical ratio was favorable and if they had previous laboratory experience with numerical discrimination.

For a long time numerical abilities were thought to be uniquely a human capacity, until researchers discovered that preverbal children, non-human primates and some other species of mammals and birds possess rudimentary abilities to judge quantities that are based on representation of number. Many authors now agree about the possible existence of phylogenetically shared core systems underlying number abilities of these animal species and our non-verbal numerical abilities (Dehaene, 1997). Here we found evidence that similar capacities are present also in fish suggesting that large, complex brains are not a necessary prerequisite for adding small numbers (within the subitizing range) and raising the intriguing possibility that foundation of numerical capacity may be evolutionarily more ancient, dating back at least as far as the divergence between fish and the land vertebrates.

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