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Spontaneous versus trained numerical abilities. A comparison between the two main tools to study numerical competence in non-human animals

Christian Agrillo*, Angelo Bisazza

Department of General Psychology, University of Padova, Italy

HIGHLIGHTS

- Numerical abilities have been reported in a wide range of non-human animals.
- Two main approaches have been adopted: spontaneous choice tests and training procedures.
- The two methodologies seem to lead to different results.
- We review pros and cons of studying spontaneous and trained numerical abilities.

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ABSTRACT

A large body of experimental evidence shows that animals as diverse as mammals, birds, and fish are capable of processing numerical information. Considerable differences have been reported in some cases among species and a wide debate currently surrounds the issue of whether all vertebrates share the same numerical systems or not. Part of the problem is due to the fact that these studies often use different methods, a circumstance that potentially introduces confounding factors in a comparative analysis.

In most studies, two main methodological approaches have been used: spontaneous choice tests and training procedures. The former approach consists of presenting to the subjects two groups of biologically-relevant stimuli (e.g., food items or social companions) differing in numerosity with the assumption that if they are able to discriminate between the two quantities, they are expected to spontaneously select the larger/smaller quantity. In the latter approach, subjects undergo extensive training in which some neutral stimuli (e.g., a quantity of dots) are associated with a reward and the capacity to learn a numerical rule is taken as evidence of numerical abilities.

We review the literature on this topic, highlighting the relevance, and potential weaknesses in controlling confounding factors obtained with either approach.

Contents

* Corresponding author at: Department of General Psychology, Via Venezia 8, 35131 Padova, Italy. Tel.: +39 0498276931; fax: +39 0498276600.
E-mail address: christian.agrillo@unipd.it (C. Agrillo).

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1. Introduction

In the last decade the study of numerical abilities has become one of the main issues in cognitive neuroscience. Numbers are an essential feature of everyday life, allowing us to conduct functions as diverse as estimating the shortest queue at the supermarket, checking if our change is correct, or designing a bridge. Behavioral and neuroimaging studies converge to indicate that humans display multiple cognitive systems for number processing. Symbolic numerical abilities are strictly related to culture and language and permit us to learn the wide range of symbols and syntax required in school mathematics. Neuroimaging studies have shown that these abilities rely on a large number of brain regions, such as the intraparietal sulcus, prefrontal cortex, cingulate gyri, the insula, and the cerebellum (reviewed in Arsalidou and Taylor, 2011). However, cross-cultural, developmental and experimental evidences indicate that humans possess other numerical abilities that are not related to language and culture. Mundurukù, an Amazonian population that lacks vocabulary for numbers beyond five, can nevertheless discriminate between much larger quantities (Pica et al., 2004). Infants can discriminate between 6 and 12 objects at six months, well before the emergence of language (Xu and Spelke, 2000). These abilities, often called non-symbolic numerical abilities (Gilmore et al., 2010; Price et al., 2012; Zebian and Ansari, 2012), permit us to discriminate 9 from 10 items in no more than 150 ms (Halberda et al., 2008). Neuroimaging studies suggest that symbolic and non-symbolic numerical abilities recruit partially different neural circuits (Holloway et al., 2010). For instance, while both symbolic and non-symbolic representations activate the right intraparietal sulcus, symbolic numerical abilities are primarily processed in the left hemisphere while non-symbolic numerical abilities recruit the right hemisphere (Chassy and Grodd, 2012).

Several lines of research indicate that our symbolic numerical abilities are based on non-symbolic numerical systems (Agrillo et al., 2013; Halberda et al., 2008; Park and Brannon, 2013). Also, deficits in the study of mathematics, such as dyscalculia, seem to be associated with low performance in non-symbolic numerical tasks (Piazza et al., 2010; Furman and Rubinsten, 2012). In this sense, the study of non-symbolic numerical abilities becomes crucial to understanding the foundation of our mathematical abilities.

Until a few decades ago, it was assumed that non-symbolic numerical abilities could only be studied in our species. Today we know that other vertebrates share the capacity to discriminate between quantities and make simple calculations (i.e., mammals: Vonk, 2014; Perdue et al., 2012; birds: Emmerton and Renner, 2006; Farnsworth and Smolinski, 2006; fish: Agrillo et al., 2014; Gómez-Laplaza and Gerlai, 2013). There are many ecological situations in which numerical abilities can be useful. Hyenas, for instance, are more willing to enter social contests when their group outnumbers that of opponents (Benson-Amram et al., 2011). Numerical capacities can be important in guiding foraging decisions such as selecting the larger amount of food (Normand et al., 2009) or the optimal quantity of preys (Panteleeva et al., 2012). The ability to compare numerosities can enable animals to select the group with the more advantageous sex ratio (Flay et al., 2009) or to dilute predation risks by getting protection within the largest group of social companions (Hager and Helfman, 1991).

As we have all experienced in everyday life, for example when searching for an uncrowded train carriage or selecting the best fruit basket, we can discriminate between different quantities without necessarily counting the number of objects in each group. Numerosity normally covaries with several other physical attributes, and animals can use the relative magnitude of non-numerical cues, such as the total area of the stimuli or the overall space occupied by the sets or their density. Human and other animals can estimate which group is larger/smaller by using these non-numerical cues (hereafter "continuous quantities", Beran et al., 2008a; Cantlon and Brannon, 2007b; Gebuis and Reynvoet, 2012; Gómez-Laplaza and Gerlai, 2012, 2013). For example, cats were able to learn to discriminate between two and three dots to get a food reward. However, as soon as the cumulative surface area was controlled for, their performance dropped to chance level, suggesting that cats primarily based their choice on continuous quantities instead of numbers (Pisa and Agrillo, 2009). Also, salamanders were able to discriminate between 8 and 16 crickets but careful controls showed that they used the overall quantity of movement of these potential preys instead of their numerosity (Krusche et al., 2010). In this sense, before assuming that a species possesses a specific numerical ability, it is necessary to strictly control for continuous quantities, a challenge that represents one of the most critical issues in this research field (see Sections 2 and 3 for more details).

Indeed, as we will see later, several non-human animals proved able to discriminate between quantities even when prevented from using continuous quantities, and numerical abilities are often very similar in distantly related species. These findings prompted a debate as to whether all animal species share the same numerical systems and if these are homologous to our non-symbolic numerical systems. This issue becomes even more relevant regarding the possibility of developing animal models to study neural circuits of number processing and the biological basis of learning disabilities in the acquisition of mathematical abilities.

Inter-specific comparisons have led to mixed results. Some studies reported similar performances in distantly related species. For instance, one study showed that New Zealand robins can discriminate between 1 vs. 2, 2 vs. 3, and 3 vs. 4, while their performance significantly decreases in 4 vs. 5 (Hunt et al., 2008) – a similar numerical acuity exhibited by distantly related species such as guppies (Agrillo et al., 2012a), and mosquitofish (Agrillo et al., 2008a). The accuracy in relative numerosity judgments of bears (Vonk and Beran, 2012), dogs (Ward and Smuts, 2007), parrots (Al Aïn et al., 2009), and angelfish (Gómez-Laplaza and Gerlai, 2011a) is affected by the numerical ratio between the matched numerosity, as commonly reported in humans (Revkin et al., 2008) and non-human primates (Beran, 2004; Cantlon and Brannon, 2007a). Even mosquitofish and college students show surprising similarities when tested with the same numerical contrasts (Agrillo et al., 2010).

Other studies, however, highlighted differences in performance among different vertebrates. For example, horses, domestic chicks, salamanders, and angelfish discriminate between groups differing by one unit and up to 2 vs. 3 (Gómez-Laplaza and Gerlai, 2011b; Rugani et al., 2008; Uller and Lewis, 2009; Uller et al., 2003), while robins, guppies, and mosquitofish discriminate between 3 vs. 4 (Agrillo et al., 2008a, 2012c; Hunt et al., 2008). Trained pigeons can discriminate up to 6 vs. 7, a numerical acuity not observed in untrained birds (Al Aïn et al., 2009; Rugani et al., 2009). Difference in performances have been reported even between closely related species: the accuracy of African elephants is affected by the numerical ratio (Perdue et al., 2012) while the accuracy of Asian elephants appears to be insensitive to the numerical ratio (Irie-Sugimoto et al., 2009; Irie and Hasegawa, 2012).

In sum, while some studies highlighted similar performance among vertebrates, others remarked upon the inter-specific differences. Part of the inconsistencies reported in the literature might be ascribed to the different methodology adopted (Agrillo and Miletto Petrazzini, 2012), such as different paradigms (e.g., spontaneous behavior vs. trained behavior), different stimuli (e.g., food, social companions, dots), and sensory modality (e.g., visual vs. auditory stimuli). In some cases, there is evidence that different methods of measuring numerical abilities can lead to different results in the same species. For instance, goldbelly topminnows could discriminate up to 2 vs. 3 companions with one experimental procedure