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Evasive responses of American shad *(Alosa sapidissima)* to ultrasonic stimuli

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Abstract: Many species of odontocete cetaceans (toothed whales) use high frequency clicks (60-170 kHz) to identify objects in their environment, including potential prey. Behavioral and physiological studies have shown that American shad, *Alosa sapidissima*, can detect ultrasonic signals to at least 180 kHz. This study demonstrates that freely swimming, American shad show a variety of behaviors in response to pure tone, ultrasonic stimulation. This response depends primarily on stimulus amplitude and, to a lesser degree, on stimulus frequency, direction and duration.

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1. Introduction

Odontocete cetaceans (toothed whales) use audition as their primary source of sensory information about their environment.[1] They use short clicks (50 to 500 μs) to echolocate and longer whistles for communication.[1,13] Sonar clicks are narrowband with peak frequencies that can be shifted by the animal between 120 and 140 kHz for the harbour porpoise (*Phocoena phocoena)* and between 70 to 130 kHz for the bottlenose dolphin (*Tursiops truncatus*).[18,21] These biosonar signals have a highly directional pattern with peak levels occurring between ± 10° in altitude and azimuth from the midline of the animal (thus the emitted signal resembles a target cone), with signal levels up to 228 dB re: 1 μPa at 1 m.[5] The biosonar signals also have a frequency contour around the odontocete head. At the periphery of the cone, the power at higher frequencies drops exponentially, leaving only lower ultrasound bands (between 30 and 80 kHz) that have any significant power.[18,21]

Clupeid fishes (herrings and shads) are among the prey of the echolocating harbour porpoises and bottlenose dolphins.[20] Although it has been assumed that odontocete prey would not be able to detect echolocation signals, it has been shown that these frequencies are within the hearing range of several species of clupeids of the genus of *Alosa*.[15] These include the American shad (*Alosa sapidissima),* which can detect ultrasound signals at rather high amplitudes (between 140 and 180 dB re: 1 μPa).[10,15] Alewives (*A. pseudoharengus*) swim away from echosounders, suggesting that Alosids may also detect the direction of ultrasound.[15]

A recent study shows that Pacific herring (*Clupea pallasii*, a member of the Clupeinae, the same family but different subfamily as the American shad) accelerate their swimming speed in response to artificial dolphin clicks.[18] However, the investigators did not examine the impact of different signal amplitudes or frequency components on behavior.

The present study investigated the response of American shad to pure tone, ultrasound stimuli, the nature of the behavioral response, and whether these responses varied with signal frequency and/or amplitude. Although the stimuli resemble only the frequency and amplitude components of the natural odontocete echolocation signal, they allow comparison of the pure frequency component with the behavior, thereby providing a “spectral analysis” of the responses. Although these experiments are limited to the test tank, they provide insight into the nature of responses of ultrasound-detecting fish to sounds of potential predators.[7,20]

2. Materials

Three groups of 10 to 38 American shad (15 to 23 cm total length) were used. Fish were kept in round tanks (fiberglass, 0.5 cm thickness, 123 cm inner diameter, water depth of 73 cm) at a 14/10h light-dark-cycle. During experiments, the tanks were illuminated by a round neon light above the center. The animals were hatched and raised in captivity and had never been exposed to ultrasound. All work was done with approval of the Institutional Animal Care and Use Committee (IACUC) of the University of Maryland, College Park.

Sounds were presented to the shad using three sound sources: two ultrasound-capable hydrophones (ITC 1042) and one underwater loudspeaker (UW 30, University Sound) (for details of setup, see separate webpage at http://www.life.umd.edu/biology/popperlab/shadavi/). Stimuli waveforms were triggered with an HP pulse generator gating a function generator (Wavetek 182A). Stimulus waveforms were monitored on an oscilloscope, amplified, and fed to the appropriate speaker. In some trials, a sonic-masking sound was applied before, during, and after ultrasound stimulation. Masking noise (band passed 0.2 - 20 kHz) was synthesized using the program Igor Pro and played through the soundcard of a PC (Yamaha). The noise signal was then amplified (Techron 5507) and fed into the loudspeaker.

For directional tests, two ultrasound speakers were mounted on opposite sides of the tank and used in random order.

For video analysis, a copy of the pulse trigger signal was played onto an AC LED mounted on top of the central light in the center of the view of the recording camera. This produced two flashes, one when the stimulus was turned on and the other when it was turned off. A color charge-coupled device (CCD) video camera (512*492 pixels, 30 frames/s, All Electronics) mounted 1.5 m above the tank monitored the fish movements and trigger signals from the stimulation on- and offset. The images were captured and digitized using a video capture board (Pinnacle DC 10+) and a personal computer (PC, AMD, Athlon). Single video frames were analyzed using Igor Pro (Wavemetrics). Swimming direction, speed, and schooling behavior of fish for the first 10 s after stimulus onset were compared qualitatively with behavior prior to stimulus.

Stimulus frequencies were varied in different trials between 20 kHz and 160 kHz. Different amplitudes were used depending on the transmission sensitivity range of the hydrophone. The sound pressure level (SPL) at the opposite side of the tank was at least 20 dB above the hearing threshold of American shad (in our experiments 175 dB to 184 dB re: 1 μPa).[15] Amplitude changes between 20 dB above hearing threshold (for American shad after Mann et al. 2001) and 184 dB SPL had no effect on the behavior. In four experiments, the stimulus amplitude was driven to the maximum nondistorted output of the hydrophone, which resulted in signals of 194 dB re: 1 μPa at 80 kHz and 180 dB re: 1 μPa at 20 kHz.

All signals were calibrated using a hydrophone (ITC 1042). The sound levels were adjusted relative to the maximum distance in the tank (approximately 1.1 m) even though the SPL was measured at different spots within the whole tank (see webpage for details). Hydrophone output was amplified (Stewart VBF-7), sampled at a rate of 1 MHz (IoTech Wavebook 512), and stored on a PC. These signals were analyzed using Matlab (Mathworks) and Igor Pro.

Videos were made before each trial to compare prestimulus behavior of the fish with the behavior during sound presentations. Stimulus frequencies were randomly chosen during each experiment, but with the majority of the repetitions biased towards the primary response frequencies of 70 to 110 kHz. During different trials, the amplitude was also switched in random order between 175 and 184 dB SPL. Each trial was followed by a silent intertrial period of at least two minutes. To reduce adaptation effects and minimize stress for the experimental animals, there was a one-hour pause between each set of 15 trials. No more than three sets of trials were run in a day. The last four (of 15) experiments used stimulus levels above 184 dB and contained all frequencies, but were focused on 70 to 110 kHz. The intertrial interval in these experiments was increased to at least eight minutes with only one set of trials daily. Due to the strong response of the fish to amplitudes above 185 dB SPL, no long duration stimulations (>1 Min) were tested at these amplitudes. Experiments with two ultrasound sources and experiments with a white noise source were conducted as described, but at SPLs below 184 dB.

3. Results

American shad were monitored for control purposes on days without experiments and 20 minutes after an experiment. In both cases, fish showed a loose circling behavior in the tank. Mm.1. Video pretrial behavior (1.4MB).

American shad showed three distinct types of behavior in response to ultrasound presentation:

Type I behavior consisted of a short shocklike stopping of motion as well as a short shock-like acceleration in the original swimming direction or a bending away from the sound source followed by a short acceleration (lasting <1s). Mm. 2. Video type I response (1.4MB).

Type II behavior consisted of a rapid bending directly away from the sound source by fish located between the source and tank center (bending always occurred in the first frame of the video at stimulus onset, <33 ms). This was followed by high acceleration (top speed of individual fish 2.9 m/s, average speed of schooling fish 0.3 m/s, measured by frame-to-frame analysis over 1s). Once the fish reached the other side of the tank, they entered a close schooling group[18] that was initially stationary. With continued stimulation, this formation of fish slowly started to move again. Mm. 3. Video type II response (1.4MB).

Type III behavior resembled a paniclike response with nondirectional (even out of the water) extreme speed (fastest fish measured was 11 m/s) and the immediate break up of schooling behavior. The fish kept swimming at this very high speed until the stimulus was turned off. The fish then slowed down and began schooling again after about 8 s. We never used stimuli longer than 3, s so do not know if the response would ultimately stop in the presence of the sound. Mm. 4. Video type III response (1.4MB).

In 15 experiments the ultrasound behavior of three groups of American shad (between 10 and 38 individuals) were observed (see Fig. 1).

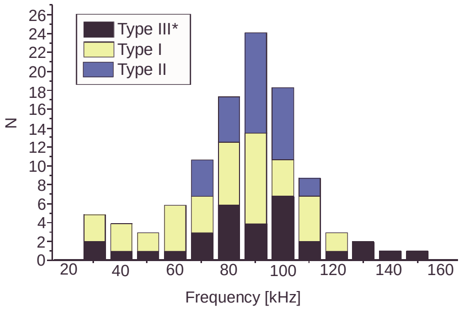

Fig. 1. Observed responses to ultrasound stimuli including tests at all amplitudes, durations, and frequencies, except noise and dual speaker experiments. A response was counted when the majority of the fish showed the same behavior. All frequencies from 20 to 160 kHz were tested in at least four experiments. *Type III response was found only when stimulus amplitude was above 185 dB re: 1 μPa.

Due to different test purposes, not all frequencies were tested the same number of times. Type I responses were found between 60 and 120 kHz. Type II responses (strongest response at stimulus amplitude below 185 db re: 1 μPa) were only found at frequencies between 70 and 110 kHz. Type III responses were found at stimulus amplitudes above 185 dB re: 1 μPa between 30 and 150 kHz (see Table 1). No Type III response was measured below 185 dB SPL.

Table 1. Response to ultrasound stimuli

Condition	Response	Frequency range of responses
Amplitude below 185 dB SPL		
Short pulses <150 ms	Type I	80-100 kHz
Short pulses 150<x<400 ms	Type I	60-120 kHz
Long pulses 1<x<4s	Type I	30-120 kHz
	Type II	70-110 kHz
Ongoing stimulation >1.5 Min	Type I	60-70 and 110-120 kHz
	Type II	80-100 kHz
White noise present		
Stimulus 0.8s<x<4s	Same as long pulses	
Amplitude above 185 dB SPL*		
Short pulses <150 ms	Type III	30-120 kHz
Short pulses 150<x<400 ms	Type III	30-150 kHz
Long Pulses 1<x<3s	Type III	30-150 kHz

*Note that at 20 kHz only 180 dB SPL could be reached. Stimulus amplitude reached maximum at 80 kHz and 194 dB.

3.1 Behavior to short pure tone stimuli

Fish were exposed to short pure tone signals (between 0.3 and 400 ms, below 185 dB re: 1 μPa) (for spectral analysis see web page) separated by at least a two minutes intertrial period. In response to stimuli below 150 ms long, fish occasionally showed type I responses between 80 and 100 kHz while they showed type I behavior in response to durations of 150 to 400 ms and frequencies from 60 to 120 kHz. Type III behavior occurred in response to amplitudes above 185 SPL between 30 and 150 kHz.

3.2 Behavior to long pure tone stimuli

With stimulation between 1 and 4 seconds (durations random length in multiples of 0.33s, amplitude 175<x<185 dB re: 1 μPa) fish showed type I responses between 30 and 120 kHz. However, in more than 70% of experiments from 70 to 110 kHz fish showed type II responses. Above 185 dB re: 1 μPa shad showed type III behavior from 30 kHz up to 150 kHz and the response continued for the duration of the stimulus. Due to the strong response we never tested longer than 3 s.

3.3 Behavior to very long stimulation

American shad were exposed to pure tone stimulation of 60 to 120 kHz for 2 minutes (amplitude 175<x<185 dB re: 1 μPa). At 60, 70, 110, and 120 kHz they started to show type I responses within 2 seconds of signal onset. While continuing to circle, the fish stayed at least one fish length away from the hydrophone. Between 80 and 100 kHz shad showed type II responses for at least the first 5 seconds of stimulation. Thereafter the newly formed close group slowly started to circle again. Note that in the video shown below the LED flash during stimulation is not related to the stimulus.

3.4 Behavior to two sound sources

Two ultrasound sources, placed on opposite side of the tank, were used alternately in random order in four experiments. Shad always showed startle responses away from the sound source. Mm. 5. Video type II directional response (1.3MB).

3.5 Behavior to ultrasound stimuli with simultaneous white noise masking

In this experiment white noise was constantly played through the loudspeaker while another hydrophone (same location in the tank) was used to present ultrasound stimuli. When the white noise was turned on the shad continued to circle but kept a greater distance from the low frequency hydrophone when passing it than when the sound was off. Fish showed the same evasive behavior to ultrasound stimulation when noise was presented. Mm. 6. Video type II response with background noise (1.4MB).

4. Discussion

With limited detailed physiological data available on the signals used by hunting odontocetes (compared to the detailed information about responses of insects to echolocating bats[14,20,21]), it seems parsimonious to assume that a high frequency, high power click train is the primary alarm signal indicating the approach of the predator to the American shad.[1,18] Even with the continuous directional information of an incoming odontocete (if shad are capable of processing the directional component of the signal), an escape seems very unlikely, given the swimming speed and endurance of the predator, unless the shad adopt some strategy to avoid the dolphins well before they get to the fish.

From the two hydrophone experiments it appears that American shad can determine the direction of the signal at least on the horizontal plane (in a tank). It has been demonstrated that *Tursiops* can discriminate targets less than 12 cm in length at 100 m distance, and that peak amplitude of the lower frequency portion of echolocation click ("sidebands") at this distance is still above the hearing threshold of American shad.[13,15] This would explain the directional, but still fast, evasive, type II behavior. A hunting odontocete is not able to constantly swim at its top speed, but instead maintains a slower and steadier travel speed while searching for prey.[19] With a constant evasive behavior in the opposite direction of the odontocete and at moderately increased speed, American shad might be able to keep away from the predator for a longer period. Thus an individual odontocete would have only a relatively small chance of detecting the fish. Perhaps to counter this behavior, odontocetes work in groups to hunt large schools of fish.[15]

Our data lead us to suggest that American shad have evolved a mechanism to make themselves less "conspicuous," or less easily preyed upon, by echolocating odontocetes. We also suggest that when shad detect ultrasound signals in the frequency range of the edges of cetacean echolocation beams (frequencies below 60 kHz did not show type II responses), they turn slowly away from the sound source. If they detect continuous echolocation frequencies in the dolphin click (between 70 and 110 kHz), they form very compact groups to decrease the opportunities for an echolocating dolphin to discriminate individual fish. Finally when a predator reaches a close enough range to attack, the fish show a random and very fast "panic" response, making it potentially difficult for the predator to focus on one individual or even to chase several individuals at once. Again odontocetes seem to have evolved a potential countermeasure to this behavior since they try to chase schools of fish into situations that decrease escape possibilities, such as into a bay or close to the water surface.[15]

Clearly, the behavior of American shad is reminiscent of the response of noctuid moths, which use ultrasound detection to avoid predation by echolocating bats.[6] Noctuids use afferent acoustic neurons from the "ear" that respond to a very broad frequency band (sonic and ultrasonic). In contrast, American shad appear to have an exclusive ultrasound "pathway" that becomes apparent when considering that there is no masking effect of the ultrasound signals with sonic white noise almost 80 dB above the sonic hearing threshold, whereas the maximum ultrasound signal presented was only 40 dB above threshold. The ultrasound transducing apparatus in American shad might be uncoupled from the sonic hearing system in the inner ear. Perhaps future investigations will reveal a new subsystem of the inner ear dedicated to ultrasound perception.

We recognize that the experiments in the tank may have elicited somewhat different responses than in wild animals responding to echolocation sounds of dolphins. Quantifiable field studies would be very difficult to do, but would show the actual responses of American shad to dolphin signals. Furthermore the behavior will have to be analyzed in detail to reveal more about possible directional processing of ultra sound in American shad.

A recent study on Pacific herring has shown that they also respond to ultrasound signals by acceleration and eventually forming closer schooling groups by "polarizing".[18] However these authors used only sound levels that were close to the threshold of at least American shad, and thus did not find the more elaborate, directional, type II responses, nor the type III "panic" responses we discovered. We would predict that the Pacific herring will show those behaviors if tested with higher amplitude signals, and that the responses we describe are ubiquitous to all ultrasound-detecting clupeids.

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