FEATURED ARTICLE

Dick Fay and Goldfish

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Do fish hear? What do fish hear? How do fish hear? These are questions that have been around since at least the times of Aristotle and Pliny the Elder. Whether or not fish are disturbed by the sounds made by fisherman has been an issue at least as far back as Issak Walton (1653; see also Rudow, 2020). However, it was not until the early 20th century that investigators in the United States, starting with Parker (1903) and his group and in Europe by von Frisch and his students (e.g., von Frisch, 1938), conclusively demonstrated that fishes can hear (see historical reviews by Moulton, 1963; Tavolga, 1971). These early studies and the ones that followed over many decades explored hearing in a number of different fish species and asked a range of questions, further demonstrating that fish can hear and suggesting that they could discriminate between sounds and suggesting that the goldfish (*Carassius auratus*; Jacobs and Tavolga, 1967, 1968; Enger, 1973; Tavolga, 1974) and Atlantic cod (*Gadus morhua*; Hawkins and Chapman, 1975) could discriminate between sounds and detect signals in the presence of masking noise.

These early studies provided information about hearing in perhaps 5 of the more than 33,000 extant fish species. However, what was lacking were in-depth investigations of hearing in fishes that would give a picture of what they could and could not do with their auditory systems in the detection and processing of sound. Nor were the data of sufficient depth on a single species to enable a comparison between the hearing capabilities of fishes and those of terrestrial vertebrates, including humans. Such an understanding was needed, however, to put fish hearing into the perspective of overall vertebrate hearing and to help understand the place of fishes in the evolution of hearing. This latter issue was of particular importance because it is clear that the auditory system of vertebrates evolved within the fishes. The basic structure of the ear and auditory central nervous system (CNS) is the same in fishes and humans (Popper and Fay, 1997; Fay and Popper, 2000).

There is, however, one body of literature on a single species that does provide the depth and breadth of knowledge of hearing that allows realistic comparisons with other vertebrate taxa and also helps put fish hearing capabilities into an evolutionary perspective. This work focused on the goldfish, which became the "white rat" of fish hearing research. The vast majority of this work was done over almost 50 years by Richard (Dick) R. Fay (**Figure 1**). Before his retirement, Dick was planning on taking a broad and integrative view of all of his goldfish

Figure 1. *Dick Fay enjoying a visit to a herring restaurant in Copenhagen (see nyhavnsfaergekro.dk). **Top:** photo of Dick with his first aquavit. **Bottom:** photo as reimagined by Tony Hawkins. © 2020, Anthony D. Hawkins, all rights reserved.*

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work so that it would further help auditory neuroscientists understand vertebrate hearing. Dick was not able to follow this path, and so the purpose of this article is to describe the breadth of these studies, with hope that some future investigators will be stimulated to bring together all of Dick's ideas and move forward from them, perhaps doing a similar range of studies in another interesting species. We should mention that Dick, who is a close friend of the three of us, has seen and approved this article and has given us valued insights into some of his thinking.

About Dick Fay

Dick retired in 2011 from Loyola University Chicago (IL) where he was a distinguished professor of psychology and a long-time member of the fabled Parmly Hearing Institute. Sisneros (2016) has provided an intriguing and thorough biography of Dick and his contributions, so they will not be included here. Dick has been a member of the Acoustical Society of America (ASA) for more than 50 years. He has an ASA Silver Medal in Bioacoustics, chaired the Animal Bioacoustics Technical Committee, and was associate editor of *The Journal of the Acoustical Society of America*.

As a graduate student working in the laboratory of Ernst Glen Wever (see acousticstoday.org/7408-2) at Princeton University (NJ), Dick discovered that a conditioned measure of respiration by the goldfish provided a reliable, valid, and relatively noninvasive measure of the fish's ability to process sound (Fay, 1969). The conditioned respiration response was a change in respiration evoked by a mild electric shock that was intermittently paired with a sound presentation. The sound presentation would, over a short period, elicit a change in respiration not unlike that elicited by the shock. Over several years, including a postdoctoral year with Georg von Békésy, the 1961 Nobel Laureate, at the University of Hawai'i (see acousticstoday.org/7302-2), Dick refined this technique and started to integrate the behavioral measures of auditory function that it provided with recordings from the auditory nerve of the goldfish. His work in Hawai'i with von Békésy (Fay, 1973, 1975) and later at the Parmly Hearing Institute at Loyola University Chicago and the Marine Biological Laboratories (MBL) in Woods Hole, MA, was heavily influenced by an almost 50-year (and still going!) friendship and collaboration with *Acoustics Today* editor, Art Popper (**Figure 2**). This collaboration is discussed in Fay and Popper (2014) and Popper and Fay (2016).

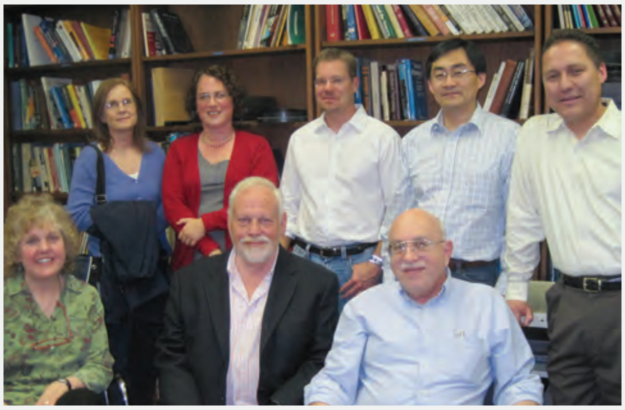

Figure 2. *Dick Fay and Art Popper in the Parmly Hearing Institute Library along with former students of one or both. Sheryl Coombs and Peggy Walton were graduate students with Art and then postdocs, and then long-time collaborators with Dick. Michaela Meyer was comentored by Dick and Art. David Zeddies was a postdoc first with Dick and then with Art. Zhongmin (John) Lu was a graduate student of Dick's and a postdoc with Art. Joseph Sisneros collaborated with Dick.* ***Seated, left to right:*** *Sheryl Coombs, Dick Fay, and Art Popper.* ***Standing, left to right:*** *Peggy Edds-Walton, Michaela Meyer, David Zeddies, John Lu, and Joseph Sisneros.*

How Dick Met the Goldfish!

Dick Fay first encountered the goldfish as a graduate student at Connecticut College (New London), and it was the subject of his first publication (Fay, 1969). In deciding to work on goldfish, Dick picked a species that is a member of a taxonomic group, the Otophysi (or Ostariophysi) that have anatomical adaptations that enhance hearing capabilities compared with most other species from other taxa. Selecting the goldfish because it hears well was, however, not the basis for choosing goldfish for study. Instead, Dick says in a video presentation (see bit.ly/3aeJOnE) that this was because he could buy them for 50 cents in any Woolworths. Other reasons for selecting goldfish were that they are very hardy and able to survive the rigors of research and handling by a young investigator. And, indeed, it was not until the work of Jacobs and Tavolga (1967), which probably was being done at about the same time as Dick was starting out (and unbeknownst to Dick), was it known that goldfish had a wider hearing range (to over 3 kHz) and better hearing sensitivity than most other fish species.

Over the course of his career, Dick conducted a wide range of investigations using psychophysical and physiological methods to ask a plethora of questions that sought to compare hearing of the goldfish with that of other vertebrates. Indeed, Dick was among the early investigators of hearing who combined psychophysical with neurophysiological measures to explore auditory processing. Of course, Dick also delved into other species (Fay et al., 1974; Lombard et al., 1981), making especially important contributions to understanding hearing in the toadfish (*Opsanus tau;* e.g., Zeddies et al., 2012; Edds-Walton et al., 2015), but those are other stories, some of which are described by Sisneros (2016) and by Yost and Popper (2016).

The Goldfish Auditory Periphery

Dick viewed his studies of auditory function in the goldfish as providing crucial information about the peripheral neural contribution to hearing. The inner ear of most fishes is typical of that of other vertebrates in having three semicircular canals as well as otolith organs. Of the latter, goldfish have a saccule and utricle as well as a third otolith organ, the lagena, which is not present in amniotes (reptiles, birds, and mammals). Each of the otolith organs has sensory hair cells that are the same as found in other vertebrates, and it is clear that these cells evolved in the earliest fishes (e.g., Coffin et al., 2004).

However, unlike most other vertebrates, the majority of bony fishes do not have otoconia in their otolith organs. Instead, the otoconial material in each end organ is in the form of a solid mass, the otolith, composed of calcium carbonate. These otoliths sit above the cilia of the sensory hair cells, separated by an otolithic membrane.

The fish inner ear does not have the biomechanical structures found in mammals. Stimulation of the hair cells comes from relative motion between the otolith mass, which is far denser than other fish tissues, and the rest of the fish's body, including the sensory epithelia (for a discussion of fish hearing and inner ear function see Popper and Hawkins, 2018, 2019; Schulz-Mirbach et al., 2019).

What the Ear Tells the Brain

The mammalian biomechanical structures provide a powerful form of the spectral/temporal processing of sound, which is transduced via the vibration of the stereocilia of cochlear hair cells into neural action potentials in the auditory nerves that synapse with the hair cells. Dick argued that because his data showed that goldfish tend to respond to changes in the parameters of sound such as frequency and intensity in ways similar to how mammals respond, then the biomechanical properties of the mammalian ear are probably not the only way for vibration to be transduced into useful information for hearing (e.g., Fay, 1969, 1970a,b, 1972). Dick also showed that auditory nerve responses measured in goldfish were very similar to those measured in mammalian auditory nerve fibers (e.g., Fay, 1978a,b; Fay and Olsho, 1979). Thus, his work revealed those aspects of the auditory nerve responses (i.e., the temporal pattern of action potentials) that provided the basis for hearing in the goldfish and in vertebrates in general.

The *Databook*

The view that goldfish hearing shared many similarities with that of other vertebrates eventually led to Dick's now famous book, *Hearing in Vertebrates: A Psychophysical Databook* (Fay, 1988). Over many years, Dick gathered all of the articles that he could find related to psychophysical measures of auditory function in all vertebrates (and as far as we know, he found them all). He then developed a system to provide a standard format for presenting what Dick believed to be the relevant psychophysical data from each and every one of these studies. He devoted thousands of hours to using a clever, manual caliber system designed to trace the data from figures in articles, resulting in numbers in a spread sheet that formed the basis of his structured presentation of the results. Bill Yost has vivid memories of Dick hunched over the apparatus hours on end, tracing the figures from an article he had just received.

As this project developed and Dick published the *Databook*, he began to appreciate that his earlier observations of the similarity in goldfish "hearing" data with that from other vertebrates was not unique to the goldfish. He was firmly convinced that vertebrates shared many common features in hearing sound. Dick compiled figures comparing psychophysical results for several common measures of hearing for all vertebrates covered in his book. By putting all of these data together in one graph, Dick showed that although there are clear differences across species in measures of the thresholds of hearing, there are also some very clear similarities. He also demonstrated that all terrestrial species have a spectral region where their thresholds are lowest; although these spectral regions vary greatly across species, the sound pressure level of a species' best sensitivity is remarkably the same (i.e., within approximately ±15 dB of 0 dB sound pressure level [SPL] re 20 μPa). Given that 183 species are represented and the range of thresholds across frequency for many species is 100 dB or more, these similarities are striking.

Many of Dick's contributions after his *Databook* was published were built on the theme of commonalities among the auditory function of vertebrates even when they had evolved different methods for processing sound. Two such related auditory functions and commonalities among species began to occupy Dick's thoughts: sound source localization and its relationship to sound source processing (i.e., often called auditory scene analysis). In the remaining available space, we describe his work on sound source localization and refer to some of his articles on sound source processing (e.g., Fay, 2008, 2009a,b).

Sound Source Localization

One of the most important features of the vertebrate auditory system is the ability to determine the direction of a sound source around the animal. However, although it is clear that terrestrial vertebrates can localize, the ability of fishes to localize sound has been debated and studied for almost 100 years, without providing a full understanding of the capabilities and mechanisms (reviewed in Fay, 2005; Hawkins and Popper, 2018)

Dick became very intrigued by sound source localization, and he was convinced that fish must also be able to localize sources. However, data showing that fish did so and how that ability depended on the properties of sound were almost nonexistent. Dick's *Databook* included only three papers that had examined directional hearing (Chapman and Johnstone, 1974; Hawkins and Sand, 1977; Buwalda, 1981). Each of these papers dealt with the same species, the Atlantic cod (*Gadus morhua*).

In the articles cited by Dick, the investigators conditioned fish (e.g., via conditioned heart rate) to respond to a difference in the angular separation of two sound sources and determined the minimum audible angle (MAA) that the fish could discriminate. The MAA is not a direct measure of sound source localization, and Dick was not sure which cues fish, especially the relatively small goldfish, might use to localize a sound source.

As pointed out by van Bergeijk (1964), the traditional cues used to explain mammalian sound source localization seem to be unlikely for a fish. For mammals, sound arrives at the two ears with an interaural time difference (ITD) that provides a cue for the azimuthal location of a sound source and/or the sound at the ear farthest from the source is less intense than that at the other ear, generating an interaural level difference (ILD) due primarily to the head producing a sound shadow for the sound arriving at the far ear. And sound is differently attenuated as a function of its frequency and the location of the sound source relative to the torso, head, and pinna. Thus, for mammals, spectral changes can provide a cue for the relative location of a sound source, especially in the vertical plane (elevation). The width of the goldfish head and the good impedance match between water and the fish's head, as well as the approximately 4.8 times faster speed of sound in water than in air, reduce the ITD and ILD cues to negligible values. Fishes have no pinna, are sensitive only to low-frequency sounds whose wavelengths are very large relative to the size of most fish, and have very poor spectral resolution, so spectral changes are almost certainly not a cue for fish sound source localization. So, if fishes do localize sources based on sound, what do they use to do so? This is the sort of challenge Dick loved, and he became aware that European scientists had suggested that it was the detection of particle motion, a vector quantity, by fishes that allowed them to determine the direction of sounds (reviewed by Hawkins, 2014).

The Fay Shaker Table

The details of what Dick did can be found in an article that he published in *Science* (Fay, 1984). Dick argued that hair cell sensitivity to sound is directional, in that the axis of vibration of hair cell stereocilia is perpendicular to the direction of the inner ear vibratory motion. So, because fish hair cells are oriented in different directions within the macula of each inner ear organ, the sensitivity of the hair cells and the nerve fibers innervating the hair cells might also be directionally dependent.

Dick set out to see if this was true. To do so required a way to change the direction of otolith motion within the inner ear. He could combine this with his expertise in measuring the neural responses of the auditory nerves connected to the hair cells and he had a way of knowing which inner ear organ a nerve fiber came from. Thus, he would be able to show if and how the sensitivity of auditory nerves depended on the directional interaction of otolith motion and hair cell orientation. That is, he assumed that the sensitivity of the neural response would depend on the relative orientation of otolith motion to the orientation of the hair cell. The relative orientation that produced the largest neural response might provide a directional cue the brain could use to help in its determination of a sound source location.

Figure 3. *Dick's original shaker table with four vibrators (**black**) moving the dish in which the fish is placed in the horizontal direction and a large vibrator under the table (**not visible**) moving the dish in the vertical direction. The table is still in use in the lab of Joe Sisneros (University of Washington, Seattle). Picture courtesy of Joe Sisneros.*

But, how does one produce otolith motion in different directions? And, how does one do so on the microscopic scale of displacements of hair cell stereocilia (100 pm to 1 μm)? The answer was the "Shaker Table" (see **Figure 3**) that was described in Dick's *Science* (1984) paper. Dick designed and then supervised the building of a specially milled stimulating "dish" to which the fish's head would be attached. The dish could be vibrated in all three directions by two pairs of shakers oriented at 90° to each other and a large vibrator to move the dish vertically. Then, three sensitive accelerometers were attached to the dish to measure its motion. Finally, an optical displacement transducer was used to confirm that the dish and the fish's head attached to the dish were moving in phase and at the required frequency (140 Hz).

It was no mean feat to get the system machined to the specifications Dick required (which was done with the help of his brother at Grumman Aircraft Company in New York) and then to perform the meticulous measurements and calculations to ensure the accuracy of the fish's head movements. Dick kept careful notes on all of the steps in the process in case another shaker table had to be built, which happened later when others wanted one for their studies (e.g., see Sisneros, 2016). Interestingly, before Dick was developing his shaker table, a device with similar shaker functions had also been developed by European scientists (Enger et al., 1973; Hawkins and Horner 1981).

The shaker table became almost a metaphor for Dick's incredible contributions. Several other studies have used this table (e.g., Lu et al., 1996; Meyer et al., 2011). Having the shaker table built was not an easy task for Dick, but Dick is not the type who is easily deterred by such matters, as is evident by the success of the shaker table and Dick's research productivity.

The results of Dick's experiment (Fay, 1984) clearly showed that the auditory nerve responses of the goldfish were directionally sensitive, with the pattern of sensitivity differing among the three inner ear receptor organs. And, as Dick concluded, "These are the essential features of a detection system that, after appropriate central processing, is capable of directional hearing, range determination, and impedance characterization." A key part of his conclusion was "after appropriate central processing." Little was known at the time about the central (brainstem and cortical areas) processing of sound by fish. So, in a typical Fay manner, Dick set out to know more.

A New Species

From the mid-1980s to the end of his career, a main topic of Dick's research was better understanding of the fish's auditory central nervous system. Over time, the bulk of this work was done during the summers in Dick's lab at the MBL. One motivation for this work was to understand how the central nervous system might process the directional information he had measured in the auditory nerve. This work, which used the toadfish, *Opsanus tau*, examined both peripheral and central processing of sound and was done in collaboration with Dick's colleague Peggy Walton (e.g., Fay et al., 1994; Fay and Edds-Walton, 2000).

Around 2003, Dick's former postdoc David Zeddies introduced him to Joe Sisneros (see **Figure 2**). One of Joe's interests was the plainfin midshipman (*Porichthys notatus*) and the female's ability to locate a calling male in shallow water. This was the sort of animal model Dick was always hoping to find, so it is not surprising that Dick, Dave, and Joe started a collaboration (e.g., Zeddies et al., 2010, 2012; Coffin et al., 2014). Although the work on the midshipman and the auditory central nervous system of fish produced a great deal of important information, an explanation of how the fish's central nervous system processes the directional information provided by the periphery has not yet been fully revealed.

Conclusion

Over his 50+-year career, Dick Fay contributed immensely to the literature on fish and vertebrate hearing through a remarkable set of research papers. (Indeed, some have suggested that this resulted in a close physical resemblance between investigator and subject; see **Multimedia1** at acousticstoday.org/fayfish.) The papers cited here, the additional papers cited in Sisneros (2016), and a number of Dick's more recent papers (Rogers et al., 2016; Sisneros et al., 2016; Mohr et al., 2017; Hawkins et al., 2019) are immensely important contributions to the auditory neuroscience literature. But, perhaps Dick's even greater contribution was his in-depth focus on one species, the goldfish, so that its auditory system is well-known enough to contribute to our overall understanding of vertebrate hearing (and not just from the comparative perspective).

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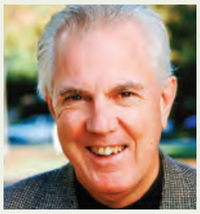

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William A. Yost is director of the Spatial Hearing Laboratory and research professor at Arizona State University, Tempe. His current research interests are sound source localization when the listener and/or the sound source move and measuring the size of the auditory scene. When Bill was hired by Loyola University Chicago (IL) in 1977 to develop a university-wide research institute based on the Parmly endowment, Dick Fay was already an assistant professor in the Psychology Department. Dick joined Bill in developing the Parmly Hearing Institute over the next 30 years, becoming director when Bill became Associate Provost for Research and Dean of the Graduate School.

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Anthony D. Hawkins now runs his own consultancy company but was originally the Director of Fisheries Research for Scotland. His research has included studies of sound production and hearing by fishes as well as other aspects of fish behavior. He first met Dick at a conference organized by Bill Tavolga, Art Popper, and Dick Fay in Florida in 1980 and has since spent time with Dick at many other conferences in the United States and Europe.

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"Humuhumu," watercolor painting by Alex Tolstoy. See more of Dr. Tolstoy's art at atolstoyart.com.