Long-term memory in fishes

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In the movie *Finding Nemo*, Dory the regal tang suffers from short-term memory. Indeed, there may be a myth out there to the effect that many fishes have only a three-second memory. This is false, of course. Fishes (regal tang included) can be taught all kinds of things ("event X is always followed by event Y", "if I do A, then event B will happen", "the way to food is along this path", "the best way to handle such a food item is like this", "predator P looks like this and smells like that") and they remember such things for many days at least, and often many weeks.

But let's not be content with weeks. Are fishes gifted enough to remember things for years? The answer is: some do, but we don't know of many cases. One reason for this scarcity is that many fish species don't even live for many years. Another reason is that a true test of long-term memory requires that once a fish has been taught something, it must not be exposed to the relevant stimulus again (it must not be "reinforced") until the test takes place. This is nearly impossible to do in the wild: how can one guarantee that a wild fish will not come in contact with a particular stimulus for many years? And even in the lab, studies on long-term memory are not popular because they take a lot of time, and professional scientists are often under pressure to publish papers rapidly. It takes a lot of fortitude to house many fish that take up space and do nothing simply in the hope that they will provide unambiguous evidence of memory during a single test a few years henceforth.

As a result, the evidence we have tends to come from anecdotes. But some of these anecdotes are quite interesting. Here is one that comes from what I consider a reliable source: Charles W. Eriksen, Professor Emeritus (Psychology) at the University of Illinois at Urbana/Champaign. After reading my book on fish behaviour, Dr. Eriksen sent me an e-mail relating some of his experiences with catfish. His message was so well written that I simply quote him here.

"About twenty years ago we built a pond near our farm house and stocked it with bluegills, largemouth bass and channel catfish. A few years later I observed a neighbour feeding the catfish in his pond. He carried a coffee can of fish pellets and would rattle the pellets in the can. At this sound the catfish could be seen coming from all directions in the pond, leaving a wake in the water. So I decided to train my catfish to come to call. Instead of rattling food pellets in a can, I thought it would be more interesting to call them by name. I shouted out "fish-fish" a number of times as I spread the pellets in the water. Within three days (trials) I had about 19 catfish coming to call. I continued to call and fed them on a somewhat regular basis for about 2 or 3 months that summer before abandoning the call and feeding in August. The next spring I started the calling and feeding again and on the very first call about 14

catfish responded. Within two days the number was up to 16 and that was the total for the remainder of the summer. Again, due to the press of other demands, I quit feeding in August.

Five years (count them, five) lapsed before I fed or called the catfish again. At the end of this time I decided to start calling and feeding catfish again. Imagine my surprise when on the very first call of "fish-fish" the wakes of at least nine fish could be seen coming through the water. And this was before I had thrown a single pellet upon the water. By the second feeding (the next day), I had 13 fish coming in to feed. These were probably the only survivors since this was the highest total I as able to count during the summer. These were from the original stocking. The habitat of the pond does not appear suitable for catfish reproduction and I have not introduced any fish since the original stocking. All of the fish are of about the same size which by now is quite considerable."

What a delightful observation! Hurray for an impromptu yet fairly rigorous experiment! Dr. Eriksen and his wife lived on the property, the pond was about 50 yards from the house, and it is seems unlikely that anybody else would have reinforced the fish, unknown to Dr. Eriksen, by calling and feeding them during the five years that intervened between the two years of training and the final "test". Outside of the special case of imprinting (see below), I know of no better example of long-term memory in fishes.

A second anecdotal example is also from a reliable source. In the foreword to the book "Fish Cognition and Behaviour", Dr. Tony J. Pitcher mentions some goldfish in his lab who were trained to choose tubes of one colour over another in order to get food. Then for one year the fish were fed normally in the absence of tubes. When, at the end of that year, the tubes were presented again, the goldfish immediately selected the one with the correct colour.[1]

Here are other observations, this time gleaned from the scientific literature. Carp that had experienced the unpleasantness of being hooked on a line were still hook-shy a year later, even though they did not see a single hook during that interval.[2] Sockeye salmon were taught that a brightening of their aquarium light signalled the imminent delivery of food at the surface – they indicated such knowledge by swimming faster and coming to the surface as soon as the light was brightened – and they still responded to such a signal 8 months past the last reinforcement. A year after the last reinforcement they still accelerated but did not come to the surface when the light was brightened, and after 2 years the response had disappeared.[3] Some rudd, *Scardinius erythrophthalmus,* and European chub, *Squalius cephalus,* were trained to accept food from the hand and mouth (!) of a person, and after a 6-month break they readily did so again, approaching that person but not others.[4] Crimson spotted rainbowfish, *Melanotaenia duboulayi*, kept in a small tank learned how to escape from a model trawl apparatus by swimming through a small hole in its center, and when tested again 11 months later they escaped promptly on the first try. (Unfortunately, as acknowledged by the author of the study, a control was missing from this experiment to eliminate the possibility that efficient escape was a function

of calmness acquired after many months in captivity rather than remembering exactly where the hole was in the trawl apparatus.) [5]

Let's slide down the scale towards memories that last several months or several weeks. In one study, rainbow trout were taught to press a bar for a food reward. Then the bar was withdrawn, the fish were hand-fed for 3 months, and finally the bar was brought back. The fish quickly pressed the bar, showing that even after 3 months they had not forgotten what the bar was about.[6] But contrast this with another study on rainbow trout, in which they were taught to accept small pieces of black-dyed liver as food. After this training, the fish were only given regular food pellets. When the liver bits were presented again 2 weeks later, the trout readily took them. However, when the liver bits were reintroduced 3 months later, the trout disregarded them.[7] So, after 3 months rainbow trout forget a food item, but they remember a press bar. Perhaps unusual objects (a press bar, or a feeding tube as in the case of the goldfish above) are better remembered than unusual food items, especially when other food items are presented in the meantime.

Limited memory for food items may be related to the fact that in some environments, food sources can be quite variable, both in space and in time. There might be a trade-off (perhaps in terms of how many neurons can be allotted to each task) between remembering about old food sources, and learning to handle new ones.

Fishes that are offered a novel food item will often ignore it at first. Eventually however, they will sample this new food, and if they find it palatable they will start eating it more regularly. If the food is live prey, the skill required to catch it and to handle it properly can then improve through learning. The fish become capable of detecting the prey at a greater distance (as indicated by orienting movement), initiating the attack on it sooner, succeeding at catching it more often, and wasting less time to position the prey correctly within the mouth before swallowing it.[8] (These improvements are realized more quickly if the fish are hungry,[9] or if only one type of prey is offered. If two types of prey are presented alternately, the fish do not learn as quickly as when pure diets are used.[10])

In sticklebacks at least, memory for food-handling skills is limited. If a stickleback that has learned how to forage for prey A is then switched to a diet of prey B for 10 days, and then back to prey A, it will handle prey A as naively as it did before the original learning. If not regularly reinforced, a stickleback forgets its foraging skills within 1-4 weeks. One study has found that three-spined sticklebacks, *Gasterosteus aculeatus*, from a land-locked freshwater pond forgot how to handle a particular prey after 25 days, but that threespines from an estuary forgot after only 10 days, and that sea sticklebacks (= fifteen-spined sticklebacks) *Spinachia spinachia* forgot after only 8 days. The authors of the study suggested that sticklebacks which come from habitats where prey populations are unstable (such as tidal zones of the sea and estuaries, as opposed to freshwater ponds) may benefit by forgetting their foraging skills more easily. By forgetting outdated skills more quickly after a given type of prey has disappeared from the environment, these fish may be able to concentrate on learning new skills more thoroughly. [11]

Forgetting about food in an environment of plenty may be excusable, but forgetting about the identity of predators is likely to carry a severe penalty – indeed, the ultimate penalty. In fact, knowing what a predator looks like is so important that many species don't even risk a first tentative encounter to learn about it. They have an innate knowledge that predators usually have wide mouths and large eyes, and they automatically avoid fishes that display these characteristics.[12] But it is also possible for fish to *learn* the precise identity of some of their predators. They can do this by witnessing other fish fleeing from the predator (see the page: Social intelligence in fishes), by associating the smell or look of a predator with the presence of alarm substance, or by direct inspection or interaction with the predator. There have been very few studies aimed at determining how well this hard-earned information is remembered. Furthermore, I am aware of no study that attempted to find the *maximum* duration of such memories. Researchers usually test a duration that is convenient within the limits of their work schedule. The durations in the next paragraph should all be preceded with "at least".

Zebra danios learned to recognize a predator and did not let it approach within a certain distance; they maintained that flight distance after 10 days without any contact with the predator.[13] Five days after being briefly placed in a tank together with a predatory lingcod *Ophiodon elongatus*, Coho salmon juveniles survived better than unexposed individuals when put in the presence of the lingcod again. [14] Two years after having been stalked by the realistic-looking model of a pike, European minnows *Phoxinus phoxinus* reacted to a similar (but larger) pike model by inspecting it more, staying in larger shoals, and hiding less than other minnows who had never seen any model before.[15] Guppies that had been chased by conspecific adults for one or two days when they were very young escaped more easily from the attacks of live cichlids about 10 weeks later, as compared to fry that had never been chased by anybody (so here the memory is not of predator identity, but of how to evade a chase).[16] Even a fry's experience of being chased by a parent, and taken into its mouth for safe carrying back to the nest, may help the fry to avoid predators several months later, as reported for some populations of sticklebacks.[17]

Fish may also remember what species are harmless. Paradise fish, *Macropodus opercularis*, commonly approach and inspect new species, presumably to determine if they are predatory or harmless. In one study, paradise fish were given the chance to inspect an innocuous goldfish. After this they were kept away from any goldfish for three months. When the goldfish was presented again at the end of those three months, the paradise fish did not pay too much attention to it. It seems they remembered what goldfish were like, and how harmless they were.[18]

Pairs of the anemonefish *Amphiprion bicinctus* defend the anemone in which they find shelter and lay their eggs. Fish ethologist Hans Fricke captured the mating partner of one such anemonefish, kept it captive in an aquarium for 30 days, and then brought it back to the field site and presented it inside a Plexiglas tube to the partner that had been left behind. At the same time he also presented other anemonefish in transparent tubes. The partner directed many more attacks to the strangers than to the

former mate, suggesting mate recognition after a 30-day absence. In a similar experiment, Fricke removed anemone owners and kept them at another location for six months before bringing them back to their original site. He released them near their old anemone but in a place where the anemone itself was out of sight. The fish immediately swam in the direction of their anemone, showing they remembered their old neighbourhood even after a 6-month absence. In a control test, strangers released to the same site did not find the anemone, showing that nothing special about the site pointed the way to the anemone and that only memory could have helped the original owners.[19]

By far the best example of long-term memory is the homing behaviour of salmon. When they are young, salmon learn the smell of the stream in which they live. Then they leave the stream to go live at sea. Several years later, they come back to their natal stream in order to spawn in it. These adult salmon find their natal stream by following their nose – the trail of the odour learned several years earlier but not forgotten. This seems to be a case of imprinting. In imprinting, the brain is hard-wired to learn something during a sensitive period early in life, and retain that information until death. This is how many species of birds, for example, after being exposed to their parents early in life, figure out what their species, and in particular their future sexual companions, should look like.

The discovery of long-term olfactory memory in salmon took place in the 1960s and 1970s and is mainly due to the work of Arthur Hasler at the University of Wisconsin. In his first experiment, Hasler caught some adult salmon, plugged the nostrils of some of them so they could not detect any odour, left other individuals untouched, and measured the success of all these fish at returning to the stream where they had been born and originally tagged. Intact fish made it home successfully whereas fish with plugged noses were recaptured more or less evenly among all of the streams of the basin. To provide further evidence, Hasler and his co-workers reared young coho salmon in a hatchery and exposed them to one of two different chemicals, morpholine and phenethyl alcool (PEA). These artificial chemicals do not normally carry biological meaning but they are odoriferous. The fish were then marked according to the chemical they had been exposed to, and released into Lake Michigan. During the spawning migration 1.5 years later, the researchers dripped morpholine into one river and PEA into another 9 km away. Convincingly, 95% of the fish that were recaptured and that had been exposed to morpholine were recovered in the morpholine-scented river, and 92% of the recaptured PEA fish were recovered in the PEA-scented stream.[20]

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