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Allis shad (*Alosa* alosa) exhibit an intensity-graded behavioral response when exposed to ultrasound

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Abstract:

Most fish cannot hear frequencies above 3 kHz, but a few species belonging to the subfamily *Alosinae* (family Clupeidae) can detect intense ultrasound. The response of adult specimens of the European allis shad (*Alosa alosa*) to sinusoidal ultrasonic pulses at 70 and 120 kHz is tested. The fish showed an intensity-graded response to the ultrasonic pulses with a response threshold between 161 and 167 dB re 1 *µ*Pa (pp) for both frequencies. These response thresholds are similar to thresholds derived from juvenile American shad (*Alosa sapidissima*) in previous studies, supporting the suggestion that these members of *Alosinae* have evolved a dedicated ultrasound detector adapted to detect and respond to approaching echolocating toothed whales.

Keywords: bioacoustics, biocommunications, ultrasonics, zoology

1. Introduction

Predator-prey interactions in the aquatic environment involve several sensory modalities such as vision, hearing, olfaction detection of water displacement with the lateral line system. These stimuli are used by predators to detect and track prey, and by the prey to detect and evade the approaching predators (Collin and Marshall 2003). Toothed whales produce directional, ultrasonic clicks with sound pressure levels of more than 220 dB re 1 μPa (pp) to echolocate prey (Au 1993). The predation pressure from toothed whales can be intense (Santos et al. 2001), and it is therefore conceivable that some prey species may have evolved sensory means to detect the powerful echolocation signals of toothed whales (Mann et al. 2001), similarly to how some moths have evolved ultrasound hearing to detect echolocating bats (Miller and Surlykke 2001).

Most fish can not hear frequencies above a few kHz (Hawkins 1981). However, some members of the subfamily *Alosinae* (family Clupeidae) have been shown to detect, respond to and process intense ultrasonic signals (Nestler et al. 1992; Mann et al. 1997; Mann et al. 2001; Plachta et al. 2004; Gregory et al. 2007). It has been suggested that this capability could be a counter-move against echolocating toothed whales (Mann et al. 2001). Studies of ultrasound detection abilities in Alosinae so far have focused on juvenile American species such as American shad (*Alosa sapidissima*) and gulf menhaden (*Brevoortia patronus*) (Mann et al. 2001), but it is not known if the capability to detect and respond to intense ultrasound is found across the entire subfamily.

One of the European members of the Alosinae, the allis shad, spawn in the rivers of the northern part of France and spend most of their life in the Bay of Biscay (Baglinière et al. 2003; Acolas et al. 2004), where a range of piscivorous toothed whales are found. However, stomach contents from the common dolphin (*Delphinus delphis*) show that even though the dolphins feed on a wide range of fish species, allis shad has not been identified as prey, despite temporal and spatial overlap of these two species (Pusineri et al. 2007). Here we test the behavioural response of the anadromous allis shad (*Alosa alosa*) when exposed to ultrasonic signals and discuss implications for avoidance of echolocation toothed whales.

2. Materials and methods

Allis shad were caught in a live fish trap at INRA Station de piégeage, Le Moulin des Princes, Pont Scorff in Le Scorff River (Brittany, France) in May 2006. 26 adults of mixed sex with body lengths (nose to tail) between 45 and 55 cm were used. All fish were released back into the river after the experiment. Experiments were conducted at the place of capture in an outdoor test tank measuring 2.1×2.1×0.37 m (length×width×depth) filled with water from the river at 13˚C.

Six groups consisting of two to five fish were exposed in two different playback sequences. Having several fish in each test group facilitated more natural shoaling behaviour, but only data from the first responding fish in each group was used to avoid the possible bias of one fish evoking a change in the swimming behaviour of the other fish in the tank. In the first sequence a 70 kHz signal was used (four groups) and in the second sequence a 120 kHz signal (two groups). The frequencies used are within the range of the centroid frequencies of echolocation clicks of toothed whales (Au 1993). Each playback sequence consisted of twelve stimulations at the two frequencies using received levels (± 4dB) at the fish of 157, 161, 167, 173, 179, 185 dB re 1 μPa (pp) with five minutes in between each exposure. The fish were exposed to the same intensity level twice. Half of the fish groups were exposed to an increasing followed by a decreasing series of intensities, and the other half to intensity steps in reversed order. This procedure made it possible to investigate if the thresholds for incrementing and decrementing exposure levels were different.

Ultrasonic pulses consisting of 50000 cycles of sine waves were transmitted from an omnidirectional HS70 transducer (transmitting efficiency of 145 dB re 1 μPa/V at 1m) for the 70 kHz pulse (pulse duration of 0.7 s) and an omnidirectional Brüel & Kjær 8105 transducer (transmitting efficiency of 145 dB re 1 μPa/V at 1m) for the 120 kHz (pulse durationof 0.4 s). The transducer was placed in the middle of the tank and connected to a tone generator Agilent 33220A via a 46 dB custom-built power amplifier.

Measurements of the sound field in the test tank were performed with a calibrated Brüel & Kjær 8105 hydrophone. Signal analysis of the pulses using Matlab 6.1 (*Mathworks*) showed that all significant energy was contained within 100 Hz around the center frequency. The tone generator produced a weak low-frequency pulse (< 10 Hz) at the beginning and end of the ultrasonic pulse. The effect of this by-product was tested using a directional Reson 2116 transducer. Furthermore, to test for the effect of low frequency by-products of the high frequency pulse each fish group was also exposed to a control sound stimuli consisting of a pure tone pulse at 2 kHz with 0.5 s duration and a sound pressure level of 160 dB re 1 μPa (pp) played with a UW30 transducer (transmitting efficiency of 110 dB re 1 μPa/V at 1m). This stimulus should be 10 dB above the hearing threshold of allis shad, as estimated from hearing measurements made on other Alosa species (Popper et al. 2004), and well below the spectral background noise in the tank (<135 dB re 1 $\mu Pa^2/Hz$). The signal should therefore be audible to the fish.

The swimming behaviour of the fish was recorded with a Profiline **CTV7040** video camera (25 frames s^{-1}) mounted 1.5 m above the water surface of the tank. The camera images were digitized to a laptop via a Grabster 400 video card using the software Ulead VideoStudio7 (Ulead Systems Inc.). Each sound stimulation was accompanied by a cue given by the operator recorded by a microphone connected to the audio input of the video card. The synchronization between video and audio was estimated to be within a few 100 ms. Single video frames were analyzed using Pinnacle studio Plus 9.3 (Pinnacle System Inc.) and MB-ruler 3.0. The swimming speed (in body lengths s^{-1}) was estimated in intervals of 0.5 s in a 6 s window starting 3 s before and 3 s after stimulation.

The 97.5 % confidence interval of the mean swimming speed for the 3 s interval before exposure was computed by pooling the data from all fish for each exposure. A behavioural response was considered present if the swimming speed after exposure was twice this value (Fig. 1).

3. Results

Allis shad showed a change in swimming speed when exposed to ultrasound played at 70 kHz and at 120 kHz (Fig. 1). Each swimming velocity is the mean of the response obtained during the increasing and decreasing sound level exposure series for each group (Fig. 1). In all but three of the twelve stimulation sequences, a significant correlation was seen between the received level and the swimming speed measured 1 s after stimulation (Student's t-test on the correlation coefficient, $p<0.05$, see Table 1). The change in swimming speed gradually declined as the sound pressure level decreased. The response threshold defined as two times the 97.5% confidence interval (threshold at 70 kHz: 0.70 BL/s and at 120 kHz: 0.66 BL/s) was between 161-167 dB re 1 μPa (pp) at 70 kHz and 161-167 dB re 1 μPa (pp) at 120 kHz (Fig. 1). When exposed to the 2 kHz control sound, none of the fish exceeded the defined response threshold (Fig. 1).

Half of the fish groups were exposed to an increasing followed by a decreasing series of intensities, and the other half to the opposite with no difference in the derived thresholds.

To make sure that the fish responded to the ultrasonic output of the transducer and not to any omnidirectional low-frequency by-products or electric noise, a directional ultrasonic transducer (Reson 2116) was used on three fish (sensu Nestler 1992). When the transducer was directed towards the fish, the fish was exposed to both the directional ultrasonic pulse and the weak, omnidirectional low-frequency by-product. Sound exposure elicited a strong response in all of the three fish when the transducer was pointed at them. When the transducer was turned 90 degrees with respect to the fish, exposing them to the weak low-frequency by-product only, no response could be detected. This shows that the fish did in fact respond to the ultrasonic stimuli and not the low frequency by-product (*sensu* Nestler et al. (1992)).

4. Discussion

Allis shad respond to ultrasonic signals in the frequency range where toothed whales echolocate. The response thresholds between 161 and 167 dB re 1 μPa pp at 70 and 120 kHz are comparable to the behavioural thresholds obtained from juvenile American shad, which showed a very weak or no behavioural response below 160 dB re 1 μPa at frequencies between 20 and 160 kHz (Mann et al. 1997). The similar thresholds of European and American species suggest that members of the *Alosinae* have evolved a dedicated ultrasound detector, possibly unique among all fish species.

The duration of 70 kHz and 120 kHz pulses of 0.7 s and 0.4 s, respectively, is three orders of magnitude longer than the duration of clicks from toothed whales (20-250 μs). We used such long pulses to make the study comparable with previous behavioural studies on ultrasound detection in other shad species (Plachta and Popper 2003). The drawback of using long-duration signals in small tanks is a varying received level caused by interference patterns and that the energy carried in the sound pulses is much larger than for a toothed whale's click at the same peak intensity.

The behavioural response thresholds measured here are at least 20 dB above the hearing threshold found for American shad using acoustic brainstem response techniques (Mann et al. 2001). Even though the fish can actually detect weaker sounds, the sound intensity apparently needs to be considerably higher before the fish responds behaviourally to the stimulus. Increased sound intensity leads to stronger behavioural responses indicating that allis shad have an intensity-graded response to the output of its ultrasound detector as indicated for American shad (Plachta and Popper 2003). The response threshold to ultrasound may reflect a trade-off between being caught and the costs associated with futile escapes (energy expenditure and lost opportunity to engage in other activities). Therefore, the response should depend on the animal’s perception of the risk (Ydenberg and Dill 1986). Allis shad may therefore use the intensity of the echolocating signals as a cue to estimate the proximity of an echolocating toothed whale: a distant toothed whale will cause lower received levels and hence only require a mild response of turning away from the predator, while high received levels of echolocation clicks would signify a close-by predator necessitating a strong and forceful escape.

Allis shad do not appear in the stomach content of the common dolphins (Pusineri et al. 2007), even though the habitats of the allis shad and common dolphins overlap in the study area. This observation, in combination with the present demonstration of a clear behavioural response when exposed to ultrasonic signals, indicates that allis shad may benefit from their ability to detect ultrasound to successfully minimise predation from echolocating toothed whales.

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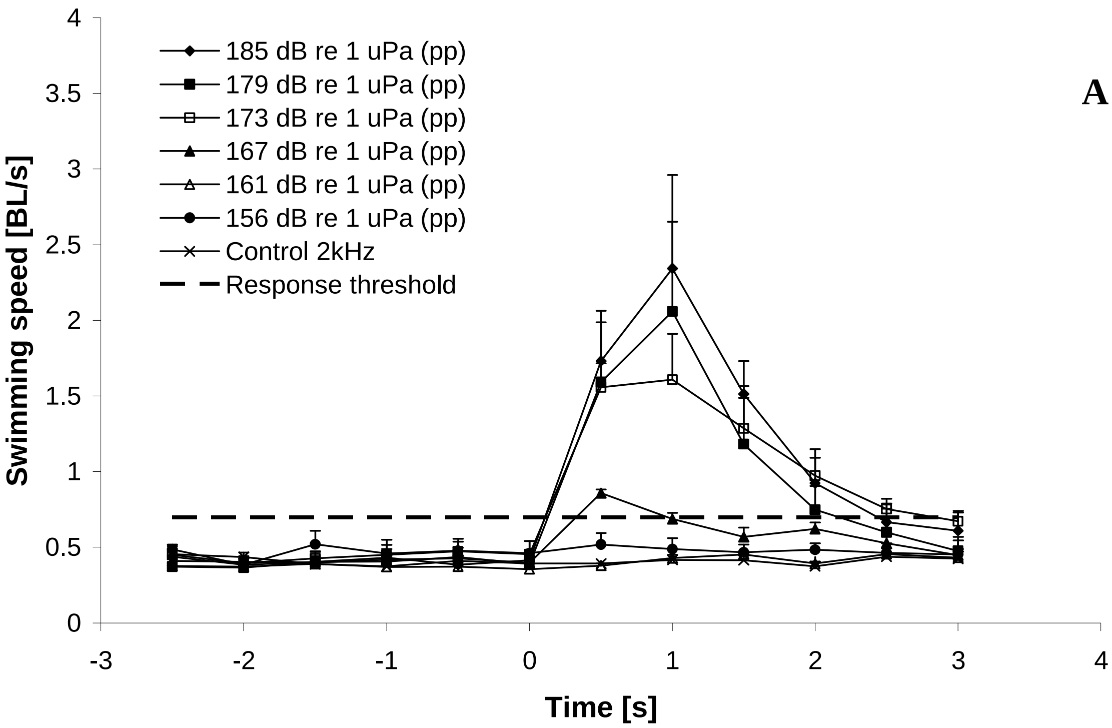
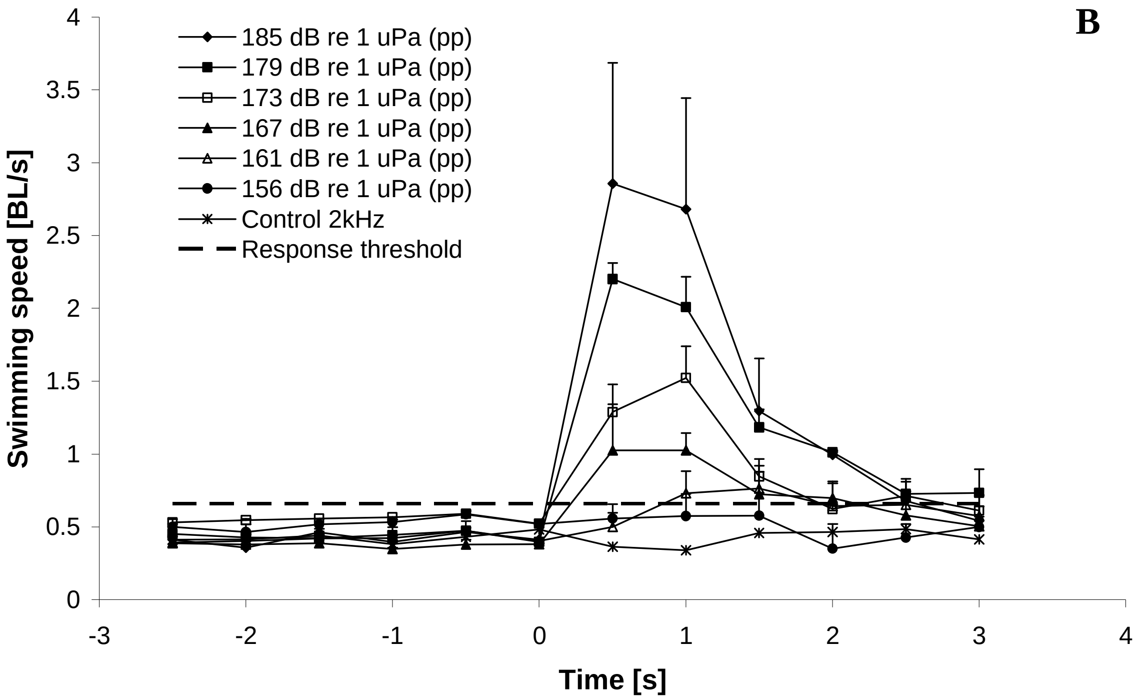
Table 1: The result of Student's t-test made on the correlation coefficient at 70 and 120 kHz for the fish responding first in each test group when exposed to an increasing and a decreasing sound pressure level. G=fish group, corr=correlation coefficient, t=t-value, significance level (marked with stars) $p<0.05$.

		70 kHz				120 kHz	
		G1	G2	G3	G4	G5	G6
Increase	r^2	0.76	0.24	0.94	0.44	0.96	0.83
	t	2.34*	0.50	5.53	0.99	6.50*	3.00*
Decrease	r^2	0.98	0.83	0.95	0.84	0.59	0.90
	t	9.32*	2.92*	6.17*	3.14*	1.50	4.10*

Figure captions

Figure 1: Allis shad swimming speed (mean +S.E.) before, during and after stimulation with ultrasound at two frequencies played at six different sound pressure levels. After each experiment the allis shads were exposed to a control sound at 2 kHz and 160 dB re 1 µPa pp. The allis shad are stimulated at the time 0 s. Swimming speed was measured with 30 s intervals. **1A**: Mean swimming speed of four fish when exposed to a 70 kHz tone. **1B**: Mean swimming speed of two fish when exposed to a 120 kHz tone.




B
185 dB re 1 uPa (pp)
179 dB re 1 uPa (pp)
173 dB re 1 uPa (pp)
167 dB re 1 uPa (pp)
161 dB re 1 uPa (pp)
156 dB re 1 uPa (pp)
Control 2kHz
Response threshold
Swimming speed [BL/s]
Time [s]
0
0.5
1
1.5
2
2.5
3
3.5
4
-3
-2
-1
0
1
2
3
4