

Fish cognition

Redouan Bshary^{1,*} and Culum Brown²

The central nervous system, and the brain in particular, is one of the most remarkable products of evolution. This system allows an individual to acquire, process, store and act on information gathered from the environment. The resulting flexibility in behavior beyond genetically coded strategies is a prime adaptation in animals. The field of animal cognition examines the underlying processes and mechanisms. Fishes are a particularly interesting group of vertebrates to study cognition for two reasons (Figure 1). First, they occupy a key position in the vertebrate phylogenetic tree: the common ancestor of the tetrapods was a bony fish. Thus, all vertebrates share key genetic features that code for the body structure, including the vertebrate brain. Similarities in brain structure and function are hence likely to be due to common ancestry. A second reason to study fish cognition is that fish have had their own independent evolution/radiation since they split from tetrapods. Bony fishes are by far the most species-rich vertebrate group. As a consequence, they provide the best options for a comparative approach that aims to link the evolution of cognition to a species' ecology. Therefore, the study of fishes may reveal general principles of ecological effects on cognitive abilities in vertebrates.

In comparative cognition, humans are often used as a reference point to determine whether other species possess similar cognitive abilities. Some researchers, in particular primatologists, use the comparative approach to find similarities due to common ancestry. Comparing all vertebrate taxa, including fishes, may thus reveal the shared cognitive tool box of vertebrates. A prime example is the recent discovery that all vertebrates share a network of brain areas that is involved in social decision making. The similarities strongly suggest that a version of this network was present in the common ancestor of all vertebrates. On the other hand, studies on fishes may

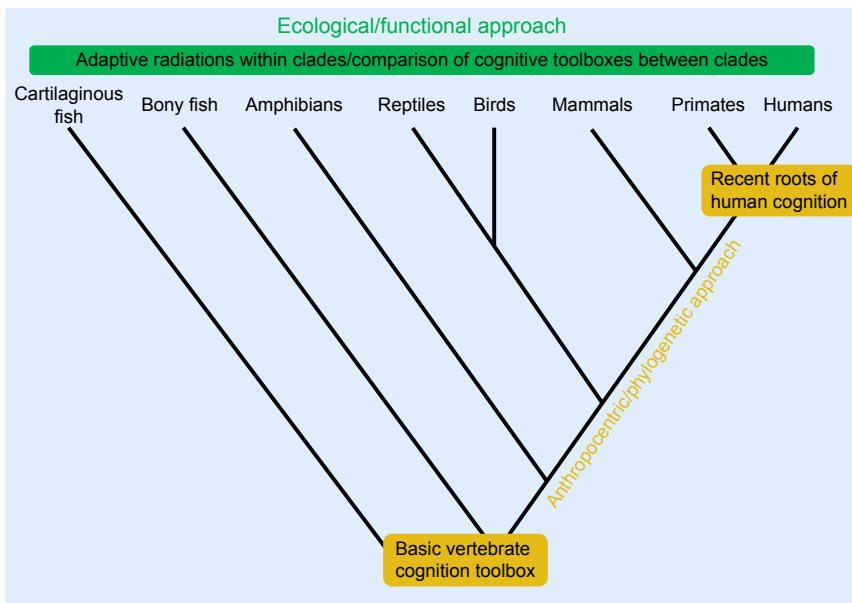


Figure 1. How research on fishes contributes to general research on cognition.

This anthropocentrically organized phylogenetic tree illustrates two non-mutually exclusive approaches to comparative cognition. The ‘anthropocentric’ or ‘phylogenetic’ approach aims to infer similarities due to shared ancestry. While typically used by primatologists interested in the evolution of cognitive processes used by humans, the study of fishes may inform us about the general shared cognition toolbox of vertebrates. The ‘ecological’ or ‘functional’ approach is rooted in standard evolutionary theory based on natural selection, which predicts that a species’ cognitive abilities are a reflection of its ecological (social and environmental) complexity. Fishes offer great opportunities to use this approach, either within taxa showing adaptive radiations or in tests for convergent evolution among vertebrates.

reveal that certain similarities between species are likely to be the result of convergent evolution. For example, a cichlid fish shares with some bird and mammal species including humans the ability to use transitive inference, i.e. the ability to conclude that if $A > B$ and $B > C$ then $A > C$. Such a similarity is best seen as independent adaptation to similar ecological conditions. Conversely, the ecological approach can be used to compare closely related fish species that occupy divergent niches in order to identify differences in cognitive abilities (cognitive ecology). Fishes have undergone multiple adaptive radiations where closely related species occupy diverse niches linked to important differences in habitat as well as social organization. Thus, one can repeatedly compare closely related species and correlate environmental factors with differences in brain structures and differences in cognitive task performance. A classic model system is that of the cichlids occupying African rift lakes. Comparisons within lakes have shown that brains and cognition have been shaped by both the physical and social environment. Comparisons between

adjacent lakes reveal amazing cases of convergent evolution of species which occupy similar niches.

Below, we provide some examples of fish cognition research. We highlight two major areas in which fish have made a substantial contribution to our understanding of the evolution of cognition: social cognition and spatial learning.

Social intelligence

It has long been argued that the large human brain and associated cognitive skills were favored by natural selection to cope with our complex social interactions. This rationale can readily be generalized to any species that lives in complex social groups. Fish are capable of individual, kin and olfactory self-recognition, the basis for most sophisticated social behaviors. In most instances, chemical cues play a very important role in the recognition process and may be reinforced by visual cues. In guppies, individuals become familiar with one another over a period of about 2 weeks. When given a choice, fish nearly always chose to shoal with familiar rather than unfamiliar individuals, and there appear

to be foraging and anti-predator benefits associated with this choice. Shoaling fish also have good numerical abilities used to track shoal size. These abilities appear to rely on two separate systems. The first is an object tracking system that enables them to keep track of up to four objects simultaneously and thus they can make very accurate judgments when comparing small quantities. The other system is more useful for comparing larger quantities and relies on the relative rather than the absolute differences between two sets. It has been argued that other vertebrates (including humans) also use these two systems. Other key findings on fish social cognition are listed below (Figure 2).

Traditions and social learning rules

Outside humans, the best experimental evidence for rather arbitrary traditions in wild animal populations stems from birdsong and coral reef fish spawning migrations. Various fish species aggregate at dawn or dusk on the reef to swim together to a site suitable for spawning. In a most spectacular experiment, entire local populations of blue-headed wrasse were exchanged between locations. Robert Warner showed that without local knowledge, the translocated populations selected new spawning sites, showing that both the old and new locations were somewhat arbitrarily chosen. Moreover, they kept the new locations for the entire 20 years of study, i.e. across generations. While the information transfer seems to be rather simple — naïve individuals may learn by following knowledgeable ones — recent research has demonstrated that nine-spined sticklebacks can use highly sophisticated updating rules, so-called ‘hill climbing’ rules, to decide whether and from whom to learn about the location of food sources. They compare their own experience with the success of observed conspecifics in order to decide where to feed. At the time, such decision rules about social learning had been only described in humans.

Social decision making

Being a member of a group has been suggested to convey advantages concerning optimal decision making. Ignorant individuals may rely and knowledgeable ones to find food or shelter and to avoid predators. Shoaling fish species yield highly suitable systems to test theories

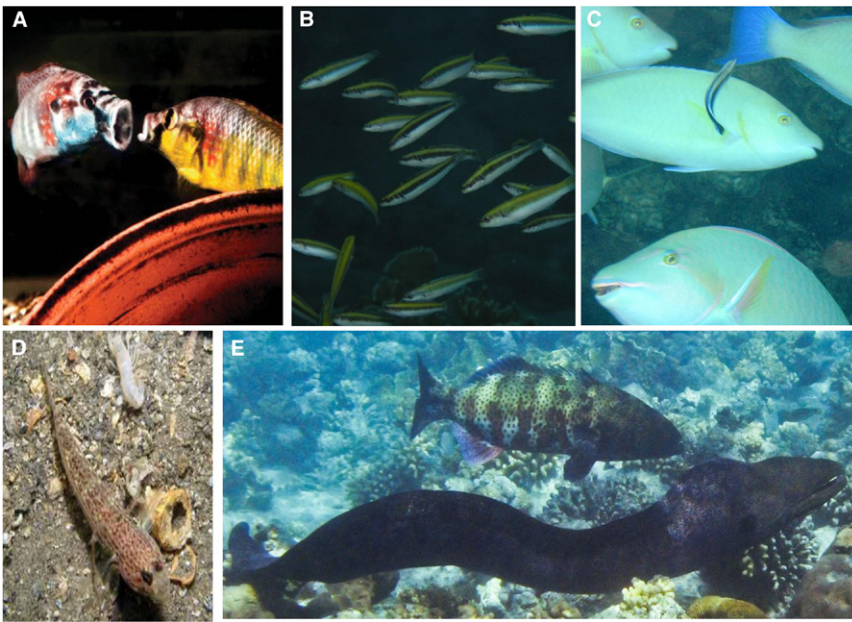


Figure 2. Examples of fish cognitive social abilities.

(A) The cichlid *Astatotilapia burtoni* uses transitive inference to predict male hierarchies. (Image: Russ Fernald.) (B) Spawning migrations in the wrasse *Thalassoma bifasciatum* as an example for arbitrary traditions. (Image: Robert Warner.) (C) Cleaner wrasse adjust service quality to the presence of bystanders. (D) Rock pool blennies use cognitive maps to jump 'blindly' between pools. (E) Groupers coordinate joint hunting with moray eels. (Image: Alexander Vail.)

concerning the precise decision rules. 'Robofish' (Figure 3), whose movement patterns are experimentally programmed and towards which real fish react relatively naturally, have been instrumental to investigate causality. Through the use of robofish, researchers have shown that single stickleback are susceptible to a leader behaving in a maladaptive way (going towards a predator), while larger groups avoid this pitfall by using a quorum response. The personality of particular individuals within the group can also greatly affect the level of influence that individual has on guiding group behavior.

Reputation as a basis of cooperation

The literature on humans emphasizes the fact that humans often achieve stable cooperation through reputation. Reputation matters as observers will only help those individuals in need who have helped others. Reputation mechanisms involve the ability to properly assess outcomes even without personal experience, and to adjust ones' own levels of cooperation conditionally on the partner's past behavior and to the presence of bystanders. In fishes, the cleaner wrasse *Labroides dimidiatus* must manage its reputation. Cleaner wrasse

remove ectoparasites from cooperating so-called 'client' reef fish but prefer to eat client mucus, which harms the fish and thus constitutes cheating. Cleaners have 2000 interactions per day. Therefore, clients visiting a cleaner may often witness the end of an ongoing interaction and invite inspection if the observed service was good but avoid cleaners that cheated. Cleaners thus have a social prestige, and they are indeed more cooperative to current clients if bystanders are present.

Shared intentionality

Humans are often highly coordinated during cooperative interactions. It has been argued that 'shared intentionality', i.e. the awareness of a common goal, is the basis for our ability to coordinate so well. Indeed, infants respond with signaling when an experimenter stops contributing in a shared activity. Interestingly, groupers of the genus *Plectropomus*, ferocious predators in coral reefs, regularly face this experimental design in nature and solve the task. These groupers hunt with speed, driving prey into crevices. Groupers solicit joint hunting with moray eels by shaking their head near the morays' head. The signal often induces the morays to start moving through

crevices, which may drive prey out into the open and make it accessible to the groupers. After a few meters, the morays naturally take the role of the human experimenter: they stop the joint activity and return to resting. Groupers respond to the situation by approaching the moray and signaling to induce further joint activity.

A particularly exciting area of research on fish cognition links brain structure and behavior within species. The cichlid *Astatotilapia burtoni* has become a model system to study the social decision network. In this species, males may repeatedly change their status from dominant to subordinate and vice versa. Experimentally induced changes in status can be used to study changes in gene expression and hormone concentrations in the brain regions associated with social decision-making, as well as the corresponding changes in social behavior.

Spatial learning

It is quite clear that there is a strong selective advantage for all vertebrates to move efficiently from place to place within their environment. Individuals are far better off learning and recalling the locations of important features, such as predators, refuge, food and mates. Fishes are capable of using a wide range of techniques to navigate including the use of a sun compass, magnetic fields, landmarks, cognitive maps and so on. They are also capable of finding the location of a foraging patch by geometric integration. Thus fishes match terrestrial vertebrates in just about every facet of navigation. Much of the research to date, however,

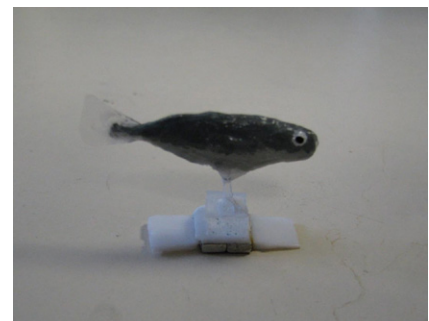


Figure 3. A powerful tool for experimental manipulation.

'Robofish', a model whose movement patterns are experimentally programmed and towards which real fish react relatively naturally, allows precise testing of fish decisions in the context of group coordination. (Image: Jens Krause.)

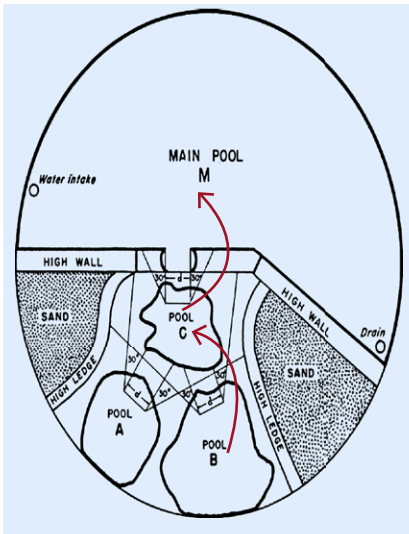


Figure 4. No leap of faith.

A cognitive map in a fish: rock-pool blennies know the precise location of low-tide pools in their home range, which enables them to leap 'blindly' from one to the other when disturbed. With permission of the publishers: Aronson, L.R. 1971. *Ann. NY Acad. Sci.* 188, 378-392.

has focused on how the environment shapes the types of cues fish tend to use. Most studies show that fish have a hierarchy of cue preferences with evidence of cue overshadowing and redundancy. For example, rock-pool dwelling gobies face the problem of finding their home pool before the tide goes out. Rock-pool species, which inhabit these stable but complex habitats, have enhanced spatial learning abilities relative to sand-dwelling species which merely move back and forth with the tides. Classic experiments demonstrated that rock-pool gobies know the location (direction and distance) of neighboring pools as they jump directly to these when disturbed, indicating the formation of a cognitive map (Figure 4). They recall the location of surrounding pools for weeks after being experimentally removed. When they are displaced, gobies quickly return to their home pool. Analysis of the brain structure of rock-pool dwelling gobies shows a far larger telencephalon (hippocampus homolog) than their sand dwelling relatives. Rock-pool gobies tend to use fixed landmarks whereas sand gobies tend to use egocentric navigation techniques. Experiments with sticklebacks have also revealed that key aspects of the environment shape cue preference, spatial learning ability and memory retention.

Controlled laboratory experiments have shown that the spatial learning abilities of fishes can be enhanced if the structural complexity of their rearing environment is increased. Interestingly one can also see a corresponding increase in brain size and neural connectivity. Thus, there is evidence that the habitat can influence cognition both during development (e.g. via neural recruitment) and via natural selection. Indeed the high degree of neural plasticity even in old age is a key feature of fish brains.

Fishes are also quite able to predict the timing of events. Like most animals they rely on various environmental cues in addition to their internal clocks. Keeping track of time is obviously important in a range of contexts, for example predicting daily prey migrations or predator activity. Fish are also capable of combining these aspects in a skill that is called 'time-place learning'. That is, they can learn both when and where an event is likely to happen.

Ethical considerations

In conclusion, fishes are highly amenable to experiments to test general concepts of cognition. A particular current advantage is that keeping fish in the laboratory, including killing subjects for brain studies, is currently more accepted than for other vertebrates. We note that this latter point appears to be increasingly anachronistic. At least in western countries, animal welfare laws do not distinguish between different vertebrate groups, meaning that fish should receive the same ethical standards of protection as birds or mammals. A crucial question in this context is in how far fishes may feel pleasure and pain. With respect to the latter, evidence accumulated over the past 10 years or so that fishes indeed feel pain. The peripheral nervous system for the detection of painful stimuli is apparently homologous among vertebrates. Also, negative stimuli like acid injections lead to prolonged alternations of behavior, strongly suggesting central nervous processes. Application of analgesic returns behavior to normal. Critics argue that the subjective experience of pain has not yet been properly demonstrated for fishes. Ideally, one would have to show that the subjective negative experience alone has negative fitness consequences in

the absence of any physical damage. Such evidence exists for pleasure: coral reef fishes regularly receive physical stimulation from cleaner wrasse that use their pectoral and in particular pelvic fins to provide a kind of massage. Such a massage yields no material benefits like parasite removal, food, access to mates or reduced predation. Nevertheless, fish with access to a soft brush at the bottom of a cleaner model have lower baseline and acute stress response cortisol levels than fish without. In humans, the success of massage therapy is evidenced by low cortisol levels. Apparently, a purely hedonistic feeling has fitness-relevant consequences in fishes. Whether such evidence will eventually lead to a better protection of fishes remains to be seen. Fishes play a special role for humans as they are the most numerous animal food source but also as a group the most common pet, and as laboratory subjects second only to mice. Thus, changes in welfare application are bound to have major effects on our daily lives. Research on the cognitive abilities of fishes should play a pivotal role by providing policy makers a sound scientific basis for their ethical assessment.

Further reading

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¹University of Neuchâtel, Institute of Biology, Emile-Argand 11, 2000 Neuchâtel, Switzerland. ²Macquarie University, Department of Biological Sciences, NSW 2109, Australia.

*E-mail: redouan.bshary@unine.ch