



Changing tides: ecological and historical perspectives on fish cognition

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The capacity for specialization and radiation make fish an excellent group in which to investigate the depth and variety of animal cognition. Even though early observations of fish using tools predates the discovery of tool use in chimpanzees, fish cognition has historically been somewhat overlooked. However, a recent surge of interest is now providing a wealth of material on which to draw examples, and this has required a selective approach to choosing the research described below. Our goal is to illustrate the necessity for basing cognitive investigations on the ecological and evolutionary context of the species at hand. We also seek to illustrate the importance of ecology and the environment in honing a range of sensory systems that allow fish to glean information and support informed decision-making. The various environments and challenges with which fish interact require equally varied cognitive skills, and the solutions that fish have developed are truly impressive. Similarly, we illustrate how common ecological problems will frequently produce common cognitive solutions. Below, we focus on four topics: spatial learning and memory, avoiding predators and catching prey, communication, and innovation. These are used to illustrate how both simple and sophisticated cognitive processes underpin much of the adaptive behavioral flexibility exhibited throughout fish phylogeny. Never before has the field had such a wide array of interdisciplinary techniques available to access both cognitive and mechanistic processes underpinning fish behavior. This capacity comes at a critical time to predict and manage fish populations in an era of unprecedented global change. © 2015 John Wiley & Sons, Ltd.

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INTRODUCTION

Fish are the most abundant vertebrate taxonomic group, with over 30,000 species colonizing virtually every water body on the Earth.¹ The diversity of fish encompasses species from the most primordial to the most complex and highly derived – from the jawless hagfish (*Myxiniidae*) to the live-bearing

seahorse (*Hippocampus* sp.). In the last decade, it has become increasingly clear that the cognitive capacities of fish can be as diverse as their morphology. In fact, cognition has in many ways shaped fishes' ability to adapt to the vast range of niches and environments that they inhabit. Fish use tools, develop cultural traditions, take turns, cheat, punish, cooperate in hunting both within and between species, communicate, and learn by watching their companions, among many other diverse skills. Paradoxically, fish as a whole have historically been far less represented in research on cognition,¹ yet the very diversity and the specializations that have made them difficult to study make them, in turn, a rich resource for understanding the evolutionary ecology of animal cognition.

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For the purposes of this review, we adopt the definition of animal cognition proposed by Shettleworth² in 2009, which describes cognition as a process by which the external world is internalized through a series of different sensory systems. The information from these systems is then processed through both learning and memory to allow the animal to interact with its environment. Accordingly, we are interested in how fish use a range of senses to detect the world around them, and how they integrate and process that information to generate appropriate responses.

Studies of cognition were traditionally conducted in the laboratory, using model species such as rats (*Rattus norvegicus*), pigeons (*Columba livia*), and, as described below, occasionally goldfish (*Carassius auratus*).^{2,3} These studies taught us a great deal about the fundamental cognitive functions in animals and laid the foundational framework for the investigation of information processing. However, this approach bypassed the evolutionary and ecological context under which animals had been selected to learn information.^{1,2,4} Fish are ideal subjects with which to address this gap; they express a considerable capacity for niche specialization over relatively short time scales that support speciation events and adaptation to challenging environments. The field of fish cognition continues to dramatically¹ expand, delivering considerable worthy material to cover. We have, therefore, chosen to selectively highlight research that captures some of the history of the field, and more recent advances that emphasize the ecological context of cognition, and show key promise for future research.

THE ECOLOGICAL BASIS OF COGNITION

Historically, goldfish occasionally featured as an early model organism used by experimental psychologists. In contrast to the more commonly employed rats and pigeons, however, an overall impression of a slow, limited cognitive capacity emerged. This may have contributed to the cultural myth that fish have a 3-second memory that is oft-repeated even today.³ In one early experiment, three goldfish were pitted against two rhesus monkeys (*Macaca mulatta*) and made to complete a reward matching task. One location awarded food 70% of the time, another only 30% of the time. The fish matched their frequency of approach to frequency of food reward, so approached the 70% target 70% of the time, and the other target 30% of the time. The monkeys, on the other hand, chose the 70% reward all of the time. As the latter is mathematically a more appropriate response because it produces greater total

reward payoff, it was concluded that monkeys were capable of making more 'rational' decisions.^{3,5} However, a decision is only as rational as the context in which it is made, and what these experiments lacked was an understanding of the ecological and evolutionary forces under which decision-making processes develop. For example, aquatic environments are often highly variable. In that context, it is likely that committing to a single source of food exclusively, even if more reliable, may not be the most appropriate response. Instead, approaching the lower food reward location to the degree matched by its payout might be the safest strategy, allowing a fish to adjust its behavior if the higher payout location suddenly became unavailable, or the lower payout location increased in its resource.

Until recently, research in animal cognition was primarily used as a means to better understand the human perspective. In an early synthesis on the subject, 'Animal Intelligence' in 1898, Thorndike states, 'the main purpose of the study of the animal mind is to learn the development of mental life down through the phylum, to trace in particular the origin of human faculty'.⁶ This foundational principle holds an inherently hierarchical view of cognition, a repeating motif descended from ideas as early and formational as Aristotle's *scala naturae*.^{1,2,4} However, this view of cognition is erroneous; cognitive processing does not develop in a vacuum. As with all evolutionary products, cognition is a mechanism developed to cope with particular problems presented by a particular niche.

The incompatibility of a hierarchical approach with contemporary evolution was pointed out thoroughly in 1969 by Hodos and Campbell, who noted 'nonetheless, this arbitrary hierarchy continues to influence researchers in the field of animal behaviour'.⁴ They argued that the infatuation of the field with making comparisons for comparison's sake showed a failure 'to distinguish between data obtained from living representatives of a common evolutionary lineage and data from animals which represent divergent lineages', adding that there is limited predictive value from such arbitrary comparisons, which has slowed the development of the field.⁴

This early argument for a more evolutionary and context-specific approach came 20 years after Schneirla called to reformulate the principles of the field, stating the 'problem of the animal psychologist' should be to 'contrive to understand how each animal type functions as a whole in meeting its surrounding conditions: what its capacities are like and how they are organized'.^{4,7} Despite these early and strident calls for a Darwinian and context-specific approach to the investigation of animal minds, the field remained

predominantly in Thorndike's perspective for almost a half century. Fricke in 1973 was a notable exception who stressed that body structure, physiology, and behavior should be considered together, as 'adaptation to a new ecological niche involves the entire gene pool of the organism'.⁸

Nonetheless, a shift to an ecological approach to cognition has emerged in the last two decades.^{9–11} Shettleworth called the two approaches the 'anthropocentric' and the 'ecological' programs,¹² although it could be argued that the goal of understanding human cognition requires an equally biological context, and human or animal cognitive and behavioral processes can only be comparable with comparable ecological contexts.^{12,13} In this review, we discuss archerfish (*Toxotes* sp.), a species faced with the problem of detecting and targeting prey through the boundary of water to air, further challenged by a competitive setting. In this case, comparing visual search patterns of archerfish and those of humans could be argued as appropriate, as both require the skill of fine visual discrimination in their individual ecological context. Remarkably, the fish's ability to solve this task with a relatively simple brain appears to be as effective as the way humans use their visual cortex for the visual search process.¹⁴ This does not imply that fish are as sophisticated as humans. Rather, it illustrates how natural selection can provide solutions to common problems presented across species, and that this can be done using different neural apparatus and mechanisms.¹⁵ By contrast, comparing the blind Mexican cave fish and human visual search patterns would be inappropriate, because these fish do not use vision as their primary means of interacting with the world. Although it seems sensible not to compare sighted to unsighted species in this example, when the difference is not so physiologically obvious, it is too often assumed that what is cognitively demanding in human systems will also be similarly so for other species. The reverse problem is also prevalent; assuming skills to be lacking solely due to the evolutionary distance from humans.² If a skill is required in the social or ecological context, then the base hypothesis should be that it will be present. Just as in a physiological context, problems of cognition can be solved by evolutionarily distinct processes, though these differences may be less obvious than ascertaining the differing evolutionary pathways that lead to a bird's versus a bat's wing. This inability to observe cognitive functioning directly makes its investigation much more difficult, as behavioral processes must be used as a proxy to understand internal state. However, we should not avoid investigation because it is more difficult, but we can approach it more carefully. When studying cognition,

it is, therefore, critical to consider the nature of the task that the animal is trying to solve, how it is relevant to the animal and its environment, and how best to ask these questions with as much clarity and precision as possible.

COGNITION AS A MEANS TO AN END

Animals face a wide range of challenges that behavior, rote or flexible, serves to solve. We have chosen to describe four general areas in which fish have developed a cognitive approach: (1) spatial orientation and navigation, (2) predation interactions, (3) communication and interspecific interactions, and (4) tool use and innovation.

These topics are by no means the only challenges that cognition addresses. They are, however, the major areas where strong selective pressure has produced cognitive function worthy of note, and they emphasize the value of considering how the environment shapes cognitive processes.

Where Am I, and Where Am I Going?

Research in spatial navigation has been particularly productive both in terms of understanding navigational processes, such as three-dimensional mapping and the integration of multiple cues, and as a mechanism to explore how contrasting environments with different demands shape cognition. Fish provide a particularly advantageous window on this approach, because the ease with which nearby aquatic habitats can become isolated from each other allows the investigation of contrasting populations of the same species while varying only a few factors.¹¹

One such opportunity was presented by distinct but nearby populations of river and pond three-spined sticklebacks (*Gasterosteus aculeatus*). Ponds are more stable environments than rivers, with landmarks and visibility levels that stay relatively constant. By contrast, rivers frequently fluctuate in water level, turbidity, and flow. A lodged branch that might be a landmark one day could easily be swept away the next. It was, therefore, hypothesized that fish would utilize navigational cues in rivers and ponds differently, and this was found to be the case.¹¹ When small plants were placed in a maze marking the doorway leading to a food reward, pond sticklebacks significantly improved performance. However, fish from the less stable riverine habitats showed no differences, indicating that they paid little attention to available local landmark cues. This is not a genetic difference between populations. When river and pond fish were each raised in the laboratory under simulated stable

and unstable environments, there was no inherent difference in the capacity of each population to learn the landmark cues.¹⁶

Similarly, lake-dwelling sticklebacks sometimes become differentiated into different niches. Limnetic individuals seek out plankton in the main water body, whereas benthic fish spend their time searching for prey on the substrate. The contrasting lifestyles and environments these fish experience were found to influence how quickly a fish could learn to use landmarks to locate a food reward, with benthic fish showing superior performance over limnetic fish.¹⁷ When drawing such comparisons, it is important to consider whether the result observed is due to superior cognitive ability or whether some artifact of experimental design may have resulted in the task being biased in favor of one of the groups. This is not an uncommon issue that can occur in comparative studies. In the above case, the experiment was designed to test the use of visual landmark cues in a food reward finding task. Benthic fish spend more time moving around a landmark-rich substrate, and are, therefore, more likely to encounter such cues as they forage compared to the limnetic fish in the water column. Thus, the use of visual landmark cues to provide direction may potentially bias the task in favor of the benthic fish.¹⁷ However, this task could be solved either by learning an appropriate turn direction, a navigation system likely to be in place in the limnetic individuals, or by following the visual landmarks as might be used by the benthic fish. An additional analysis of the cues used showed that both groups could use the landmark information, indicating that the original result was not an artifact. With this established, we can hypothesize that this kind of spatial task may be more common for benthic fish as they learn the position of different foraging patches or food replenishment rates and this may underlie their superior performance in the task.¹⁷ Results such as these highlight the importance of recognizing the ecological background of the animals being tested and making the biological relevance—and potential biases—of the task an important part of both the design of the experiment and the interpretation of the results.

More variable than rivers are intertidal habitats. Challenges caused by the change in tides and periodic reduction of shelter have forged a strong capacity for spatial memory. Despite being conducted almost half a century ago, one of the most impressive examples of spatial ability in fish was described by Aronson in the frillfin goby (*Bathygobius soporator*).^{18,19} These small gobies are able to map the topography of the intertidal zone with remarkable accuracy during high

tide, learning the locations of the depressions that will retain water when the tide goes out. If at low tide, the goby is threatened by a predator (or an enthusiastic scientist), it is able to jump from its present pool to a remaining, often unseen, destination with extreme precision. If it continues to be threatened, it continues jumping from one neighboring pool to the next in order to make a complete escape. More recently, another intertidal fish, the shanny (*Lipophrys pholis* L.), has been investigated to determine what cues the fish use to map the intertidal zone. Burt de Perera and Guilford showed that the shanny can encode the position of shelters in each pool both in terms of local cues (internal to the pool) and by more distant global cues that lie outside the bounds of the pool.²⁰ When tested for cue preference, they found that the fish showed individual variation in terms of local versus global information utilization.

This variation at the level of the individual demonstrates a flexible approach to problem-solving. There will often be more than one solution to any given problem, and the ideal solution may depend on highly variable factors, particularly in changeable, intertidal habitats. In these situations, cognitive flexibility will be highly beneficial and could be a mechanism to help cope with change. This flexibility can also lead to differences in the way individuals learn information about their environment, which might also influence the solutions they ultimately adopt.

Being a highly visual species, it is easy for us as humans to imagine visual landmarks as the primary means of accessing spatial information. However, vision is just one sense with which fish can learn about their environment. Auditory, olfactory, electrosensitivity, and pressure sensitivity, among others, are all the means by which fish collect spatial information. These cues are not restricted to adult individuals. Larval and juvenile fish must also learn about their surroundings. In particular, auditory cues have been shown to be extremely important for developing fish embryos of species such as the reef-dwelling cardinalfish (Apogonidae). When hatched, the larvae move into the water column where they feast on abundant plankton for a few weeks to months until they are large enough to migrate back to their natal reef to settle. As vision is not available during the initial development, the embryos must have some other means by which they can identify their natal reef. Developing larvae during the egg stage have been shown to solve this problem by learning the sounds specific to their reef and using these cues to help them home.²¹

Developing coral reef larvae are not the only fish that must cope without the sense of vision. *Astyanax mexicanus* is a species of freshwater tetra that lives

in a region of north-eastern Mexico dominated by a soluble rock prone to weathering such that sinkholes and caves are abundant. Lineages of this species occupying caves have lost their eyes and so must devise ways to navigate in complete darkness.²² It was previously thought that the only method by which the blind Mexican cave fish could navigate was by sensing the hydrodynamic disturbances produced by its own forward movement. These disturbances stimulate the lateral line, an array of specialized mechanoreceptors that line the head and body, providing specific information about pressure fields around the fish.²³ In novel environments, the fish move faster to gain information, but this mechanism poses obvious risks. In early 2014, it was discovered that the cavefish utilize mouth suction to generate flows additional to those produced solely by the forward motion of the body. By rapidly opening and closing their mouths, they create pulses of pressure that deliver additional information back to the lateral line in a way comparable to echolocation. In an unfamiliar arena, the fish increased the rate at which they moved their mouths.²⁴ Mouth suction is a highly evolutionarily conserved feature of teleost fishes, necessary for both prey capture and respiration,^{24–26} and this is a clear example of how an evolutionarily ancestral trait can be co-opted in a novel fashion to provide unique avenues for the collection of environmental information. Examples such as these can be used as an opportunity for further investigation in other species with similar ecological constraints, as the ancestral mechanism may be similarly adapted in other descended lineages.²⁴

Unlike many terrestrial species that operate predominantly within a two-dimensional habitat, fish can make use of a third dimension. Determining the vertical position in the water is, therefore, an important piece of information, and one that cannot be reliably solved by vision. The obvious cue is hydrostatic pressure; however, until 2010, it was not believed that fish had a mechanism by which to sense absolute pressure.²⁷ This is because the volume of gas in the swim bladder is varied, so although it has long been known that fish are sensitive to pressure changes,^{28,29} it was assumed that any absolute measure could not be inferred without a long-term static reference.^{30,31} Recently, however, a mechanism was described whereby absolute depth could be inferred by means of short, rapid ascents, such that the vertical speed is combined with the rate of change of swim bladder volume.³⁰ Although this mechanism has still only been theoretically described and is yet to be physiologically examined, the ecological hypothesis would suggest that such a constant and critical habitat cue would have some mechanism of utilization.³¹ In this

way, consideration of the cues available in the ecological context of a species can act a predictive mechanism for future investigation.

Animals that move in a complex environment are constantly integrating pieces of information to map and navigate the world around them. Considering the diverse mechanisms by which fish are able to achieve this skill, even within a single species, the importance of integrating different sources of information becomes clear. Though from an investigative point of view, it can become difficult to tease out precisely the manner in which different cues are utilized, naturally constrained systems such as the blind Mexican cave fish navigating without the sense of vision show great promise as an avenue for future understanding of information acquisition and integration. Additionally, the diversity of isolated but geographically proximate aquatic habitats provides a great opportunity to continue to elucidate the ways in which landscape shapes cognition in the future.

Eating While Avoiding Being Eaten

Predation is one of the most unforgiving selection pressures. A single mistake can cost a fish's life, making trial-and-error an often rapidly terminated process. Consequently, antipredator defenses, in their many forms, are typically acquired quickly.³² This may be in the form of a template-matching mechanism to recognize specific predators³³ or one trial learning, to list two possibilities. In the latter case, a prey fish can learn a novel predator from a single encounter of damage-released alarm cue from a conspecific fish paired with either sight or scent of the predator.^{33–35} Fish are particularly interesting in this arena because they have indeterminate growth. What might have previously been a serious predator could be outgrown and harmless at a later stage. Additionally, many species have complex life histories including larval and pelagic stages, habitat shifts, or migrations. Ecological changes such as wet versus dry seasons can dramatically alter a landscape even in a highly localized species. Any of these variables may result in the introduction of new or the loss of old predators.³³ Therefore, although template-like mechanisms of predator recognition may allow a fish to survive in the immediate future, it is possible that they can become too prescriptive at a larger scale in which a diversity of potential predators coexist and change with time. As a result, a degree of flexibility and higher orders of cognition become important, allowing a prey fish to adapt and alter responses as necessary according to their immediate environment.³³

If a fish survives an initial predator encounter, it would be highly adaptive to be able to learn more

from the interaction than to simply avoid that particular predator. Fathead minnows (*Pimephales promelas*) conditioned to recognize lake trout (*Salvelinus namaycush*) also condition to two other species of salmonid, though they do not generalize to more distantly related predatory species. There is evidence that prey fish can generalize both chemical and visual cues to related predators.^{36–38} Being able to generalize from one predator encounter to closely related but different species is likely to be adaptive, as phylogenetically close predators may well have a common prey that they hunt in a similar manner.

The necessity for a rapid learning response to predators presents a particularly unique cognitive problem when the initially learned information is incorrect. This can occur either when a nonthreatening stimulus is mistaken for threatening or, more dangerously, when a predator with real threat potential is mistaken to be nonthreatening. In these circumstances, the initial, rapidly learned response must be updated as better information becomes available. Mitchell et al. investigated latent inhibition mechanisms and predator learning in juvenile coral reef fish.³⁹ Latent inhibition refers to the situation when a familiar stimulus takes longer to acquire meaning than a new stimulus. They found that when damselfish were pre-exposed to predator odor on a number of occasions prior to being exposed to both predator odor and alarm cue, the prey fish initially failed to recognize predator odor as a threat. However, after four to six simultaneous exposures of predator odor and alarm cue, the damselfish were able to learn that the predator odor signaled danger. This result demonstrates that a measure of cognitive flexibility can exist even in an environment where rapid learning is critical, allowing fish the capacity to respond to changing conditions.³⁹

There are interacting effects of hunger and pre-exposure to predator odor as well. The state of an animal can influence the level of risk that it is prepared to take in the presence of predators. Observations of pre-settlement coral reef larvae showed that fish kept on different levels of food ration will respond in different ways to threat when facing a potential predator. Fish on a low ration diet were generally more active, moved farther away from shelter, and expressed bolder behavioral responses overall than those on a high food ration diet. When placed on a patch reef and monitored for survival, fish without pre-exposure to predator odor had very low survival, while fish with previous experience were more likely to survive. Interestingly, fish on a low ration diet but exposed to a predator odor had a similarly low level of survival, suggesting a trade-off between the current internal state and the propensity for risk-taking.⁴⁰

This is particularly important to take into account when investigating cognition, as it can be easy to assume that results are a cognitive effect, when the variation may actually be due to a difference in motivation or, in this case, a willingness to take risks.

Living alongside predators can also shape more general aspects of cognition. Brown and Braithwaite compared the Panamanian bishop fish (*Brachyrhaphis episcopi*) from four pairs of high and low predation sites across four rivers.⁴¹ Fish from high predation sites were slower to solve a spatial task and took longer to locate a food reward and access the shelter across a series of trials. In comparison, the low predation fish were faster at acquiring this task and made fewer mistakes in the process. It may seem counterintuitive that fish from high predation site areas showed poorer learning when presumably an ability to learn quickly might be advantageous in a high predation environment. Closer inspection suggests that the low predation site fish were able to explore and use the cues within the maze more flexibly, and this appears to have given them an advantage in learning the location of the food reward and shelter. It is possible that this result is specific to this kind of task; however, it may be indicative of more general differences. Other work on the same system has also shown differences in temperament between high and low predation populations, such that high predation populations tend to be bolder and more active.⁴² Work with mammals has shown that bolder individuals tend to establish relatively inflexible routines and are not very sensitive to small changes in the environment.⁴³ If bolder animals pay less attention to changes in the environment, their capacity to acquire new information in the first place may be hampered. This would certainly support the apparent superior cognitive skills of fish from low predation sites. Considering the ecology of the environments from which these fish were sourced, it also seems likely that the low predation site fish have the liberty of taking their time as they explore and learn about their environment owing to the comparatively decreased threat of predation, and this could also aid their learning. Alternatively, there may be trade-offs between investing in learning about potential predation versus other aspects of the environment.

Given the nature of the many kinds of antipredator interactions, there is also an underlying physiology that comes into play associated with glucocorticoids and other such behavior-altering neuroendocrine factors known to be associated with interference in learning.^{44,45} This makes predator interactions particularly difficult to analyze from the perspective of cognition, as it can be difficult to fully interpret

what physiological changes actually mean. Despite the difficulty, this interplay is well worthy of study, particularly because of the importance of predation as an ecological and evolutionary driver. Cleaner fish, so named because they remove ectoparasites from client fish, are a particularly unique system in which to investigate predator interactions because they choose to regularly interact with predator fish.⁴⁶ The Atlantic cleaner goby (*Elacatinus* sp.) was found to have increased cortisol levels when in the presence of a predatory client. The goby also approaches a predatory client faster than a nonpredatory client, and they stay with them longer than they would with a nonthreatening client.⁴⁷ This finding is fascinating; however, it is as yet unclear what precisely is driving the change in physiological and behavioral response between predatory and nonpredatory clients. Several possibilities come to mind. First, physiological and endocrine factors produced in response to the predator may cause the cleaner fish to become bolder and prolong the interaction, with no direct decision-making involved. Alternatively, fear rather than boldness may drive the change, and the presence of the predator may cause a heightened state of awareness that makes the cleaner fish seek additional reassurance about the status of the client. Finally, the longer interactions could be a more complex cognitive process such that the cleaner fish is seeking to communicate its willingness to cooperate with a predatory client. Further investigation in this system shows great promise toward elucidating the driving factors behind non-predation-related interactions between predators and nonpredators as well as for gaining greater understanding of the interplay between physiology and cognition.

Prey fish have evolved multiple ways of coping with the dangers posed by predators and many of these strategies employ learning and memory processes that vary in their degree of complexity.³² How prey fish respond to different kinds of predator allows us to tease apart the relative contribution of simple versus more complex cognitive processes associated with predator interaction. Other observations suggest that some of these responses are likely modulated by affective state (e.g. states of fear or arousal) that is likely to further influence what is learned and remembered.^{48,49} Predator interactions clearly show considerable potential for clarifying the interplay between cognition and physiology.

Meeting of Minds: Interactions With Those Around You

The aquatic environment is a much noisier and overall a more communicative place than is often thought.

Not only do fish use reef sounds as a homing device²¹ but they have also developed many sophisticated methods of producing sound with which to communicate. In fact, the very basis of vocal, acoustic communication in vertebrates as a whole is thought to be derived from mechanisms present in the early fishes.⁵⁰ Communication is a particularly interesting means to explore the interplay between physiology and cognition. It is easy to imagine the evolutionary scenario where more complex cognitive processing develops from base sensory capacity. Less often considered, however, is the potential for the interplay of cognition and habitat to be a driver of physiology. Nonetheless, this may be just as likely to be a driver of physiological development as vice versa.

As a case for consideration, the plainfin midshipman (*Porichthys notatus*) is particularly famous for its hum.^{51,52} A portion of the male midshipman population, known as Type I males, have a large acoustic repertoire, which they use to court females and in aggressive or defensive interactions with other individuals.⁵³ Some have described them as sounding like 'an orchestra of mournful oboes'⁵¹ but can at times be so loud that San Francisco houseboat owners have grumbled about their homes vibrating from the sound at night.⁵² While entertaining (at least for those not attempting to sleep in a houseboat), this acoustic intensity presents a practical problem for the midshipman, who, without some mechanism of regulation, would deafen themselves preventing them from hearing predators or conspecifics. To cope with this, at the same time that the muscles around the swim bladder contract to instigate the hum, a signal is sent to desensitize both the neurons located at the hair cells in the inner ear as well as along the mechanosensory lateral line, both of which are used for sensing auditory signals. This simultaneous signaling not only serves to tell the fish that the sound is their own, but also allows them to protect their acoustically receptive organs so precisely, even when they emit a sound, that sensitivity to all other acoustic signals remains unaffected.⁵³

This remarkably refined physiological mechanism may be driven by a cognitive need from two directions: first, the need to communicate with potential mates and other males and second, to nonetheless maintain the capacity to sense and respond to the threat of predation or other signals in the environment. A similar mechanism for dimming the lateral line sensitivity to specific stimuli is also thought to be a method by which fish can dampen the 'noise' caused by water movements resulting from their own motions,^{53,54} allowing better quality information about the surrounding environment. This illustrates the potential capacity for the consideration of

cognitive drivers to act as a predictive framework for physiological constructs as well.

Plainfin midshipmen and other toadfishes are by no means the only fish to produce acoustic signals. Even several species of the weakly electric fish, cited below for their highly derived electric communication technique, have been shown to produce a variety of acoustic signals, such as ‘grunts’, ‘moans’, ‘growls’, ‘pops’, and ‘hoots’ during courtship and territorial defense.⁵⁵ Although the physiological mechanisms and the behavioral context of acoustic communication are now relatively well established in isolation, the decision-making pathways and cognitive processes behind such communication is an area surprisingly understudied and ready for a cross-disciplinary context-sensitive approach to investigation.

Even more common are instances of visual and olfactory communication. Fish use olfactory cues to selectively shoal with familiar conspecifics,⁵⁶ and fish often use visual information to learn about the social relationships of those around them.⁵⁷ When fish compete with one another for access to various resources, individuals often come into conflict. Being able to recognize or remember the dominant and subordinate relationships between individuals within a group would clearly be beneficial to prevent unnecessarily resource-expensive conflict. A system in which this has been studied extensively is the Siamese fighting fish (*Betta splendens*). Here, it is possible to stage fights between different males, and allow observer fish to see which individual is the winner and which the loser. Fighting fish will aggressively swim toward an individual perceived as a loser, and, therefore, subordinate. Alternately, it will produce an avoidance response toward an individual perceived as dominant, behavior that can be used to measure a fighting fish’s evaluation of an opponent’s social standing. In staging these fights, it was found that fighting fish are indeed able to eavesdrop on the interaction, and will then use that information appropriately in its own later interactions with those fish.⁵⁷

This work was taken one step further with African cichlids (*Astatotilapia burtoni*). Males of this species are aggressive and highly territorial and, like the Siamese fighting fish, will engage in fights to defend territories. In this study, a series of interactions were staged such that observer fish were taught a sequence: Fish A beat Fish B, Fish B beat Fish C, C beat D, and D beat E.⁵⁸ Grosenick et al. wanted to determine whether the observer fish could learn the logical progression in that sequence, a process known as transitive inference. If the fish could do so, then when they observe Fish A and E together, they should recognize that A will be dominant to E.

When that interaction was staged, that was exactly how the observer fish responded. One possible explanation for this result, however, is that the observer fish had always seen Fish A win and Fish E lose. Therefore, it is possible that the observer fish simply label the conspecifics as either winners or losers. Pitting Fish B and D against one another is a better test of transitive inference because the observer fish have seen both fish win and lose an equal number of times. Only if the fish understand the progression of the sequence will they have the capacity to perceive Fish B as dominant to D, a task they successfully completed.⁵⁸ Transitive inference is a psychological process that we see in ourselves, but it takes human children 4 years before they can develop the necessary cognitive skills to understand those relationships.⁵⁹

Conditions can be turbid in an aquatic environment, in which case visual cues will not be reliable, acoustic communication can be overwhelmed, and depending on the rate of flow, olfactory cues can become misleading. As a result, some species have evolved a method of communication using electric pulses. Weakly electric fish have an organ that discharges to produce a sinusoidal electric signal.⁶⁰ The signal is used to sense objects in their environment,⁶¹ for species recognition⁶² as well as for communication.^{63–65} We will focus on three genera of weakly electric fish, *Apteronotus*, *Eigenmannia*, and *Gymnarchus*, illustrated in Figure 1. While both *Eigenmannia* and *Gymnarchus* derive their electric organ (EO) from the muscle tissue, *Apteronotus* derives it from the neural tissue.⁶⁰ However, phylogenetically, *Eigenmannia* and *Apteronotus* are more closely related New World species, whereas *Gymnarchus* is an Old World species. All are descended from a common, nonelectrosensing ancestor. Thus, the capacity for electrosensing has convergently evolved in all three species.⁶⁰

The capacity to modulate the EO discharges is important when two individuals are emitting at a very similar frequency, which interferes to create a signal unintelligible to either party. When this occurs, individual fish will modulate their own signal either up or down, known as the jamming avoidance response (JAR).^{61,66} In order to enact the JAR, however, a fish must determine whether to be the one to increase or decrease its frequency (in effect, to solve the awkward problem humans frequently encounter in hallways to determine who ought to move to the left or the right). Because the ideal solution to this problem lies in consistency, this constitutes a very good example of a deterministic, but nonetheless cognitive, decision-making process.

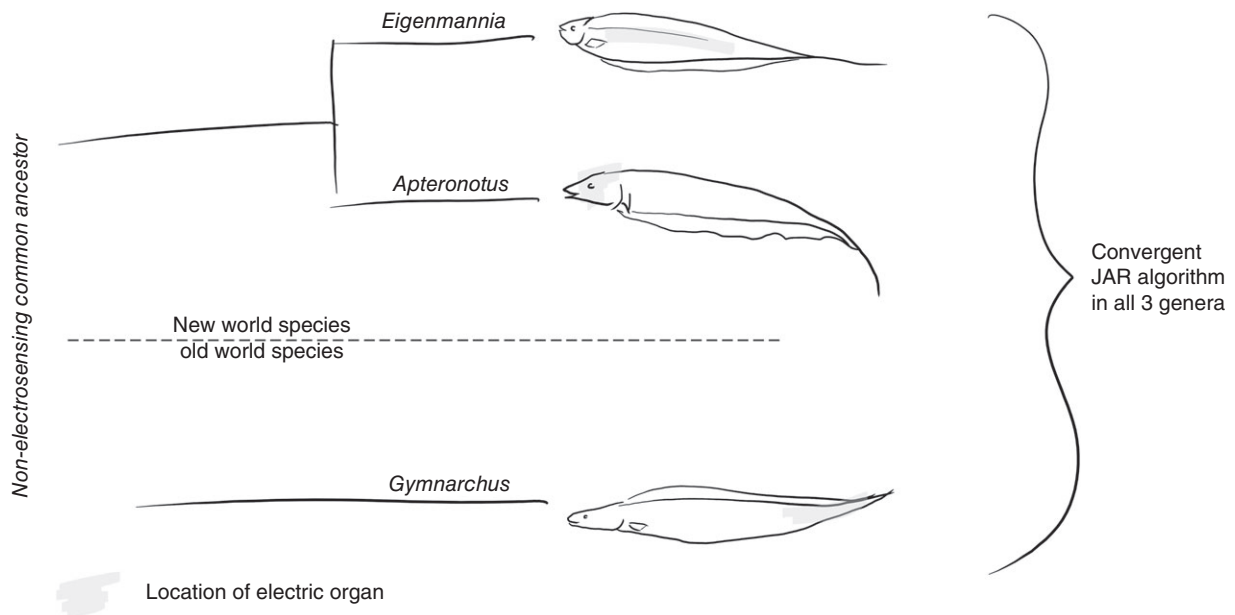


FIGURE 1 | Convergent evolution of the electric organ and Heiligenberg jamming avoidance response algorithm in three genera of weakly electric fish: *Apteronotus*, *Eigenmannia*, and *Gymnarchus*.

This process is exceptionally well documented, and is known as the Heiligenberg JAR algorithm. In this algorithm, the fish with the higher initial frequency will increase its signal, while the fish with the lower initial frequency decreases its signal, thereby solving the jamming issue.⁶¹ The neural mechanism by which the fish detect whether they have a higher or lower frequency is more similar in *Apteronotus* and *Eigenmannia*,⁶⁷ mirroring their closer phylogenetic relationship. *Gymnarchus*, on the other hand, utilizes a very different neural pathway. Nonetheless, it has been shown that all three species ultimately utilize the same Heiligenberg algorithm to decide whether to increase or decrease their frequency to solve the jamming problem.^{15,68,69} This is particularly illustrative because it provides a definitive example where convergently evolved structural mechanisms (the EO)⁶⁰ have resulted in a similarly convergent overlaying decision-making pathway.¹⁵ This area shows particular promise because the mechanistic underpinnings have been so thoroughly investigated,^{60,61} providing a strong foundational framework on which to develop further cognitive studies and examine the evolutionary contexts in which common decision-making pathways can form.

Cleaner fish also provide a fascinating case study in communication and interspecific interaction. Some cleaner fish will remove ectoparasites opportunistically, while others develop specific stations where a pair of fish will work together.⁴⁶ These stations are often so popular that clients will line up and wait

their turn to be cleaned. For the most part, cleaner fish will stick to ectoparasites; however, some species will ‘cheat’ by taking a bite of the more nutritious scale and mucous instead.⁷⁰ Cheating behavior also makes for subtle and interesting dynamics between both the cleaner and the client as well as between the cleaner partners. A cheating cleaner can be spotted by the shudders or jolts from the bitten client fish.⁷¹ If they are bitten too often, a client can retaliate either by ending the interaction or by punishing the cheater by aggressively chasing it. While in line, clients will watch the cleaner fish and if they perceive a pair to be cheating too often, the clients will choose a different station.⁷² Cleaner fish are apparently aware of this danger, however, as they have been found to be more cooperative when they are aware of an observer.⁷³ Punishment occurs not only from client to cheater. If only one of the cleaner pair cheats, both partners lose if the client chooses to swim away from the interaction. As a result, sometimes one partner will punish the other for cheating, and making the partner less likely to cheat in the future.^{70,74}

Additionally, cleaner fish are known to engage in ‘tactile stimulation’ in order to pacify a client after a bite.⁷⁵ In this behavior, the cleaner fish touches the client with dorsal and pectoral fins, and no mucous or ectoparasites are consumed. This behavior has been found to lower cortisol levels,⁷⁶ and in one study, it was associated with both an increased interaction duration and a decrease in the aggressive chasing by the client fish used to punish cheaters. Cleaner fish also

appear to provide tactile stimulation more often to predatory clients,⁷⁵ and it has been suggested that this may reduce predatory interactions toward bystanders at the cleaning station.⁷⁷

In a study involving cleaners that do not operate on stations, Oates et al. found a negative correlation between cheating and frequency with which clients encounter cleaners (*Labroides bicolor*).⁷⁸ For this to arise, the fish necessarily have some understanding of their geographic location within their home range, and when in less frequented areas, their tendency to cooperate is lowered, leading to an increased incidence of cheating in the periphery of their territory. Although it is still unclear whether this is a simple associative process or a complex interaction of spatial cognition with social recognition, being able to link location with the degree of cooperation expressed is an interesting cognitive feature. In cleaner fish systems, both clients and cleaners learn and remember individuals and status. The capacity to communicate intent, as well as to potentially manipulate interactions, as seen by the use of pacifying tactile stimulation, shows an extraordinary degree of interspecific awareness. Further research exploring the influence of social structure systems on cognition in fish will be an arena of fascinating future development (Box 1).

BOX 1

COOPERATIVE HUNTING: BETWEEN AND AMONG US

Cooperation is an area of particular interest for those investigating both the human and the animal mind. In an ecological context, cooperative behavior has repeatedly evolved in three-dimensional open habitats.⁷⁹ This provides a very interesting framework in which to investigate the circumstances under which cooperation develops, and the diversity of fishes again lends a prime opportunity for such effort. Here, we highlight two examples of cooperative hunting: one within and the other between-species.

Pack Hunting in the Weakly Electric Fish

The clear water of Lake Malawi allowed the opportunity for Arnegard and Carlson to observe simultaneous behavior and electric signaling of a weakly electric fish, the Cornish jack (*Mormyrops anguilloides*) in the wild.⁶⁵ They observed that the fish remained dormant during the day but started aggregating and hunting in small groups

at night. These groups were found to be composed of the same individuals across nights, suggesting a form of pack hunting behavior. Additionally, the fish were occasionally observed to be synchronizing their electric discharges with great precision, believed to be a pack cohesion signal, particularly as the behavior was primarily observed when the individuals returned to their group after a temporary separation.

The Grouper and the Moray Eel

Complex coral reef habitats have numerous places for small prey fish to hide when pursued by a large predator like a grouper (*Plectropomus pessuliferus*). These pursuits often end in frustration for the grouper when the prey fish retreat to crevices too small to follow. In such circumstances, the grouper will occasionally initiate a group hunt with a giant moray eel (*Gymnothorax javanicus*), whose hunting strategy is to follow their prey into holes. The grouper will swim to an eel's burrow and signal by means of rapid head shaking. If inclined, the eel joins the grouper and swims in close proximity to the place where the grouper lost its prey. The grouper will indicate the location of the hiding prey by angling its head coupled with more vigorous head shakes. As the eel goes in pursuit, the grouper will wait above the coral. Sometimes the eel corners the prey, other times the prey fish is flushed back into the open where the grouper waits ready to ambush it.⁸⁰

Tools and Targets: Interactions With the Environment

Despite the long-held belief that tool use is a defining feature separating humans from all other species,^{81,82} tool use is not only present but also remarkably widespread throughout the animal kingdom.^{83–85} A growing recognition that tool use goes far beyond Hominidae has created a problem with regard to definitions. As the debate has been well covered elsewhere,^{83–86} we will not delve extensively into it here. It is generally agreed that the early definitions of tool use (such as those proposed by van Lawick-Goodall⁸⁷ in 1970, Alcock⁸⁸ in 1972, and adapted by Beck⁸⁹ in 1980) were fairly arbitrary in character, with Beck's most widely adapted definition requiring that a tool be disassociated from the surrounding environment and held, in some manner, by the user.⁸⁹ This creates the uncomfortable distinction by which an otter bashing a rock against a shellfish is

considered to be tool use, but the same animal bashing the shellfish against a rock is not. Fortunately, Beck later adapted the definition to include such situations where the user exerted control over the tool, whether or not it remained attached to the substrate, though this, of course, in turn spawned the question of what, precisely, ‘control’ ought to indicate.⁸³ Fish create a definitional conundrum because they lack grasping appendages and given that their environment is more viscous and buoyant, the physics of mechanically operating an object is entirely different from what is possible in air.^{84,90,91} In the case of anvil use in an aquatic environment, it may be both evolutionarily and cognitively more appropriate to maintain primary ‘control’ over the object of interest, because putting a food item down runs the risk that it will float away while a crushing tool is obtained. Paško suggested that investigations of tool use in fish should not overlook the complexities of manipulating objects within the aquatic environment.⁹⁰ Thus, Goodall’s original definition—that of the use of an external object in the attainment of an immediate goal—would seem an appropriate definition as that would work both in an out of water,⁸⁴ so this is the definition that we will adopt.

Although cognition is almost always absent from definitions of tool use considered over the last 40 years, it is typically assumed that some degree of higher order cognition is required.⁸⁴ Such an assumption may have originated from the cultural imagery of the early human stepping from the mists of instinct into the *sapiens* of the stone age, stone axe as both a symbol and a motivation for his intellectual advancement. Thus, when Jane Goodall described tool use in primates in 1960, it came as a shock to many, and anthropologist Louis Leakey famously telegraphed her, ‘Now we must redefine tool, redefine man, or accept chimpanzees as human’.(Ref 92, p. 212) Today, in addition to primates, there is evidence of tool use in bears,⁹³ elephants,⁹⁴ sea otters, dolphins,⁹⁵ mongooses,⁹⁶ woodpecker finches,⁹⁷ crows,^{98,99} owls,¹⁰⁰ octopuses,¹⁰¹ ants,¹⁰² and wasps,¹⁰³ among other species. However, just as any other measurable behavior, these examples of tool use vary from rigid, deterministic patterns of behavior through to fully flexible cognitive problem-solving.⁸⁴ This is certainly no reason to discard tool use as a valuable and potentially vibrant arena of cognitive study. In fact, determining when tool use is cognitive and when not is a fascinating and elucidating area of investigation, ripe for an ecological approach.

Observing tool use in fish is challenging because our terrestrial habitat overlaps very little with them, and it is difficult for us to spend long periods of

time in an aquatic environment. Therefore, repeating Jane Goodall’s extensive hours of unobtrusive observation¹⁰⁴ in the field with her troupe of chimpanzees is far from straightforward for fish. Nonetheless, it is not solely the logistical difficulties that have limited the opportunities for the observation of tool use in fish. Instead, the pervasive idea of cold-blooded and dim-witted fish has meant that we have not expected to see it, and so did not look to find it. Then, even when it was found, it did not occur to us to describe the behavior as such.

In fact, the earliest documented instance of tool use in fish was published in a manual on the keeping and breeding of the brown hoplo catfish, *Hoplosternum thoracatum*, 3 years before Goodall shocked the world with her observations of chimpanzees.^{105,106} The fish glues its eggs to a leaf and then will pick up the leaf like a tray and carry it to the safety of a foam nest if threatened, an action which satisfies even the strictest definition of control as the tool is directly manipulated by the mouth. Similarly, in the mid-1970s, it was found that both male and female South American cichlids will pick up and ‘test’ multiple leaves before they select one on which to lay their eggs. If threatened, the fish pick up the leaf and move it to a more protected location.^{107,108} In 1971, Fricke found that the wrasses *Cheilinus trilobatus* and *Coris angulate* used rock anvils to smash open sea urchins, returning to a particular stone repeatedly within their territory.¹⁰⁹ Additionally, he observed the rippled triggerfish *Balistes fuscus* blowing a stream of water directly under sea urchins to dislodge them from their positions on the rock and flip them over. Once the underside was exposed, they would bite the oral disc where few spines are present. The fish also learned the size of urchin that it could successfully manipulate. By means of choice experiments, Fricke determined that only the smaller urchins within the fish’s tolerances would be selected. The orange-lined triggerfish (*Balistapus undulates*), on the other hand, was observed breaking the urchin’s spines until it could be grasped, at which point the fish lifts the urchin and swims upward. After reaching a certain height, the urchin is dropped, and the fish can swim under the falling prey to access the underside to bite and kill it.^{8,109} That these examples were not cited as tool use at the time they were published is an indication of the assumptions in play regarding expectation of both behavior and cognitive faculties of nonhuman species in that era.

In 1995, another example of anvil use by a labrid fish was published when a yellowhead wrasse (*Halichoeres garnoti*) was seen breaking scallops on a rock, and was finally described as an example of tool

use in fish.¹¹⁰ Subsequently, photographic evidence of anvil use has been observed in a blackspot tuskfish (*Choerodon schoenleinii*)¹¹¹ and a six-bar wrasse⁹⁰ as well as a video footage of an orange-dotted tuskfish (*Choerodon anchorago*).¹¹² That all examples have been observed in Labridae, which also includes species of cleaner fish previously described, suggests that cognitive flexibility may be a primary component of niche adaptation in this family, and other examples of interesting cognitive capacity may be observed with further investigations into this group.

A recent example of innovative potential tool use in fish has been found in Atlantic cod (*Gadus morhua*).¹¹³ Pulley-operated self-feeders were placed above the fish tanks such that the fish could operate them by biting and pulling on the string as the fish swam forward. To access the food, the fish had to release the string and swim to the food inlet position. To allow individuals to be identified, the fish had an external bead tag attached on the right side of their anterior dorsal fin. In two different tanks, fish accidentally entangled their bead with the pulley mechanism, such that the feeder was triggered, after which the fish became disentangled. After these initial accidental entanglements, three fish (across two different tanks) learned to hook their bead in the trigger mechanism to activate the feeder, and the series of movements was both coordinated and fine-tuned over the course of more than 100 repetitions of the behavior across each fish. By using the tag to trigger the device, the fish could more quickly arrive at the food inlet point than when the fish triggered the device by mouth¹¹³ and thus beat its competitors to the food. This observation is particularly interesting because it showcases how we may make assumptions about cognitive inability from behavior, but in fact, physical constraints may be a primary limiting factor of behavior. As it is impossible to observe cognitive functioning directly, we rely on external, behavioral measures as a proxy. Thus, in the field of cognitive science, finding both the right questions and the best methods with which to answer these questions is essential to shed light on the inner workings of animal minds (Figure 2).

Archerfish (*Toxotes* sp.) are a particularly promising group for addressing such questions in an ecologically relevant way. These fish are opportunistic hunters and they inhabit a variety of mangrove and freshwater habitats throughout the Asia and south Pacific region. Using a specialized groove in the roof of their mouth, the fish precisely shoot jets of water at an aerial prey.¹¹⁴ This task presents a suite of interesting cognitive challenges that archerfish have contended with in order to access their prey. Almost all aspects

of the archerfish's hunting skills are learned,^{114–117} and young archerfish fire 'charmingly weak shots' that improve with time and practice.¹¹⁴ The sensory systems must be sufficiently sophisticated to cope with refraction at the air–water interface,¹¹⁵ and fish must be able to visually discern camouflaged targets against complex backgrounds,¹⁴ estimate distances to determine shot feasibility, and judge three-dimensional speed of targets.^{116,117} While matching the force of water jet to the size of prey is an automatic, evolutionarily inbuilt process,¹¹⁸ determining the absolute size of the prey that might influence where an insect falls into the water must be learned.¹¹⁵

All these tasks are completed in a highly competitive environment in which a neighboring fish will rapidly steal the fallen prey as soon as it hits the water. As a result, the archerfish must additionally be able to predict where its prey will fall, and will complete what is known as a 'predictive start' within 100 milliseconds of successfully making a shot so that they can reach the fallen prey before other fish. The most efficient path is still taken even when obstacles are en route, but if there are no competitors, the fish swims to its prey without the rapid start response.¹¹⁹ The predictive start is evolutionarily derived from a highly conserved 'c-start' mechanism, critical in predator escape responses throughout fish phylogeny, with well-known neural circuitry.¹²⁰ Using such highly conserved systems for novel cognitive processing is similar to the example of the blind Mexican cave fish where ancestral mouth-opening behaviors were utilized to improve navigation. Perhaps due to the highly social nature of the group, a large degree of social learning is shown in the fish as well. When an observer fish watches a demonstrator learn to shoot a novel moving prey item over several trials, the observer fish can then accurately complete the task the first time it tries.¹¹⁶

The accuracy displayed by the archerfish in both targeting and retrieving the prey is critical in their ecological and social context. If their predictive c-start is imprecise, they have wasted effort as another will reap the reward, or, in a worst case scenario, it could make the fish more vulnerable by potentially making predators more aware of their presence with no benefit. It is interesting, therefore, to investigate what happens when the information available to the fish is compromised. When forced to target in situations of low light intensity, the fish will take more time aiming for their target, and will choose to shoot less often, but the accuracy of each shot shows no difference. In this way, the fish are taking more time to ensure a more accurate response.¹²¹

A very simple neural circuit is responsible for these processes.¹¹⁷ When we try to solve a similar

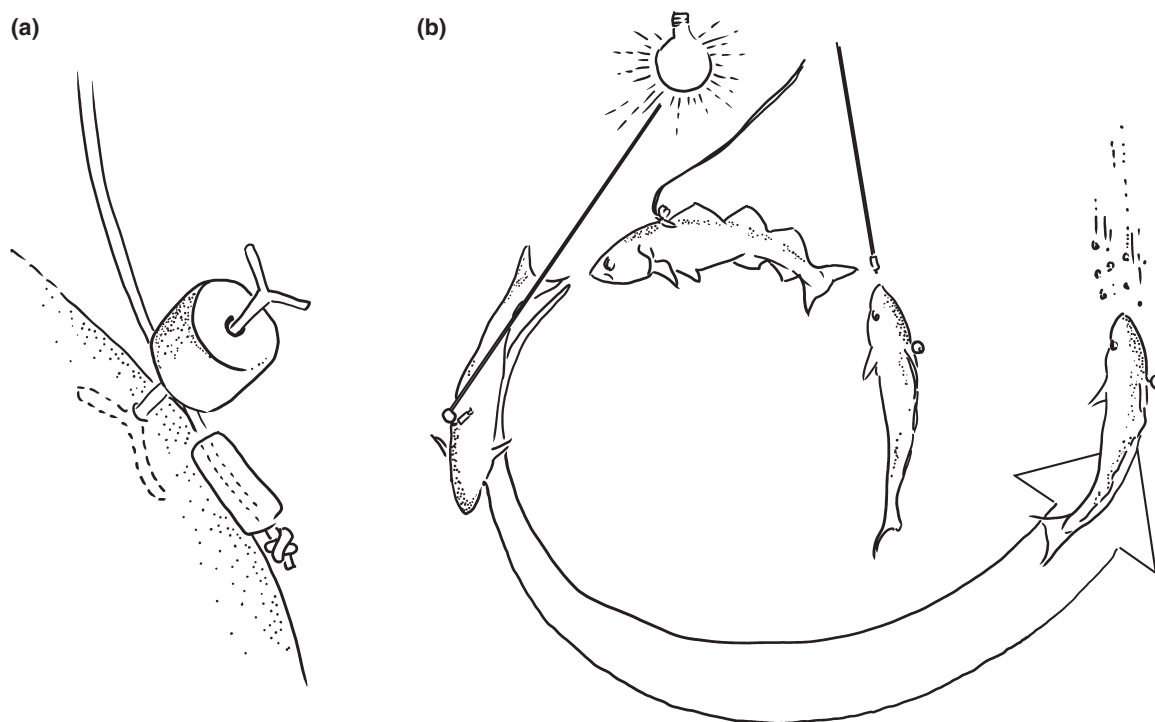


FIGURE 2 | (a) Diagram of tag bead attached to anterior dorsal fin. (b) Direction of movement. First, the fish approaches trigger pulley and positions the bead such that it catches the trigger pulley. Then, the fish swims forward, activating the trigger, and finally releases the bead and swims to the location where food is dispensed. (Reprinted with permission from Ref 113. Copyright 2013 Springer)

kind of task, our brain's visual cortex is used; however, a study in which both humans and archerfish were provided a comparable task matching the target against varying degrees of cryptic background revealed that the fish produce a visual search strategy indistinguishable from that used by humans.¹³ Both species generally start by scanning areas closest to the individual doing the observing, then continue searching areas in a stepwise fashion from that point. Thus, through distinct evolutionary pathways, a much simpler mechanism delivers in archerfish the same results as the more complex mammalian visual cortex. This capacity for complex decision-making coupled with the simplicity of the neural network of the fish gives the archerfish considerable promise as a model system for understanding the complex decision-making process in vertebrates. The nature of the hunting methods of the archerfish also provides a unique tool to access cognitive function, as the archerfish will flexibly learn to shoot at almost any target that will provide a food reward.¹¹⁴ This opportunity was recently used to begin investigating higher order cognitive capacities of archerfish.¹²² Fish were set concept learning tasks, including 'match-to-sample' or 'odd-one-out' tasks as well as a four-way 'alternative forced-choice' task. Researchers found that the fish were poor at matching to sample tests, and had only some success at

identifying the odd one out. However, they were highly successful at the four-way alternative forced-choice task. These differences in performance across the different kinds of task seem likely to be based on the ecological relevance of the different tasks to the fish. It may not be as ecologically relevant for an archerfish to reidentify something similar to what they have seen before, as in the 'match-to-sample' task. Alternatively, identifying the item different from what was seen before (the 'odd one out') and recognizing a conditioned stimulus from a wide range of unfamiliar options may be much more relevant tasks considering the evolutionary ecology of the fish.¹²²

Despite the field of tool use being somewhat tied in definitional knots, examples of this activity in fish range from basic to complex, and some examples indicate that higher order cognitive processing is involved. Exploring this variety is an area that may provide considerable insight into the spectrum of cognitive capacity and flexibility in the future.

CONCLUSION

Investigation into the field of animal cognition and fish cognition, in particular, is primed to enter a Renaissance of activity. The wide availability of histological, genetic, molecular, and behavioral techniques

combined with a context-specific approach allows for an unprecedented degree of integrated, interdisciplinary investigation into cognitive processing. This capacity could not come at a better time. Understanding the internal processes whereby fish interact with their environment can provide critical insight into the active management of aquatic systems under a

state of increasingly rapid change. Finally, basing the investigation of cognition on the ecological context in which it is developed not only provides insight into the inner workings of fish cognition, but also sets a practical framework from which we can develop sound prediction and theory in the field of cognitive science.

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