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Review

Numerical abilities in fish: A methodological review

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ABSTRACT

The ability to utilize numerical information can be adaptive in a number of ecological contexts including foraging, mating, parental care, and anti-predator strategies. Numerical abilities of mammals and birds have been studied both in natural conditions and in controlled laboratory conditions using a variety of approaches. During the last decade this ability was also investigated in some fish species. Here we reviewed the main methods used to study this group, highlighting the strengths and weaknesses of each of the methods used. Fish have only been studied under laboratory conditions and among the methods used with other species, only two have been systematically used in fish—spontaneous choice tests and discrimination learning procedures. In the former case, the choice between two options is observed in a biologically relevant situation and the degree of preference for the larger/smaller group is taken as a measure of the capacity to discriminate the two quantities (e.g., two shoals differing in number). In discrimination learning tasks, fish are trained to select the larger or the smaller of two sets of abstract objects, typically two-dimensional geometric figures, using food or social companions as reward. Beyond methodological differences, what emerges from the literature is a substantial similarity of the numerical abilities of fish with those of other vertebrates studied.

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1. Introduction

Several field studies suggested that numerical abilities are useful for mammals and birds to solve different problems in their natural environment. For instance, chimpanzees (*Pan troglodytes*, Wilson et al., 2002), lions (*Panthera leo*, McComb et al., 1994) and feral dogs (*Canis lupus familiaris*, Bonanni et al., 2011) are more willing to engage in fights when their group outnumbers that of opponents. Number judgments are important for anti-predator strategies as the probability of being captured by predators diminishes when individuals join a larger group of social companions (e.g., redshanks, *Tringa totanus*, Cresswell, 1994); for this reason, several species prefer to join a larger group of social companions when exposed to predators (e.g., Cresswell and Quinn, 2011). Numerical abilities

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can provide benefits in mate choice too (Wedell et al., 2002); for instance, the ability to count the number of conspecifics enables bank voles (*Myodes glareolus*) to adjust their reproductive strategy to the level of sperm competition, with males producing more sperm in the presence of multiple competitors (Lemaitre et al., 2011). Foraging decisions represent another ecological context in which animals can take advantage of numerical abilities; it has been shown that New Zealand robins (*Petroica australis*, Hunt et al., 2008) and rhesus monkeys (*Macaca mulatta*, Hauser et al., 2000) can select the larger amount of food in order to optimize food intake.

It is likely that similar selective pressures in favour of the ability to select the larger/smaller group of objects are present in other organisms; and indeed, the quantificational abilities in other taxonomic groups, particularly bony fish, have been recently investigated. Several fish species are known to join the larger shoal when exploring a potentially dangerous environment in order to reduce the risks of being predated (Hager and Helfman, 1991; Pritchard et al., 2001; Svensson et al., 2000). The risk of an individual fish being caught diminishes as the quantity of individuals in the group increases, a phenomenon typically called the 'dilution effect' (Foster and Treherne, 1981). Also, living in larger shoals makes it more difficult for a predator to single out an individual prey ('confusion effect', see Landeau and Terborgh, 1986) and increases the possibility of detecting predators ('many eyes effect', Pulliam, 1973). Many piscine predators suffer a low capture success rate when attacking groups of prey (e.g., Krause and Godin, 1995). Indeed some studies have found a preference for attacking individual prey or smaller groups (Milinski, 1977a, 1977b; Morgan and Godin, 1985; but see Botham et al., 2005 for the reverse preference) showing that the capacity to discriminate the larger/smaller shoal is present in both prey and predators.

Numerical abilities may also provide benefits in resource competition as it was found that banded killifish (*Fundulus diaphanus*) form smaller shoals when food is available, probably to reduce the competition for food resources (Hoare et al., 2004). In species with parental care, a further advantage of estimating quantities is the possibility to adjust parental behaviour as a function of the number of the progeny, and it has been recently demonstrated that female convict cichlids (*Amatitlania nigrofasciata*) in the presence of fry groups differing in number attempt to recover preferentially the fry from the larger group in order to increase their fitness (Forsatkar et al., 2016). Lastly, the capacity to discriminate the sex ratio of social groups in mosquitofish (*Gambusia holbrooki*) and guppies (*Poecilia reticulata*) is thought to allow males to adjust their reproductive strategies to the existing level of sperm competition (Lindström and Ranta, 1993; Smith and Sargent, 2006).

These kinds of studies give us little information about the exact mechanisms used by animals to solve numerical problems. For instance, in the above examples animals could have used non-numerical mechanisms to discriminate the larger or smaller quantity. They could for example have compared continuous quantities that co-vary with numbers, such as cumulative area occupied by the objects, their density, or the convex hull (that is, the overall space occupied by the most lateral objects of the groups). To understand whether animals really use numerical information and to shed light on the cognitive mechanisms that underlie these abilities it is therefore necessary to conduct controlled experiments in the laboratory.

A wide range of techniques has been developed to investigate these issues in mammals and birds. For example, laboratory studies strictly controlling for continuous quantities (e.g., cumulative surface area or density) demonstrated that several mammals (e.g., chimpanzees *Pan troglodytes*: Garland et al., 2014; dogs: West and Young, 2002) and birds (New Zealand robins, Garland et al., 2012; parrots *Psittacus erithacus*, Pepperberg, 2006) can solve most quantitative tasks by using numerical information only. The strengths and limitations in the use of these different methods have been the subject of a recent review (Agrillo and Bisazza, 2014). Because of their morphology, the type of locomotion, the size of the species commonly used and the fact that they live in an aquatic medium, fish cannot be easily investigated with some of the techniques developed for studying warm-blooded vertebrates and in recent years specific methods have been developed to study the numerical ability of fish.

In this paper, we review the methods that have been used to investigate numerical abilities in teleost fish and summarize the results that have been obtained. In particular, we focus on the comparison between the two main methods that have been adopted in studying fish, spontaneous choice tests and discrimination learning procedures, highlighting the strengths and weaknesses of each approach and comparing the results obtained using these two different methodologies.

2. Methodology for the study of quantity discrimination in fish

Although a wider range of methodologies have been used in mammals and birds (Hauser et al., 2002; West and Young, 2002), without exceptions we can split the literature on numerical abilities in fish into two main methodological approaches: spontaneous choice tests and discrimination learning procedures.

2.1. Spontaneous choice tests

Spontaneous choice tests typically take advantage of the natural tendency of an animal to prefer more or less of something. The subject is presented with two sets containing different numbers of biologically-relevant stimuli. In mammal and bird studies, pieces of food represent the most common type of stimuli presented in these tests. For instance, one study tested the spontaneous ability of rhesus monkeys to choose the larger quantity of plums presented on two separate plates (Sulkowski and Hauser, 2001). The assumption underlying these tests is that, if animals are able to discriminate between the two quantities, they are expected to select the most advantageous option in terms of food intake (in this case the larger quantity). In fish research, two types of stimuli have been used: social companions (shoal quantity discrimination) and food items (food quantity discrimination).

2.1.1.1. Shoal quantity discrimination

Social companions are by far the most common type of stimuli used in these tests with fish. This is due to the fact that sociality is the main anti-predatory strategy for many fish and the advantages of living in a group tend to increase as the number of individuals in the group increases. As a consequence, individual fish that are inserted in an unfamiliar and potentially dangerous environment tend to join other conspecifics and, if two shoals are present, they show a strong tendency to join the larger shoal (Buckingham et al., 2007; Hager and Helfman, 1991; Mehlis et al., 2015). Several studies have taken advantage of this anti-predator behaviour to assess the limits of quantity discrimination. Typically, a single subject is inserted into an unfamiliar empty tank where two groups of social companions are visible. The visual contact of a potential predator is not necessary as the unfamiliar environment is sufficient to increase subjects' motivation to join the larger group. The proportion of time spent near the larger shoal is recorded as a measure of quantity discrimination (Fig. 1a).

Using this procedure, it was found that mosquitofish (*Gambusia holbrooki*) can discriminate groups differing by one unit up to 4 items (1 vs. 2, 2 vs. 3, and 3 vs. 4, but not 4 vs. 5; Agrillo et al., 2008a). A closely-related species, the guppy (*Poecilia reticulata*), exhibits the same limit when tested in similar conditions