REVIEW

Soundscapes and the sense of hearing of fishes

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Abstract
Underwater soundscapes have probably played an important role in the adaptation of ears and auditory systems of fishes throughout evolutionary time, and for all species. These sounds probably contain important information about the environment and about most objects and events that confront the receiving fish so that appropriate behavior is possible. For example, the sounds from reefs appear to be used by at least some fishes for their orientation and migration. These sorts of environmental sounds should be considered much like “acoustic daylight,” that continuously bathes all environments and contain information that all organisms can potentially use to form a sort of image of the environment. At present, however, we are generally ignorant of the nature of ambient sound fields impinging on fishes, and the adaptive value of processing these fields to resolve the multiple sources of sound. Our field has focused almost exclusively on the adaptive value of processing species-specific communication sounds, and has not considered the informational value of ambient “noise.” Since all fishes can detect and process acoustic particle motion, including the directional characteristics of this motion, underwater sound fields are potentially more complex and information-rich than terrestrial acoustic environments. The capacities of one fish species (goldfish) to receive and make use of such sound source information have been demonstrated (sound source segregation and auditory scene analysis), and it is suggested that all vertebrate species have this capacity. A call is made to better understand underwater soundscapes, and the associated behaviors they determine in fishes.

Key words: acoustic daylight, auditory scene analysis, soundscape, sound source segregation.

INTRODUCTION
“What do goldfish listen to?” This question has been often asked by people trying to understand the experimental results demonstrating an acute sense of hearing and sound discrimination in a fish species (goldfish) (reviewed in Fay 1988) that does not vocalize or apparently make use of sound communication in the usual sense. This question would never have been asked if the species in question had been known as a vocalizer, because there is an obvious answer: that the only sound signals known to be biologically significant, that we know of, are vocalizations. However, because this answer cannot be applied to goldfish, there appears to be a mystery. This mystery could be seen to be partially answered by the definition of communication (Myrberg 1981) as including eavesdropping on other vocal species, and simply listening to other biological acoustic events in the environment (interception). However, the essential mystery has remained. Why are goldfish so especially competent in these listening tasks? The sense of hearing tends to be viewed as a species characteristic: a species-specific adaptation to detect and make use of vo-
calization sounds to increase fitness. This is the rationale used by proponents of the “matched filter hypothesis” (Capranica and Moffat 1983), which hypothesizes that the ear and hearing are specially adapted for receiving conspecific communication sounds. The observation that goldfish have an acute sense of hearing, yet do not vocalize, does not provide evidence in favor of this hypothesis.

It cannot be denied that an important function of the sense of hearing (or any sensory modality) in any organism is to help determine the objects and events in the environment so that the animal may behave appropriately with respect to them. There are many psychophysical observations on goldfish showing that this species’ sense of hearing has many features in common with our human sense of hearing, and with those of other vertebrate animals (Fay 1988), having widely differing vocalizations produced in very different acoustic environments. What is the explanation for this conservative nature of vertebrate hearing, given the unique characteristics of vocalizations across the animal kingdom? In the present paper, an attempt is made to provide a way to view this mystery that may lead to a deeper understanding of hearing in goldfish, in other fishes, and perhaps in vertebrates generally.

WHAT DO WE HUMANS LISTEN TO?

I begin with introspection. What do we humans listen to? A hearing impaired person would answer “speech, of course.” After all, this is the rationale and ultimate test for most treatments for impairment, including hearing aids and cochlear implants. However, try to imagine listening without speech, as if you were in a mute society. Is there no other function for hearing? The answer, I believe, is “certainly.” The sounds characteristic of any environment (soundscape) combine to make up a sort of scene that helps to establish our sense of place and our orientation to it (e.g. Krause 2002): they let us know where we are and about most of the events occurring nearby. The sound of wind or rain in the environment tell us about the landscape. The sounds of flowing water tell us that there is a stream nearby, and something about its dimensions and flow rate. The sounds of waves on a shore tell us about the size of the body of water and the state of the weather, and the composition of the beach or shore. If we are indoors, we listen to the unique “sound” of each room to identify it, and sometimes we deliberately produce a sound (we ensonify the environment) to tell us the dimensions of the room, and something about its reflectivity and reverberation when vision is not enough. We can “tap” on an object to determine whether it is made of wood, metal or plastic given the sounds produced. Environmental sounds also arise from objects and events of all kinds (e.g. footfalls, and perhaps the identity and intentions of their sources), and can signify safety, interest, or danger. These things are what we listen to, and likely are the same kinds of things that non-human animals listen to. An argument can be made about the great biological significance of such immediate and constant information about the environment impinging on an organism, compared with the specific subset of environmental sounds composed only of con-specific vocalizations.

If it can be accepted that environmental information of this kind is important for survival, then there is no need to ask what the mute goldfish listen to, or to hypothesize that the ear and auditory system are simply a set of filters matched to specific vocalization sounds. Unfortunately, there has been little research on natural soundscapes, particularly underwater ones, and we know very little about aquatic acoustic ecology, or the uses of information that animals extract from environmental sounds. However, it seems clear that these natural, biotic and abiotic sources do not have the well-predicted frequencies and temporal patterns of vocalizations, but rather have the general characteristics and variation of most sources in the natural world. To be well adapted to hear them would seem to require rather general signal processing capacities rather than capabilities fixed for detecting any one specific signal, as suggested by the matched filter hypothesis. Of course, computational filters could exist in the brain so that specific acoustic patterns could be better recognized and trigger greater attention, but the auditory periphery is more likely to be adapted for the more general signal processing tasks required for every-day listening.

ACOUSTIC DAYLIGHT

Another related concept that focuses on the natural sounds that surround all organisms is that of acoustic daylight (Buckingham 1999). Originally exploited as an imaging technology, this idea also suggests the biologically significant value of detecting and processing ambient sound underwater that is likely to be used by fish and other marine organisms. The idea is that all underwater sound sources, such as surface or breaking waves, precipitation, animal sounds, and the various sources of anthropogenic noise, ensonify the underwater environment much like the world is bathed in light by the sun. The reflection, scattering and reverberation inherently
contained in this “noise” field contains important information that could be used by marine organisms to orient themselves, and to obtain information about the environmental contents. Noise is usually seen as interfering with signal detection, or as something to be reduced for better signal detection, but the concept of acoustic daylight suggests that the ambient noise field itself has the potential to be exploited for imaging the environment. It is logical that fishes have probably exploited this information source, and if so it could be the kind of thing that “fish listen to.”

There has been only one experimental attempt to investigate this concept as applied to fishes (Lewis & Rogers 1992), based on some psychophysical work on goldfish by Fay et al. (1983). Studies on humans show that when a flat spectrum white noise is added to a copy of itself with a small delay (as if there were an echo), the resultant signal (rippled noise, repetition noise, or cosine noise) has a pitch determined by the delay, for delays ranging from 0.5 to 50 ms (Yost et al. 1978). The pitch is equal to the delay. Fay et al. (1983) investigated the perception of this rippled noise by goldfish. They determined that goldfish can easily discriminate between this rippled noise and the unrippled, flat-spectrum noise, much as human listeners do (for delays between 1 and 20 ms). This is equivalent to a goldfish detecting a sound reflecting object in a noise field using the ongoing echo from the object. The echo delay (pitch for humans) is proportional to the object distance, and the “strength” of the rippled noise perception is proportional to the object’s size or target strength. Lewis and Rogers (1992) hypothesized that a fish can detect a nearby fish through detection of the fish’s resonant swimbladder reradiating the ambient noise, arriving at the receiver fish from a specific location and with a delay with respect to the ambient noise, much like an echo. Conditioning experiments using a sound source to simulate a swimbladder reradiating the noise confirmed this hypothesis.

**REEF SOUNDS**

Another example of the uses of environmental sounds for orientation comes from the several experiments on the role of reef sounds in attracting juvenile fish back to their reefs, where they will settle to spend most of their adult lives (e.g. Simpson et al. 2005; Montgomery et al. 2006). Fish larvae grow in deeper water, and then return to their reefs to settle and reproduce. The evidence is that when these fish return to settle on their reefs, they use the “sound” of the reef for directional orientation. In Simpson et al. (2005), the research team built 24 patch reefs near Lizard Island on the Great Barrier Reef. They used an underwater loudspeaker for broadcasting reef noises, including the sounds of snapping shrimps and fish calls, on half of the patch reefs. The other patch reefs did not have the loudspeakers broadcasting reef sounds. Larvae settled in greater numbers on noisy patch reefs than on silent reefs. In addition, damsselfish were preferentially attracted to reefs broadcasting high-frequency sound, predominantly of shrimps, rather than the low-frequency sound, predominantly of fish.

These are the only experiments that I am aware of that demonstrate the potential usefulness of acoustic daylight or soundscape in fish perception and behavior. However, Tavolga (1976) observed that the sea catfish (Arius felis L.) can use the echoes from self-generated sounds to orient competently in a complex lab maze-like environment. Therefore, the small amount of existing evidence supports the notion that fish can use the echoes from nearby objects and the ambient noise field for perception of environmental features and for orientation. I believe that this is what fish listen to.

**DIRECTIONAL HEARING**

The capacity for directional hearing is not a necessity for determining sources and the processing of soundscapes, but is useful for source segregation and scene analysis. Sound source localization capacity by fishes is uncertain, with a confusing and relatively long and large literature (Fay 2005). However, there is one sort of experiment that is very clear and closely related to the notion of soundscape perception: directional release from masking studies, or experiments on “the cocktail party problem” (Hirsch 1948; Cherry 1950). The fundamental observation consists of the selective “hearing out” of one voice heard among multiple sources, as in a cocktail party, and the tendency for persons with hearing impairment in one ear to avoid cocktail parties. This notion was translated to a masking study with cod and haddock in which the threshold for a pure tone signal was determined in the presence of an independent white noise source. When the signal and noise sources are independent and placed at different azimuths or elevations, the signal can become more detectable or detected at a lower signal-to-noise ratio that depends on the angular separation between the signal and noise sources (Chapman & Johnstone 1974; Hawkins & Sand, 1977). This means that there are apparently direction-dependent detection channels in the fish auditory system, and that sound sources from different directions activate separate (at least somewhat independent) neural elements.
These directional channels have been confirmed in physiological studies in the goldfish (Carassius auratus L.) saccular, utricular and lagenar nerves (Fay 1984), in the oyster toadfish (Opsanus tau L.) periphery, medulla and midbrain (Edds-Walton & Fay 1997, 2004; Edds-Walton et al. 1999; Fay & Edds-Walton 2004) in the eighth nerve of the sleeper goby (Dormitator latifrons Richardson, 1844) (e.g. Lu & Popper 2001; Lu et al. 2003; Lu & Buchser 2004), and in the plainfin midshipman (Porichthys notatus Girard, 1854) (Weeg et al. 2002). All species of fish can detect the direct, particle motion component of sound, and this is thought to be required for this ability. The direction of acoustic particle motion would be expected to be different for every source location with respect to the fish, so the soundscape would be expected to be very complex and information-rich for fishes, and to have multiple dimensions (particle motion vectors) that we humans would be unaware of, and that would be undetectable using typical hydrophone recordings.

PERCEPTION OF SOUNDSCAPES OR AUDITORY SCENES

Assuming for the moment that important and useful information for orientation can be found in many natural soundscapes, the capacity to usefully process this information by the auditory systems of animals also would seem to be necessary (Slabbekoorn & Bouton 2008). We know much on this topic from studies on human listeners, and the capacity has been named “auditory scene analysis” (Bregman 1990). The human auditory system has the capacity for resolving the auditory scene into the collection of individual sound sources (and reflectors) that make the scene up. The process of sorting the simultaneous and successive acoustic components into those that probably arose from individual sources, and then perceptually synthesizing the individual sources from those components that naturally occur together (or are characteristic of specific sources) is called auditory source segregation. Sound source segregation is an obvious capacity of the human auditory system; for example, it is the capacity that permits us to “hear out” the individual musical instruments comprising an orchestra with surprisingly few errors, unless the composer has attempted to be devious or ambiguous in combining sounds from various instruments. This capacity does not depend critically on the ability to localize the sources (binaural analysis or directional hearing) because we can accomplish perfectly good source segregation when listening to a monaural recording, or by listening with only one ear. The result of this segregation operation is that we are aware of the orchestra’s soundscape, even though there is no necessity for there to be a spatial component to the perception. This is effortless, and is termed pre-attentive because it does not even depend critically on focusing the listener’s attention (however, see Carlyon et al. 2001). Therefore, human beings can make perfectly good use of soundscapes or auditory scenes for their perceptions and orientation.

But what about nonhuman animals? Do fishes have these perceptual abilities to process the soundscape usefully? This has been an important research question in the past decade among those interested in animal behavior and the sense of hearing. The first experiment on a non-mammal (European starling) to demonstrate source segregation and scene analysis was by Hulse et al. (1997). The method consisted of operantly training starlings to peck a key for food in response to 10-sec recordings of birdsongs. Starlings were initially trained to discriminate between stimuli made up of sample mixtures of one species’ song combined with another (essentially, two concurrent sources to be perceived independently). One type of stimulus always included the examples of the starling’s own song, and another type consisted of samples of songs of two species other than starlings. The birds were trained to discriminate examples of the first stimulus type from the second. Starlings learnt to discriminate with at least 85% accuracy. The authors concluded that a capacity for source segregation was the most likely explanation for the discrimination. In other words, the starlings behaved as humans would be expected to behave in “hearing out” individual sources against a chaotic background made up of various bird vocalizations. Later experiments demonstrated that this sort of behavior does not depend on special abilities to process the starling’s own song, and also occurs when using abstract tones as stimuli (MacDougall-Shackleton et al. 1998). Since these studies were undertaken, experiments have been carried out on primates (e.g. Izumi 2002), goldfish (Fay 1992, 1998, 2000), and even insects (Schul & Sheridan 2006), which have confirmed this capacity for sound source segregation and auditory scene analysis. It is probably the case that all species have this capacity.

SOUND SOURCE DETERMINATION BY GOLDFISH

These abilities have been repeatedly demonstrated for goldfish. In 1964, van Bergeijk asked, “given that a fish...
can discriminate between sounds A and B when they are presented separately, can he still discriminate either one when both are presented simultaneously? Or do the two sounds blend to form a new entity (such as a chord)?” (page 296). He went on to comment, “Quite clearly, it is an important question; if a fish should be unable to discriminate a particular sound among several others …., then sound production in fish would be of very limited use in communication among fishes.” He summarizes these questions as being an attempt to gauge the subjective structure of the fish's sense of hearing. Fay (1992) first showed that two tones (166 and 724 Hz) were indeed heard out or determined (probably perceptually segregated) when presented simultaneously. These experiments made use of the method known as stimulus generalization (Mostofsky 1965). In this type of experiment, animals are conditioned to respond to a specific stimulus (a two-tone complex), and are then tested for response to a set of novel stimuli (single tones) that might or might not have frequencies in common with the two-tone conditioning stimulus. The extent to which fish respond to a given stimulus in the generalization test was an indication of the perceived similarity between the conditioning and test stimuli. The generalization function of frequency showed two response peaks at the frequencies corresponding to the presence of the two tones in the conditioning stimulus. This experiment was the first to provide an answer to van Bergeijk's important question about sound source segregation by fish.

Since that time, there have been more studies on the goldfish's capacity for source segregation and auditory scene analysis. In the next generalization experiment, the stimuli were synthetic filtered tone pulses repeated at various rates. They were meant to mimic the sorts of sounds fishes make when communicating, but it is doubtful that a goldfish would ever have encountered these sorts of vocalization sounds in everyday life. The segregation hypothesis was that a simple mixture of pulse trains (a high frequency pulse repeated at 85 pulses per second (pps), and a low-frequency pulse repeated at 19 pps) would be segregated into individual sources based on a different spectral envelopes and repetition rates. The sounds were brief, pulsed sinusoids (238 and 625 Hz), creating a “low-frequency” and “high-frequency” pulse. Then the pulses were repeated at various rates between 19 and 85 pps. The main experiment consisted of two groups of eight animals conditioned to a simultaneous mixture of two pulse trains, the high-frequency pulse repeated at 85 pps, and the low-frequency pulse repeated at 19 pps. One of the groups was then tested for generalization to the low-frequency pulse repeated at rates between 19 and 85 Hz, and the other group was tested using the high-frequency pulse repeated at the same range of rates. The results for the two groups showed two, oppositely sloped, generalization response gradients. The group tested with the low frequency pulse produced a gradient that sloped downward as a function of repetition rate, with the most robust responses at the lowest repetition rates. The group tested with the high-frequency pulse had a gradient that sloped upward as a function of repetition rate (the largest response at the highest repetition rate). These results demonstrated that goldfish correctly associated a particular spectral envelope and repetition rate (i.e. information about the two mixed pulse trains was obtained independently). Auditory source segregation provides the best description and explanation of these results. These findings on goldfish were extended with additional experiments, demonstrating that segregation occurred more robustly when the spectral difference between pulse trains increased (Fay 2000). In these new experiments, 625-Hz filtered pulses alternated, with pulses having different center frequencies (500 to 240 Hz) for a total alternating pulse rate of 40 pps (see Miller & Heise 1950). Animals were tested for generalization to the 625 Hz pulse alone, repeated at a variety of rates between 20 and 80 pps. If these alternating pulses were segregated into two streams (a high frequency and low-frequency stream), then the generalization behavior should resemble that following conditioning to a pulse presented at half the repetition rate of the conditioning pulses (20 pps). The results were consistent with the segregation of the alternating pulses with large frequency separation (625–240 Hz), but not with the small frequency separation (625–500 Hz).

These experiments with goldfish demonstrate perceptual behaviors that are indistinguishable from what would be expected from human listeners under similar circumstances. The best description of these behaviors is that they are examples of concurrent auditory source segregation. Therefore, we can be confident in believing that goldfish, and fishes in general, are capable of sound source segregation, as we understand it for human listeners. Because others have come to the same conclusion with respect to monkeys, starlings (and birds in general), and even insects, it seems likely that all animals have the capacity for source segregation and, therefore, some form of auditory scene analysis, or scene analysis in general (all senses include a sort of scene analysis). Therefore, scene analysis and source segregation are phenomena of biological interest and significance that can be studied in
a comparative and evolutionary context.

It must be pointed out, however, that there is some resistance to these conclusions because scene analysis appears to some to be a cognitive capacity that would likely only occur in large-brained animals, or to be a special adaptation for dealing with conspecific vocalizations in those animals that vocalize. The latter opinion follows loosely from the “matched filter” hypothesis that assumes that the auditory sense functions primarily as part of a communication system to receive communication sounds. The above experiments refute this prediction; neither large brains, an auditory cortex, or species-specific vocalizations are required to demonstrate this phenomenon in various species.

SUMMARY AND CONCLUSIONS

I have attempted to alert the reader to alternatives to the view that animal vocalizations have determined or adapted the important characteristics of auditory systems throughout the evolution of vertebrates. However, it remains nearly true that vocalization sounds are the only sounds that have known biological significance. I have pointed out that this “knowledge” arises from a profound ignorance of the other possible sounds and sources that probably have biological significance to fish and all vertebrate animals: the soundscapes that bathe all organisms as “acoustic daylight.” This condition has existed for all time and for all species. The notion of environmental soundscapes as most probably important sources of information to the organism is suggested here. Through the experimental paradigms of stimulus generalization, a capacity for sound source segregation has been demonstrated in primates, birds, fish, and even insects. Environmental information exists to be exploited for proper behavior with respect to audible sound sources and events, and fish have the capacity to exploit it for general orientation. It seems logical to assume that this is what fish and other species listen to.

REFERENCES


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