Numerical Abilities in Fish

Subjects: Others

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Encoding of numerical information has been shown to provide several advantages to animal species, including those which are more evolutionary distant to humans, such as fish. Recently, we combined behavioral tasks with molecular biology assays (e.g. c-fos and egr1 and other early genes expression) showing that the thalamus and the caudal region of dorso-central part of the telencephalon seem to be activated upon change in numerousness in visual stimuli. In contrast, the retina and the optic tectum mainly responded to changes in continuous magnitude such as stimulus size.

fish cognition numerosity cognition

1. Introduction

The concept of numerosity refers to the cardinality and ordinality of a group of items, and it represents a basic characteristic of the stimuli in the environment 1223. Widespread research has been done to gather evidence of a non-verbal and non-symbolic capacity for the understanding of the number concept in humans [4][5] as well as in other animal species [6][7][8][9]. It has become apparent that the human capacity to accurately count and perform precise arithmetic arose from a much basic mechanism, likely shared with many animal species, such as mammals [10]. amphibians [11], reptiles [12], birds [13][14] and fish [15][16][17].

This system, labeled as "number sense" [18] or "Approximate Number System" (ANS) [18][19][20], is capable of accurately representing numerosities obeying to the Weber's law, which states that the change of a stimulus that is barely noticeable is a constant ratio of the original stimulus [21]. As to numerosity, this means that the distinguishability of two numerosities decreases as the magnitude of the numbers increases [22][23], the so-called "numerical size effect" [24].

It has been shown that the number sense arises very early during development. In humans, newborns and infants are able to discriminate numerosity of small sets [4][8][25][26]. A few hours old chicks (Gallus gallus) are capable of discerning different numerosities [8][13][27][28][29]. Newborns and juvenile fish can be trained to discriminate numerosity [30][31][32].

Since many species display numerical abilities, it has been hypothesized that these abilities guarantee important biological benefits. Numerical skills promote animal's survival by conferring advantages in food supply [33][34], social interaction [35] and avoiding predation [36][37][38][39].

Given that evolutionarily distant species differ widely in brain organization and complexity, how could they develop similar numerical abilities? This could be either the outcome of common ancestry from which they inherit it, or the outcome of convergent evolutionary processes promoted by similar selective pressures ^{[40][41]}.

Several techniques have been used to investigate numerical abilities in mammals ^{[42][43][44]} and birds ^{[14][27][45][46][47]} ^[48]. The most used paradigms were spontaneous choice tests, habituation-dishabituation techniques and operant techniques. Similar methods were used for fish.

2. Spontaneous Choice Tests

This procedure exploits the natural ability of fish to discriminate between two groups of biologically relevant stimuli that differ in numerosity, usually food or social companions. The rationale behind this task is that subjects are motivated to choose the larger (or smaller) group since it offers greater survival advantages (higher energy intake or protection).

Compared to other stimuli, fish are mostly attracted by social companions. Several fish species group together (shoal) so to avoid or protect against predation ^[49]. When shoals have different numbers of companions, fish prefer joining the larger one ^{[37][50][51]}. Exploiting this tendency, many studies have investigated quantitative abilities.

Mosquitofish (*Gambusia holbrooki*) appear to be able to discriminate between groups of conspecifics that differ by one unit up to four items (1 vs. 2, 2 vs. 3 and 3 vs. 4, but not 4 vs. 5; ^[52]). Guppies (*Poecilia reticulata*) show comparable behaviours ^[15].

Fish are also capable to distinguish between large numerosities (higher than four): swordtails (*Xiphophorus elleri*, ^[50]), guppies ^[15] and mosquitofish ^[52] discriminate two different quantities with a 0.50 ratio (e.g., 8 vs. 16) but not with a 0.67 ratio (e.g., 8 vs. 12), whereas angelfish (*Pterophyllum scalare*) discriminate up to a 0.56 ratio (5 vs. 9; ^[53]). It has also been shown that fish can exploit quantity discrimination to pick up a more profitable shoal depending on the sex of the composing individuals ^[54].

In all these tests stimuli are fully visible at the moment of the choice, thus fish could use continuous quantities to choose the larger shoal. Experimental strategies have been devoted to control for the role of continuous quantities, such as the total activity of the moving stimuli. Since many fish species live in a range of temperatures and their activity increases as water temperature would rise, by varying the water temperature between a larger and a smaller shoal, it is possible to balance somewhat the total activity of the two groups.

A technique to prevent fish from exploiting continuous quantities consists in first presenting two different numerical shoals at the same time and then at test limiting by occlusion the visibility of some items (i.e., one or more stimuli from the larger group are concealed to the testing fish, leaving the same number of stimuli visible in the two shoals). Using this method, zebrafish proved to choose the larger shoal in numerical comparisons involving both small (1 vs. 2 and 2 vs. 3, but not 3 vs. 4) and large numerosities (4 vs. 6, 4 vs. 8 but not 6 vs. 8), with a

discriminative accuracy that depended on the ratio between the sets to be discriminated ^[17]. Similar results were obtained in 27 days post fertilization (dpf) zebrafish larvae in 1 vs. 8 and 1 vs. 3 comparison ^[32]. Redtail splitfin fish (*Xenotoca eiseni*) tested in small numerical comparisons (1 vs. 2 and 2 vs. 3, but not 3 vs. 4) showed similar performance ^[16]. Of course, one could argue that the use of continuous physical variables was not apparent here at test but it was coded during initial exposure, and thus maintained in memory.

Another method to control continuous quantities in spontaneous choice tests consists of an "item-by-item presentation" procedure. This paradigm has been used in mammals (e.g., chimpanzees; ^[55]) and in birds (e.g., chicks; ^[46]) and consists in a sequential (or simultaneous as control) presentation of elements belonging to each group that prevent subjects a global viewing of the whole contents of the groups. Specifically, in order to solve the task, animals need to keep track of each item to form a representation of the contents of the groups and compare the two quantities.

Besides the use of conspecifics as attractive stimuli, spontaneous choice tests can be used for assessing discriminative judgments between different food quantities. Since more food leads to a better chance of survival, animals are expected to select a larger amount. This method is however less commonly used in fish, due to methodological difficulties in delivering and controlling food because of olfactory cues released in the water. A study in guppies investigated the ability to identify the larger number between two sets of food flakes pasted onto plastic cards. Fish picked up the larger food quantity in 1 vs. 4 and 2 vs. 4 (up to a 0.5 ratio) comparisons, while failing in 2 vs. 3 and 3 vs. 4 [56]. Further experiments showed that guppies paid more attention to cumulative surface area of food items rather than number, showing attraction to the larger food item even when belonging to a set with the smaller overall quantity. In spontaneous foraging tasks, angelfish showed to prefer the numerically larger food set as long as the items were sized identically, with an accuracy that depended on the numerical ratio between the two quantities [57]. However, variables such as the size and density of the food items played an important role [58][59], suggesting that numerical and continuous physical cues may not be considered separately but instead are combined by fish to maximize food intake [60].

3. Operant Training Procedures

Spontaneous discrimination takes advantage of ecological and naturalistic setups to investigate quantity discrimination abilities. However, the limitations of this method are apparent, and concern factors such as lack of motivation and difficulty in stimulus control. Discriminative failure may be driven by a lack of motivation, especially when the discrimination involves large numerosities: it is important for animals to maximize the intake strategy when dealing with few items (according to the optimal foraging theory; ^[33]), but it might not be so relevant when dealing with large numerosities, when both amounts would offer enough energy.

Another issue is related to the difficulty in controlling continuous physical variables that co-vary with numerosity using naturalistic stimuli. Some cues are not easily controllable (e.g., when using social stimuli, the overall movement and the volume of the conspecifics is hard to be taken into account). Besides, the control of some

variables does not exclude possible side effects that may influence spontaneous preference, e.g., larger pieces of food may elicit higher attraction ^{[56][58]}.

Some of these issues may be more easily overwhelmed using artificial and well-controlled stimuli combined with operant procedures. Typically, in training procedures animals are requested to discriminate between different sets of elements with different numerosity by choosing the one associated with a reward (usually food). Differently from spontaneous choice, using discrimination learning procedures it is possible to keep the animal' motivation high irrespective of the numerosities presented, allowing experimenters to accurately test the actual discriminative limits of the animals' numerical competence. Agrillo et al. ^[61] trained mosquitofish (*Gambusia holbrooki*) to discriminate between sets of visual elements (2 vs. 3) and choose the one associated with a reward (i.e., social reward). Mosquitofish proved able to discriminate between the two sets, showing however a drop of performance when either the cumulative surface area or the overall space occupied by the elements was equalized ^[61]. Similar results were obtained when mosquitofish were trained with large numerosities (higher than four elements; ^[62]), suggesting that some physical properties are spontaneously used in the learning discrimination process by fish. However, no discrimination impairment was noticed when non-numerical physical cues were simultaneously controlled for during the training ^[61].

In order to check whether processing numerosity would be more cognitively demanding than processing of continuous quantities (and thus used as a "last resort" strategy, see ^[63]), mosquitofish were trained in a 2 vs. 3 discrimination by making available either only continuous variables or only numerical information, or both simultaneously. Fish improved their performance when both numerical and physical information positively correlated than when only one of the two information were differing. However, no difference was found between the two latter conditions, suggesting that numerical information is not more cognitively demanding than other types of information ^[64].

The influence of non-numerical variables has been recently investigated in archerfish (*Toxotes* sp.). In a magnitude discrimination task between two groups of dots differing in number, archerfish showed that choice for sets with more/less dots was mainly modulated by non-numerical magnitudes (i.e., overall surface, overall perimeter, density, convex hull, average diameter) that positively correlated with number. Fish tended to select the group containing the larger non-numerical magnitudes and smaller quantities of dots, choosing the larger group of dots only when it was positively correlating with all non-numerical magnitudes ^[65].

Recent evidence suggests that zebrafish learning performance is strongly influenced by stimulus conspicuosness ^[66]. Similarly, guppies' numerical ability is improved when the stimulus saliency is enhanced by the presence of moving targets ^[67] and is worsened using an automatic conditioning chamber compared to that observed in more naturalistic settings ^[68]. It is therefore important to take into account that different methods may work well for one species but not for others, and that differences in performance may be related to procedural differences rather than cognitive limitations.

Quantitative abilities have been demonstrated in blind cavefish (*Phreatchthys andruzzii*) ^[69] trained to discriminate groups of sticks differing in numerosity in a circular thank subdivided in eight equal sectors. The experiment showed that, using the organs of lateral lines, blind cavefish proved able to discriminate between 2 vs. 4 objects when both numerical information and continuous quantities were simultaneously available, with a drop of performance when presented with stimuli controlled for continuous quantities. However, if trained from the beginning only with stimuli controlled for non-numerical quantities, cavefish proved able to learn the discrimination relying solely on numerical information.

Overall, it appears that fish numerical performances are comparable to those of mammals ^[70], birds ^{[27][71][72]}, amphibians ^{[11][73]}, reptiles ^[12] and invertebrates such as bees ^{[74][75][76]}, although discrimination accuracy is often lower than in other species such as primates ^{[77][78]} and parrots ^[79]. In these latter cases, however, animals are usually trained for a massive number of trials (thousands of trials), while fish training is usually limited to less than 100 trials. In fish, extensive training can increase numerical performance accuracy as seen in guppy ^[80] and goldfish ^[81]. Goldfish can achieve high accuracy levels (>90% correct) when exposed to extensive training (approximately 1200 trials), with performances similar to those of birds ^[79] and primates ^{[77][78]}.

4. Neural Correlates of a Sense of Continuous Magnitude in Zebrafish

The ability of fish to assess quantity (magnitude) in the continuous domain has been widely studied in zebrafish (see **Figure 1**).



Figure 1. Neural correlates of continuous magnitude estimation in zebrafish. (**A**) Time line of development of continuous magnitude sense in zebrafish embryo and larva. (**B**) Scheme of retinotectal pathways involved in object size discrimination in zebrafish larvae using ethological relevant stimuli. (**C**) The retina and optic tectum are involved in object size classification of visual stimuli in habituation/dishabituation experiments in adult zebrafish brain. See main text and **Table 1** for references.

Table 1. Summary of the main findings connected to neural correlates of continuous and discrete quantity discrimination in zebrafish.

	Stage	Findings	Literature Data
Sense of Magnitude	72 hpf	Retinal Ganglion Cells (RGCs) respond to Large Size Object	[<u>82][83]</u>
	84 hpf	Retinal Ganglion Cells (RGCs) respond to Small Size Object	[<u>84][83]</u>
	5–8	Optic tectum contains different population of neurons involved in large	[<u>85</u>]

	Stage	Findings	Literature Data
	dpf	and small size object discrimination	
		Retinal Ganglion Cells (RGCs) afferents synapt with Deeper layer of Optic Tectum for Large Size Object	
		Retinal Ganglion Cells (RGCs) afferents synapt with Superficial layer of Optic Tectum for Small Size Object	
	5–8 dpf	Size-based categorization of visual targets and involvement of Optic tectum in approach/avoidance behaviors	[<u>86][87</u>]
	5–7 dpf	Receptive field outputs and visuo-motor response in relation to object size changes	[<u>88]</u>
	9 dpf	Size-based categorization of visual targets similar to adult life	[<u>83</u>]
	Adult	Retina responds to change in size of a visual Stimulus	[<u>89</u>]
		Optic Tectum responds to change in size of a visual Stimulus	
Sense of Number	Adult	Thalamus responds to change in numerosity of a visual Stimulus	[<u>89]</u>
		Telencephalon responds to change in numerosity of a visual Stimulus	
	Ad [82]	The caudal region of the central part of <i>area dorsalis telencephali</i> (Dc) responds to change in numerosity of a visual Stimulus	[<u>90]</u>
		Numerosity-based categorization of a visual Stimulus and involvement of Dc in approach/avoidance behaviors	

tectal dendrites and connectivity (from 84 hpf to 9 dpf; ^[83]). Following the evidence that vertebrate retina contains distinct populations of retinal ganglion cells sensitive to object size ^{[91][92]}, Preuss et al. ^[86] studied distinct populations of tectal neurons involved in the discrimination between small- and large-size objects. Using calcium imaging of retinal ganglion cells (RGC) afferents to optic tectum and artificial stimuli which were previously shown to evoke different swimming patterns ^{[93][94]}, they showed that RGC afferents and tectal superficial interneurons arborize in distinct retinorecipient layers of the tectal neuropil playing a critical role in object size classification ^[85]. It was suggested that small-size-selective retinal inputs would arrive at superficial layers of tectal neuropil while large-size-selective ones to deeper layers connecting the size-based categorization of visual targets to the role played by the tectum in approach/avoidance behaviors ^{[85][87]}. Barker and Baier ^[86], combining optogenetics, imaging and single-cell reconstructions, identify specific interneurons in the optic tectum that are tuned to object size, influenced by prey-selective RGCs inputs and thus guiding behavioral choice (approach or avoidance). Finally, Helmbrecht and colleagues ^[88] extended this research by identifying how the segregation of the outputs generated by the receptive fields is converted into a visual-motor response processed by premotor nuclei located in the hindbrain of zebrafish larva.

Habituation/dishabituation experiments associated with measurements of early gene (IEGs) expression were performed on adult zebrafish by Messina et al. ^[89]. Animals were first habituated to a set of stimuli (small dots) and

then faced (dishabituation) to a similar stimulus with a change in size (threefold increased or decreased). A selective change in the expression of the immediate early genes c-fos and egr-1 in retinal and optic tectum tissues with respect to a group facing the familiar control stimulus was observed ^[89]. Overall, these findings indicate a conservative role of retina and optic tectum in the elaboration of continuous quantities in embryonic and adult zebrafish.

5. Neural Correlates of a Sense of Discrete Magnitude (Number) in Zebrafish

Recently, zebrafish studies have expanded our knowledge about the neural correlates of quantity estimation to discrete quantities (numerosity) (see **Figure 2**).



Figure 2. Neural correlates of numerosity cognition in zebrafish. (A) Possible timeline of development of number sense in zebrafish. (B) Schematic representation of telencephalic and thalamic nuclei activated upon a change in visual numerosity in zebrafish adult brain. (C) Molecular biology analyses revealed that the caudal region of central part of the area dorsalis telencephali (Dc) responds to change in numerosity of visual stimuli in adult zebrafish brain.

Combining a spontaneous habituation/dishabituation paradigm with molecular biology techniques, we explored the major brain regions involved in numerosity discrimination in adult zebrafish ^{[89][90]}. Briefly, adult zebrafish were habituated to artificial stimuli (three or nine small red dots that changed in individual size, position and density while maintaining their numerousness and overall surface from trial to trial). During the dishabituation phase, separate groups of fish faced a change in number (nine or three dots with the same overall surface) or different types of change in the stimuli (change in shape or in size) or no change at all (control group). The evaluation of the expression levels of immediate early genes, as specific markers of neural activity, revealed a main role of the thalamus and telencephalon in the elaboration of numerosity ^[89]. These results are consistent with reports of an activation of thalamic regions in number estimation in human infants using fMRI ^[95] as well as of an involvement of telencephalic/pallial structures revealed using single cell recording in primates ^{[96][97][98][99][100]} and corvids ^{[101][102]}.

Further research aimed to explore more in detail the pallial regions involved in numerosity estimation. This showed a specific activation in the most caudal part of the dorso-central (Dc) area of telencephalon for changes in numerosity, whereas the more rostral part responded to changes in shape ^[90]. To what extent this area could be considered as an equivalent of the mammalian parietal and prefrontal cortex ^{[104][105][96][106][103]} or of the nidopallium caudolaterale of corvids ^{[105][101][102][103][107]} is difficult to say. Whether zebrafish Dc is equivalent or homologous to regions in the mammalian and avian pallium ^{[40][108]} will require further investigation.

Intriguingly, the increased expression of IEGs in Dc with change from small to large numbers and the opposite trend from large to small numbers suggested that a higher or lower activation of Dc could be associated with motor execution (approach or avoidance) in association with the direction of the change in numerosity ^[90]. This was in agreement with behavioural measures. These results were also in line with hodological studies reporting that the major descending pathway of fish pallium to optic tectum and medulla oblungata are located in Dc ^{[109][110][111][112]}

Further research is needed to identify the neural circuits associated with discrete quantity estimation and elaboration in adult and larval zebrafish. In particular, the details of the ascending and descending pathways of Dc with the thalamus and the motoric areas need to be established, and our lab is currently working on this.

References

- 1. Piazza, M.; Izard, V. How Humans Count: Numerosity and the Parietal Cortex. Neuroscientist 2009, 15, 261–273.
- 2. Dehaene, S. Varieties of numerical abilities. Cognition 1992, 44, 1–42.
- 3. Piazza, M.; Pica, P.; Izard, V.; Spelke, E.S.; Dehaene, S. Education Enhances the Acuity of the Nonverbal Approximate Number System. Psychol. Sci. 2013, 24, 1037–1043.

- 4. Antell, S.E.; Keating, D.P. Perception of Numerical Invariance in Neonates. Child Dev. 1983, 54, 695–701.
- 5. Izard, V.; Sann, C.; Spelke, E.S.; Streri, A. Newborn infants perceive abstract numbers. Proc. Natl. Acad. Sci. USA 2009, 106, 10382–10385.
- 6. Agrillo, C.; Piffer, L.; Bisazza, A.; Butterworth, B. Evidence for Two Numerical Systems That Are Similar in Humans and Guppies. PLoS ONE 2012, 7, e31923.
- Carey, S.; Xu, F. Infants' knowledge of objects: Beyond object files and object tracking. Cognition 2001, 80, 179–213.
- 8. Vallortigara, G. Born Knowing; MIT Press: Cambridge, MA, USA, 2021.
- 9. Xu, F.; Carey, S. Infants' Metaphysics: The Case of Numerical Identity. Cogn. Psychol. 1996, 30, 111–153.
- 10. Cantlon, J.F.; Brannon, E.M. Basic Math in Monkeys and College Students. PLoS Biol. 2007, 5, e328.
- 11. Stancher, G.; Rugani, R.; Regolin, L.; Vallortigara, G. Numerical discrimination by frogs (Bombina orientalis). Anim. Cogn. 2014, 18, 219–229.
- 12. Gazzola, A.; Vallortigara, G.; Pellitteri-Rosa, D. Continuous and discrete quantity discrimination in tortoises. Biol. Lett. 2018, 14, 20180649.
- 13. Rugani, R.; Vallortigara, G.; Regolin, L. Numerical Abstraction in Young Domestic Chicks (Gallus gallus). PLoS ONE 2013, 8, e65262.
- 14. Rugani, R.; Vallortigara, G.; Regolin, L. From small to large: Numerical discrimination by young domestic chicks (Gallus gallus). J. Comp. Psychol. 2014, 128, 163–171.
- 15. Agrillo, C.; Petrazzini, M.E.M.; Tagliapietra, C.; Bisazza, A. Inter-Specific Differences in Numerical Abilities Among Teleost Fish. Front. Psychol. 2012, 3, 483.
- 16. Stancher, G.; Sovrano, V.A.; Potrich, D.; Vallortigara, G. Discrimination of small quantities by fish (redtail splitfin, Xenotoca eiseni). Anim. Cogn. 2013, 16, 307–312.
- 17. Potrich, D.; Sovrano, V.A.; Stancher, G.; Vallortigara, G. Quantity discrimination by zebrafish (Danio rerio). J. Comp. Psychol. 2015, 129, 388–393.
- 18. Hersh, R.; Dehaene, S. The Number Sense: How the Mind Creates Mathematics. Am. Math. Mon. 1998, 105, 975.
- 19. Feigenson, L.; Dehaene, S.; Spelke, E. Core systems of number. Trends Cogn. Sci. 2004, 8, 307– 314.
- 20. Gallistel, C.; Gelman, R. Non-verbal numerical cognition: From reals to integers. Trends Cogn. Sci. 2000, 4, 59–65.

- 21. Nieder, A. A Brain for Numbers: The Biology of the Number Instinct; MIT Press: Cambridge, MA, USA, 2019.
- 22. Moyer, R.S.; Landauer, T.K. Time required for Judgements of Numerical Inequality. Nature 1967, 215, 1519–1520.
- 23. Restle, F. Moon Illusion Explained on the Basis of Relative Size. Science 1970, 167, 1092–1096.
- 24. Longo, M.R.; Lourenco, S.F. Spatial attention and the mental number line: Evidence for characteristic biases and compression. Neuropsychologia 2007, 45, 1400–1407.
- 25. Starkey, P.; Cooper, R.G. Perception of Numbers by Human Infants. Science 1980, 210, 1033– 1035.
- 26. Starkey, P.; Spelke, E.S.; Gelman, R. Numerical abstraction by human infants. Cognition 1990, 36, 97–127.
- 27. Rugani, R.; Regolin, L.; Vallortigara, G. Discrimination of small numerosities in young chicks. J. Exp. Psychol. Anim. Behav. Process. 2008, 34, 388–399.
- 28. Rugani, R.; Regolin, L.; Vallortigara, G. Summation of Large Numerousness by Newborn Chicks. Front. Psychol. 2011, 2, 179.
- 29. Rugani, R.; Cavazzana, A.; Vallortigara, G.; Regolin, L. One, two, three, four, or is there something more? Numerical discrimination in day-old domestic chicks. Anim. Cogn. 2013, 16, 557–564.
- 30. Piffer, L.; Petrazzini, M.E.M.; Agrillo, C. Large Number Discrimination in Newborn Fish. PLoS ONE 2013, 8, e62466.
- 31. Gatto, E.; Lucon-Xiccato, T.; Savaşçı, B.B.; Dadda, M.; Bisazza, A. Experimental setting affects the performance of guppies in a numerical discrimination task. Anim. Cogn. 2016, 20, 187–198.
- Sheardown, E.; Torres-Perez, J.V.; Anagianni, S.; Fraser, S.E.; Vallortigara, G.; Butterworth, B.; Miletto-Petrazzini, M.E.; Brennan, C.H. Characterising Ontogeny of Numerosity Discrimination in Zebrafish Reveals Use of Multiple, Numerical and Non- Numerical Mechanisms. bioRxiv 2021.
- 33. Stephens, D.W.; Krebs, J.R. Foraging Theory; Princeton University Press: Princeton, NJ, USA, 1986.
- 34. Ward, C.; Smuts, B.B. Quantity-based judgments in the domestic dog (Canis lupus familiaris). Anim. Cogn. 2006, 10, 71–80.
- 35. Mc Comb, K.; Packer, C.; Pusey, A. Roaring and numerical assessment in contests between groups of female lions, Panthera leo. Anim. Behav. 1994, 47, 379–387.
- 36. Wilson, D.J.; Bromley, R.G. Functional and numerical responses of predators to cyclic lemming abundance: Effects on loss of goose nests. Can. J. Zool. 2001, 79, 525–532.

- 37. Hager, M.C.; Helfman, G.S. Safety in numbers: Shoal size choice by minnows under predatory threat. Behav. Ecol. Sociobiol. 1991, 29, 271–276.
- 38. Cresswell, W. Predation in bird populations. J. Ornithol. 2010, 152, 251–263.
- 39. Wedell, N.; Gage, M.J.; Parker, G.A. Sperm competition, male prudence and sperm-limited females. Trends Ecol. Evol. 2002, 17, 313–320.
- 40. Nieder, A. Neuroethology of number sense across the animal kingdom. J. Exp. Biol. 2021, 224.
- 41. Nieder, A. The Evolutionary History of Brains for Numbers. Trends Cogn. Sci. 2021, 25, 608–621.
- 42. Beran, M.J.; Smith, J.D.; Redford, J.S.; Washburn, D.A. Rhesus macaques (macaca mulatta) monitor uncertainty during numerosity judgments. J. Exp. Psychol. Anim. Behav. Process. 2006, 32, 111–119.
- 43. Jordan, K.E.; MacLean, E.; Brannon, E.M. Monkeys match and tally quantities across senses. Cognition 2008, 108, 617–625.
- 44. Beran, M.J.; Parrish, A.E. Visual nesting of stimuli affects rhesus monkeys' (Macaca mulatta) quantity judgments in a bisection task. Atten. Percept. Psychophys. 2013, 75, 1243–1251.
- 45. Al Aïn, S.; Giret, N.; Grand, M.; Kreutzer, M.; Bovet, D. The discrimination of discrete and continuous amounts in African grey parrots (Psittacus erithacus). Anim. Cogn. 2008, 12, 145–154.
- 46. Rugani, R.; Fontanari, L.; Simoni, E.; Regolin, L.; Vallortigara, G. Arithmetic in newborn chicks. Proc. R. Soc. B Boil. Sci. 2009, 276, 2451–2460.
- 47. Rugani, R.; Regolin, L.; Vallortigara, G. Imprinted numbers: Newborn chicks' sensitivity to number vs. continuous extent of objects they have been reared with. Dev. Sci. 2010, 13, 790–797.
- Bertamini, M.; Guest, M.; Vallortigara, G.; Rugani, R.; Regolin, L. The effect of clustering on perceived quantity in humans (Homo sapiens) and in chicks (Gallus gallus). J. Comp. Psychol. 2018, 132, 280–293.
- 49. Hamilton, W. Geometry for the selfish herd. J. Theor. Biol. 1971, 31, 295–311.
- 50. Wong, B.; Rosenthal, G.; Buckingham, J. Shoaling decisions in female swordtails: How do fish gauge group size? Behaviour 2007, 144, 1333–1346.
- 51. Mehlis, M.; Thünken, T.; Bakker, T.C.M.; Frommen, J.G. Quantification acuity in spontaneous shoaling decisions of three-spined sticklebacks. Anim. Cogn. 2015, 18, 1125–1131.
- 52. Agrillo, C.; Dadda, M.; Serena, G. Choice of Female Groups by Male Mosquitofish (Gambusia holbrooki). Ethology 2008, 114, 479–488.
- 53. Gómez-Laplaza, L.M.; Gerlai, R. Can angelfish (Pterophyllum scalare) count? Discrimination between different shoal sizes follows Weber's law. Anim. Cogn. 2010, 14, 1–9.

- 54. Agrillo, C.; Dadda, M.; Serena, G.; Bisazza, A. Do fish count? Spontaneous discrimination of quantity in female mosquitofish. Anim. Cogn. 2008, 11, 495–503.
- 55. Beran, M.J.; McIntyre, J.M.; Garland, A.; Evans, T.A. What counts for 'counting'? Chimpanzees, Pan troglodytes, respond appropriately to relevant and irrelevant information in a quantity judgment task. Anim. Behav. 2013, 85, 987–993.
- Lucon-Xiccato, T.; Petrazzini, M.E.M.; Agrillo, C.; Bisazza, A. Guppies discriminate between two quantities of food items but prioritize item size over total amount. Anim. Behav. 2015, 107, 183– 191.
- 57. Gómez-Laplaza, L.M.; Díaz-Sotelo, E.; Gerlai, R. Quantity discrimination in angelfish, Pterophyllum scalare: A novel approach with food as the discriminant. Anim. Behav. 2018, 142, 19–30.
- 58. Gómez-Laplaza, L.M.; Romero, L.; Gerlai, R. The role of item size on choosing contrasted food quantities in angelfish (Pterophyllum scalare). Sci. Rep. 2019, 9, 1–12.
- 59. Gómez-Laplaza, L.M.; Gerlai, R. Food density and preferred quantity: Discrimination of small and large numbers in angelfish (Pterophyllum scalare). Anim. Cogn. 2020, 23, 509–522.
- 60. Gómez-Laplaza, L.M.; Gerlai, R. Food Quantity Discrimination in Angelfish (Pterophyllum scalare): The Role of Number, Density, Size and Area Occupied by the Food Items. Front. Behav. Neurosci. 2020, 14, 106.
- 61. Agrillo, C.; Dadda, M.; Serena, G.; Bisazza, A. Use of Number by Fish. PLoS ONE 2009, 4, e4786.
- 62. Agrillo, C.; Piffer, L.; Bisazza, A. Large Number Discrimination by Mosquitofish. PLoS ONE 2010, 5, e15232.
- 63. Davis, H.; Pérusse, R. Numerical competence in animals: Definitional issues, current evidence, and a new research agenda. Behav. Brain Sci. 1988, 11, 561–579.
- 64. Agrillo, C.; Piffer, L.; Bisazza, A. Number versus continuous quantity in numerosity judgments by fish. Cognition 2011, 119, 281–287.
- 65. Leibovich-Raveh, T.; Raveh, A.; Vilker, D.; Gabay, S. Magnitude integration in the Archerfish. Sci. Rep. 2021, 11, 1–10.
- 66. Gatto, E.; Lucon-Xiccato, T.; Bisazza, A.; Manabe, K.; Dadda, M. The devil is in the detail: Zebrafish learn to discriminate visual stimuli only if salient. Behav. Process. 2020, 179, 104215.
- 67. Agrillo, C.; Petrazzini, M.E.M.; Bisazza, A. Numerical acuity of fish is improved in the presence of moving targets, but only in the subitizing range. Anim. Cogn. 2013, 17, 307–316.

- 68. Gatto, E.; Testolin, A.; Bisazza, A.; Zorzi, M.; Lucon-Xiccato, T. Poor numerical performance of guppies tested in a Skinner box. Sci. Rep. 2020, 10, 1–9.
- 69. Bisazza, A.; Tagliapietra, C.; Bertolucci, C.; Foà, A.; Agrillo, C. Non-visual numerical discrimination in a blind cavefish (Phreatichthys andruzzii). J. Exp. Biol. 2014, 217, 1902–1909.
- Jaakkola, K.; Fellner, W.; Erb, L.; Rodriguez, M.; Guarino, E. Understanding of the concept of numerically "less" by bottlenose dolphins (Tursiops truncatus). J. Comp. Psychol. 2005, 119, 296– 303.
- 71. Rugani, R.; Vallortigara, G.; Regolin, L. The use of proportion by young domestic chicks (Gallus gallus). Anim. Cogn. 2014, 18, 605–616.
- 72. Rugani, R.; McCrink, K.; De Hevia, M.-D.; Vallortigara, G.; Regolin, L. Ratio abstraction over discrete magnitudes by newly hatched domestic chicks (Gallus gallus). Sci. Rep. 2016, 6, 30114.
- 73. Krusche, P.; Uller, C.; Dicke, U. Quantity discrimination in salamanders. J. Exp. Biol. 2010, 213, 1822–1828.
- 74. Bortot, M.; Agrillo, C.; Avarguès-Weber, A.; Bisazza, A.; Petrazzini, M.E.M.; Giurfa, M. Honeybees use absolute rather than relative numerosity in number discrimination. Biol. Lett. 2019, 15, 20190138.
- 75. Bortot, M.; Regolin, L.; Vallortigara, G. A sense of number in invertebrates. Biochem. Biophys. Res. Commun. 2020, 564, 37–42.
- 76. Bortot, M.; Stancher, G.; Vallortigara, G. Transfer from Number to Size Reveals Abstract Coding of Magnitude in Honeybees. iScience 2020, 23, 101122.
- 77. Tomonaga, M. Relative numerosity discrimination by chimpanzees (Pan troglodytes): Evidence for approximate numerical representations. Anim. Cogn. 2007, 11, 43–57.
- 78. Beran, M.J. Monkeys (Macaca mulatta and Cebus apella) track, enumerate, and compare multiple sets of moving items. J. Exp. Psychol. Anim. Behav. Process. 2008, 34, 63–74.
- 79. Pepperberg, I.M. Ordinality and inferential abilities of a grey parrot (Psittacus erithacus). J. Comp. Psychol. 2006, 120, 205–216.
- 80. Bisazza, A.; Agrillo, C.; Lucon-Xiccato, T. Extensive training extends numerical abilities of guppies. Anim. Cogn. 2014, 17, 1413–1419.
- 81. DeLong, C.M.; Barbato, S.; O'Leary, T.; Wilcox, K. Small and large number discrimination in goldfish (Carassius auratus) with extensive training. Behav. Process. 2017, 141, 172–183.
- 82. Easter, S.S.; Nicola, G.N. The development of vision in the zebrafish (Danio rerio). Dev. Biol. 1996, 180, 646–663.

- 83. Niell, C.M.; Smith, S.J. Functional Imaging Reveals Rapid Development of Visual Response Properties in the Zebrafish Tectum. Neuron 2005, 45, 941–951.
- 84. Niell, C.M.; Meyer, M.; Smith, S.J. In vivo imaging of synapse formation on a growing dendritic arbor. Nat. Neurosci. 2004, 7, 254–260.
- 85. Preuss, S.J.; Trivedi, C.; Berg, C.V.; Ryu, S.; Bollmann, J.H. Classification of Object Size in Retinotectal Microcircuits. Curr. Biol. 2014, 24, 2376–2385.
- 86. Barker, A.; Baier, H. Sensorimotor Decision Making in the Zebrafish Tectum. Curr. Biol. 2015, 25, 2804–2814.
- 87. Abbas, F.; Meyer, M.P. Fish vision: Size selectivity in the zebrafish retinotectal pathway. Curr. Biol. 2014, 24, R1048.
- 88. Helmbrecht, T.O.; Maschio, M.D.; Donovan, J.C.; Koutsouli, S.; Baier, H. Topography of a Visuomotor Transformation. Neuron 2018, 100, 1429–1445.e4.
- Messina, A.; Potrich, D.; Schiona, I.; Sovrano, V.A.; Fraser, S.; Brennan, C.H.; Vallortigara, G. Response to change in the number of visual stimuli in zebrafish: A behavioural and molecular study. Sci. Rep. 2020, 10, 1–11.
- Messina, A.; Potrich, D.; Schiona, I.; Sovrano, V.A.; Fraser, S.E.; Brennan, C.H.; Vallortigara, G. Neurons in the Dorso-Central Division of Zebrafish Pallium Respond to Change in Visual Numerosity. Cereb. Cortex 2021.
- 91. Levick, W.R. Receptive fields and trigger features of ganglion cells in the visual streak of the rabbit's retina. J. Physiol. 1967, 188, 285–307.
- 92. Ölveczky, B.P.; Baccus, S.A.; Meister, M. Segregation of object and background motion in the retina. Nature 2003, 423, 401–408.
- 93. Bianco, I.H.; Kampff, A.R.; Engert, F. Prey Capture Behavior Evoked by Simple Visual Stimuli in Larval Zebrafish. Front. Syst. Neurosci. 2011, 5, 101.
- Trivedi, C.A.; Bollmann, J.H. Visually driven chaining of elementary swim patterns into a goaldirected motor sequence: A virtual reality study of zebrafish prey capture. Front. Neural Circuits 2013, 7, 86.
- 95. Kovas, Y.; Giampietro, V.; Viding, E.; Ng, V.; Brammer, M.; Barker, G.; Happé, F.G.E.; Plomin, R. Brain Correlates of Non-Symbolic Numerosity Estimation in Low and High Mathematical Ability Children. PLoS ONE 2009, 4, e4587.
- 96. Nieder, A. The neuronal code for number. Nat. Rev. Neurosci. 2016, 17, 366–382.
- 97. Nieder, A.; Freedman, D.J.; Miller, E.K. Representation of the Quantity of Visual Items in the Primate Prefrontal Cortex. Science 2002, 297, 1708–1711.

- 98. Nieder, A.; Merten, K. A Labeled-Line Code for Small and Large Numerosities in the Monkey Prefrontal Cortex. J. Neurosci. 2007, 27, 5986–5993.
- 99. Piazza, M.; Izard, V.; Pinel, P.; Le Bihan, D.; Dehaene, S. Tuning Curves for Approximate Numerosity in the Human Intraparietal Sulcus. Neuron 2004, 44, 547–555.
- 100. Nieder, A. Coding of abstract quantity by 'number neurons' of the primate brain. J. Comp. Physiol. A 2012, 199, 1–16.
- 101. Ditz, H.M.; Nieder, A. Neurons selective to the number of visual items in the corvid songbird endbrain. Proc. Natl. Acad. Sci. USA 2015, 112, 7827–7832.
- 102. Ditz, H.M.; Nieder, A. Numerosity representations in crows obey the Weber–Fechner law. Proc. R. Soc. B Boil. Sci. 2016, 283, 20160083.
- 103. Nieder, A. Evolution of cognitive and neural solutions enabling numerosity judgements: Lessons from primates and corvids. Philos. Trans. R. Soc. B Biol. Sci. 2018, 373, 20160514.
- 104. Piazza, M.; Eger, E. Neural foundations and functional specificity of number representations. Neuropsychologia 2016, 83, 257–273.
- 105. Viswanathan, P.; Nieder, A. Neuronal correlates of a visual "sense of number" in primate parietal and prefrontal cortices. Proc. Natl. Acad. Sci. USA 2013, 110, 11187–11192.
- 106. Viswanathan, P.; Nieder, A. Spatial Neuronal Integration Supports a Global Representation of Visual Numerosity in Primate Association Cortices. J. Cogn. Neurosci. 2020, 32, 1184–1197.
- 107. Wagener, L.; Loconsole, M.; Ditz, H.M.; Nieder, A. Neurons in the Endbrain of Numerically Naive Crows Spontaneously Encode Visual Numerosity. Curr. Biol. 2018, 28, 1090–1094.e4.
- 108. Lorenzi, E.; Perrino, M.; Vallortigara, G. Numerosities and Other Magnitudes in the Brains: A Comparative View. Front. Psychol. 2021, 12.
- 109. Yamamoto, N.; Ito, H. Fiber connections of the anterior preglomerular nucleus in cyprinids with notes on telencephalic connections of the preglomerular complex. J. Comp. Neurol. 2005, 491, 212–233.
- Ishikawa, Y.; Yamamoto, N.; Yoshimoto, M.; Yasuda, T.; Maruyama, K.; Kage, T.; Takeda, H.; Ito, H. Developmental Origin of Diencephalic Sensory Relay Nuclei in Teleosts. Brain Behav. Evol. 2007, 69, 87–95.
- 111. Harvey-Girard, E.; Giassi, A.C.; Ellis, W.; Maler, L. Organization of the gymnotiform fish pallium in relation to learning and memory: IV. Expression of conserved transcription factors and implications for the evolution of dorsal telencephalon. J. Comp. Neurol. 2012, 520, 3395–3413.
- 112. Ito, H.; Yamamoto, N. Non-laminar cerebral cortex in teleost fishes? Biol. Lett. 2008, 5, 117–121.

113. Rodríguez, F.; Quintero, B.; Amores, L.; Madrid, D.; Salas-Peña, C.; Salas, C. Spatial Cognition in Teleost Fish: Strategies and Mechanisms. Animals 2021, 11, 2271.

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