Cognition in fishes

[Introduction to a special issue of Behavioural Processes on Cognition in Fishes]

Noam Miller

Department of Psychology, Wilfrid Laurier University, 75 University Ave. West, Waterloo, ON, N2L 3C5, Canada

Email: nmiller@wlu.ca

1. Introduction

Fish make up more than half of all vertebrate species and inhabit an amazing range of aquatic environments, from fast-moving rivers to evaporating tide pools to the anoxic ocean floor (Nelson et al., 2016). Over the course of their evolution, fish have developed remarkable physical adaptations to thrive in these environments. Fins, to take just one example, have been stiffened and jointed for skipping through mud, lengthened into wings for gliding above the ocean surface (where aquatic predators cannot follow), and shaped into a tube to serve as reproductive organs.

Unsurprisingly, fish have evolved a correspondingly wide range of behaviors and cognitive skills to cope with this ecological diversity (Bshary & Brown, 2014), and the past several years have seen an explosion in research on fish cognition (Figure 1). Much of the initial research catalogued the cognitive abilities that fish possess, following schemata developed for mammalian and avian species. As the papers in the current issue demonstrate, researchers are now uncovering the mechanisms by which these cognitive feats are achieved, tracing the evolution of different behavioural solutions to environmental challenges, and charting the conditions under which various abilities are displayed.
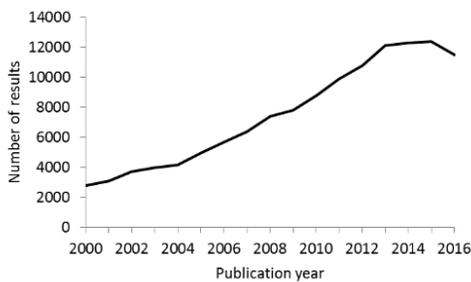
Figure 1: number of publications on fish cognition. The graph shows the number of results returned from a search for "fish cognition" on Google Scholar, by publication year, for the years 2000-2016 (the search was conducted on February 23, 2017).

Fish show divided-attention effects when foraging (silver perch, *Bidyanus bidyanus*, Warburton & Thomson, 2006), have long-term (Carp, *Cyprinus carpio*, Beukema, 1970; Sockeye salmon, *Oncorhynchus nerka*, Tarrant, 1964) and episodic-like memories (zebrafish, *Danio rerio*, Hamilton et al., 2016; see also Gerlai, 2017), and display circadian rhythmicity in their behaviour (reviewed in Reebs, 2002). They can acquire time-place associations (Angelfish, *Pterohyllum scalare*, Gómez-Laplaza & Morgan, 2005), perform transitive inferences (cichlids, *Astatotilapia burtoni*, Grosenick et al., 2007), and show audience effects in modulating their foraging (cleaner wrasse, *Labriodes dimidiatus*; Bshary & Grutter, 2006). Fish form complex spatial representations of their environments (Gobys, *Bathygobius soporator*, Aronson, 1951, 1971; reviews in Odling-Smee et al., 2006), including learning its geometry (goldfish, *Carassius auratus*, Broglio et al., 2000). Some species form and use tools in flexible ways (archerfish, *Toxotes jaculatrix*, Gerullis & Schuster, 2014) or engage in elaborate courtship displays (three-spine sticklebacks, *Gasterosteus aculeatus*, Tinbergen, 1952) which sometimes include the construction of nests (reviewed in Barber, 2013).

In all these fields and many others, the recorded abilities of fish have been quickly catching up to those of better-studied taxa. In a few disciplines, however, fish have become the model species of choice. For scientists studying animal numerical abilities, 'personalities', and social or collective behaviours (and the

growing intersections between these areas), research on fish has often led the way in understanding the mechanisms and evolution of cognition.

2. Numerical abilities

As reviewed in the current issue by Agrillo et al. (2017), a number of fish species have numerical skills that compare favourably with those of mammals. Fish display spontaneous numerical abilities in choosing a group to join – usually choosing the most numerous option – but can also be trained to perform numerical discriminations between arbitrary cues. Guppies (*Poecilia reticulata*), for example, prefer to join a group of 5 vs. 4 conspecifics (Lucon-Xiccato et al., 2017) and mosquitofish (*Gambusia holbrooki*) can learn to exit an enclosure through a door bearing 4 rather than 8 dots (Agrillo et al., 2010). Agrillo et al. (2017) note that these two methodologies may partially engage different cognitive systems. Intriguingly, the threshold number or ratio that fish can discriminate often depends on details of the experimental method, for example on the distance the fish must move to indicate a choice (Lucon-Xiccato et al., 2017).

Over 20 species of fish have been shown to have some numerical abilities (Agrillo et al., 2017, Table 1) and in the current issue DeLong et al. (2017) add another species to this list: goldfish. The authors demonstrate that when given a large number of training trials, as in the training regimes used with other species, goldfish can achieve performance rates comparable to those seen in mammals and birds. As in humans – and possibly other species – there is evidence that fish employ two distinct number systems for small and large numerosities (reviewed by DeLong et al., 2017), yet surprisingly, the authors find no ratio dependence in the discrimination ability of goldfish (i.e., fish are not better at discriminating larger ratios) in either small (1-4) or large (5-15) number ranges. This raises further intriguing questions about the existence of multiple number systems in fish, and suggests that future behavioural studies in fish may yield important insights into the mechanisms of numerical abilities in other taxa as well.

3. Personality

Many animal species display individual differences that are consistent across situations, often referred to as behavioural syndromes (Sih et al., 2004) or animal 'personalities'. Some of the earliest demonstrations of these effects were in fish. For example, male three-spined sticklebacks that react more aggressively to an intruder in their breeding territory also react more aggressively than average to a predator (Huntingford, 1976), suggesting that some of the fish are 'bolder' than others. Fish have continued to be extensively utilized in such research, resulting in a detailed characterization of the axes along which animal personalities vary (reviewed in Conrad et al., 2011) and providing plenty of data for speculations on their evolution (Dingemanse & Reale, 2005; Wolf & Weissing, 2012).

In addition to differences in personality many animals, including humans, also vary in their cognitive abilities (Sih & del Giudice, 2012). In the current issue, Lucon-Xiccato and Bisazza (2017) review the growing evidence for consistent individual differences in cognition amongst fish. As they show, recent research has begun to elucidate the mechanisms of variation in cognitive abilities by exploring, for example, their relationship to environmental conditions (such as varying predation pressure; Beri et al., 2014) and sex differences. Such cognitive variation among individuals can also be related to differences

in personality (reviewed in Lucon-Xiccato & Bisazza, 2017). In the current issue, S. White et al., (2017) map out these interactions using spatial learning in the brook trout (*Salvelinus fontinalis*), demonstrating that bold fish are slower to learn a four-arm maze than shyer conspecifics, which suggests an adaptive link between cognitive and behavioural strategies (e.g., bolder fish may spend less time in the same place, thus reducing their need to learn to navigate it).

In addition to individual behavioral traits, it is likely that in group-living species the personality composition of a group also has a large effect on the success of its members (Sih et al., 2004; Dingemanse & Wolf, 2013). Increased variance in behavior among individuals may be advantageous for groups, resulting in selective forces that maintain variation in personality (Wolf & Krause, 2014). Thus, studying personality across social – and not just environmental – conditions is imperative. In the current issue, Guayasamin et al. (2017) show that zebrafish exploration of a novel tank is altered when they are paired with another fish, and that the degree by which a fish adapts its behavior to that of its partner depends on whether that partner is more or less 'bold' than itself. Personality, then, is at least partially a social construct (Wolf & Krause, 2014).

Uncovering the mechanisms behind these interactions – between personality, cognition, group composition, and behavior – is a complex task. Barber et al. (2017) review one area of study in which these mechanisms can be studied. Personality differences, as well as variation in cognitive abilities and group membership, may affect a fish's likelihood of being infected by parasites. These parasites, in turn, often change their host's behavior in a number of quite well-studied ways and, in some cases, fish may avoid parasitized group members to reduce parasite transmission rates (Barber et al., 2000). This suggests a complex feedback loop between fish personality, behavior, and reaction to infection (see Figure 1 in Barber et al., 2017). Teasing apart the components of this system, and taking advantage of the wealth of data on the neurophysiology of parasite effects on host behavior (Adamo, 2012), may prove a key method to expose the mechanisms by which personality and behavioural plasticity function.

4. Social behavior

Many species of fish live in groups of various sizes, from breeding pairs to schools of tens of thousands (herring, *Clupea* spp., Radakov, 1973) and studies of fish dominate the experimental literature on vertebrate collective movement and decision-making (Pavlov & Kasumyan, 2000). Many species of fish show individual recognition of group-mates (Grosenick et al., 2007), form complex social networks (Croft et al., 2005) or hierarchies (Salmon, *Oncorhynchus kisutch*, Ejike & Schreck, 1980), or hunt cooperatively (Lionfish, *Dendrochirus zebra*, Lönnstedt et al., 2014).

Fish have been used extensively in studies of social learning (Pike et al., 2010), the development of 'cultural' practices (Warner, 1988; Laland & Williams, 1998), and in exploring how group-living animals combine personal and social information (Ward et al., 2011; Miller et al., 2013). Additionally, as noted above, the strong tendency displayed by many fish species to join and remain with groups of conspecifics has been used to develop behavioural assays for exploring their numerical skills (Agrillo et al., 2017), personality (Guayasamin et al., 2017), and learning (e.g., Al-Imari & Gerlai, 2008).

Amongst the many advantages of living in groups (Krause & Ruxton, 2002), one key mechanism is the improved problem-solving ability of larger groups, often referred to as 'swarm intelligence' or 'the wisdom of the crowd' (Krause et al., 2010). In this issue, Ioannou (2017) highlights some of the theoretical confusion that has crept into this field and lists the alternative explanations for improved decision-making by larger groups that must be considered and controlled for in the study of swarm intelligence mechanisms. This analysis should serve future researchers as a framework for categorizing collective effects, similar to those used in the study of social learning (Hoppitt & Laland, 2011).

One type of information that can be gathered from conspecifics in a group concerns the quality of available mates (Krause & Ruxton, 2002). Female guppies, for example, have been shown to prefer a male that they observed interacting with another female over one that was alone (Godin et al., 2005) and female Siamese fighting fish (*Betta splendens*) prefer the winner of a contest between two males that they watched (Doutrelant & McGregor, 2000). In the current issue, D. White et al., (2017) show that personality plays a key role in these processes. Female guppies that score higher on a test of sociability are also more likely than less sociable fish to copy the mate-choice of another female.

Balshine et al., (2017), in the current issue, utilize the incredible diversity of Lake Tanganyika cichlids to explore the evolution of these social systems in fish. They compare two closely related species, one of which, *Neolamprologus pulcher*, is a cooperative breeder in which subordinate group-members assist the breeding pair in raising their offspring. The other species, *Telmatochromis temporalis*, do not form groups. In a series of lab experiments and observations in the field, the authors show that *N. Pulcher* individuals spend more of their time in social interactions. Interestingly, they also find that members of this grouping species are more likely to use submissive displays to terminate a conflict, rather than fleeing, a difference which is likely instrumental in allowing larger groups to exist.

5. Neural mechanisms

In addition to our rapidly increasing understanding of their behavioral ecology and cognition, fish are an increasingly favoured taxon for studies of neural, genetic, and molecular mechanisms (Gerlai, 2003). Several fish genomes have been sequenced (e.g., zebrafish, guppies, cod, sticklebacks, rainbow trout) and a wide range of genetic manipulation tools are now available for some species. Zebrafish, for example, are frequently used as models for human diseases and for drug discovery (Dooley & Zon, 2000; Meshalkina et al., 2017). Meshalkina et al. (2017) focus on the zebrafish and demonstrate how bringing behavioral, pharmacological, and genetic techniques to bear on one problem can lead to an understanding (of learning, in this case) that bridges the span from molecular to cognitive levels. Gerlai (2017) shows in more detail how one specific sub-type of learning, relational learning, can be explored in zebrafish at the genetic, neuronal, and behavioral levels.

6. Conclusion

The five experimental papers in the current issue utilize six different species of fish, and all the papers cite research on many dozens more. Researchers are taking advantage of the immense diversity of fish species to do what comparative cognition was intended to do: expose the mechanisms and evolutionary processes that shape cognition by contrasting and comparing the behaviors of multiple species. There is,

of course, much more still to do (for example, all the experimental papers in the current issue – and a large proportion of the literature – focus on freshwater species). Research on fish behavioural processes is still in its early stages, and has barely begun to expand into the underlying neural mechanisms. However, our growing toolbox for manipulating and observing fish behavior will soon also allow the neural bases of many other behaviors to be explored (as argued by, e.g., Bshary et al., 2014). As the papers in this issue demonstrate, despite profound differences between their environments, the organization of fish cognition is remarkably similar to that of terrestrial vertebrates, and the continued study of fish behaviour will provide important insights into the fundamental mechanisms and evolution of cognition.

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