

Auditory brainstem response in a harbor porpoise show lack of automatic gain control for simulated echoes

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Abstract: The auditory brainstem response (ABR) response to simulated echolocation clicks was studied in a harbor porpoise, *Phocoena phocoena*, to determine the relationship between the animal's perceived echo strength and the simulated target distance. In one experiment the click level at the listening post was kept constant while delay was changed, in another, the level was varied to approximate spreading losses. Results of both experiments indicate that there is no automatic gain control in the hearing system of this harbor porpoise.

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1. Introduction

The auditory brainstem response (ABR) technique is being used more often for studying hearing in toothed whales (odontocetes) mainly because it is noninvasive and the suction cup EEG electrodes are easy to apply. With this method an acoustic stimulus is presented to the animal several hundreds of times. The collective electrical response (ABR) of the brain is time locked to the stimulus, recorded and averaged. The ABR response is particularly pronounced when elicited by short, broadband stimuli, such as a dolphin echolocation click. The brief click presumably activates many independent auditory channels.¹ The method is therefore suited for the study of echolocation. One study relevant to the results reported here showed that the amplitude of the ABR measured in a false killer whale, *Pseudorca crassidens*, remained unchanged when elicited by echoes from a physical target at different distances even though the level of the outgoing click was constant.^{2,3} This result seems to indicate that this odontocete might possess some form of automatic gain control (AGC) in its hearing system, as proposed for echolocating bats.⁴⁻⁷ Such a mechanism regulates the amplitude of the perceived echo over range to the target. In bats both peripheral and central mechanisms provide automatic gain control.^{8,9} Contraction of middle ear muscles during the intense vocalization protects the inner ear and the gradual relaxation of this protective mechanism contributes to the increased sensitivity for targets at longer distances. If a similar mechanism were present in odontocetes it would have to operate at a much faster time scale due to the higher speed of sound in water and to the much shorter signals used by odontocetes. Little is known about middle ear function in odontocetes.¹⁰

In this study we addressed the question of a possible AGC mechanism in the auditory system of a harbor porpoise. We used a target simulator, which allows for easy uncoupling of the simulated echo amplitude and the simulated target distance. Two experiments were run. In the first the amplitude of the simulated echo was kept constant regardless of the delay. In the second experiment the amplitude of the simulated echo was adjusted slightly less than would be predicted for two-way spherical spreading losses. We found no evidence for an AGC mechanism in a trained harbor porpoise.

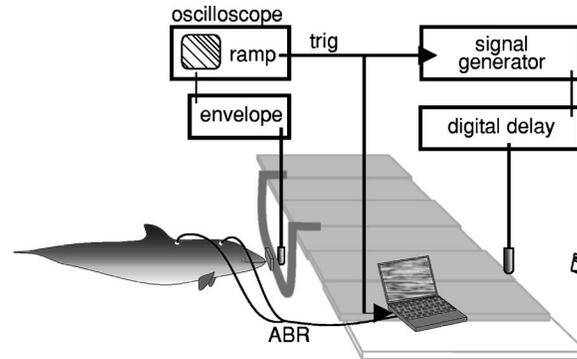


Fig. 1. Schematic of the set-up and some of the equipment used to produce simulated echoes and record ABRs. The small ghost to the right of the transmitting hydrophone symbolizes the simulated target at one possible virtual location. The schematic is not to scale.

2. Methods

We used a 9-years old male harbor porpoise, Eigil, who was born in the wild but lived most of his life in captivity. The experiments were carried out at Fjord and Bælt in Kerteminde, Denmark. Eigil was trained to station 1 m below the water surface with his rostrum on a small plastic square (the listening post) where he could station there for up to 90 s (see Mm. 1.). Before going to the listening post he was fitted with silver electrodes in suction cups, one behind the blowhole and the second near the dorsal fin, the reference electrode. He always vigorously echolocated during trials producing clicks at rates up to 300 Hz. There were normally four to eight trials per session and one or two sessions per day.

The simulated echo was the sampled step response from a 1/3-octave filter set at 125 kHz. This signal is very similar to a porpoise click in time frequency structure due to the fact that both are minimum phase bandpass signals.¹¹ The simulated echo was stored in and delivered by an Agilent arbitrary waveform generator (33220A). The porpoise's echolocation clicks were transduced by a Reson TC4013 hydrophone placed 0.5 m in front of the listening post. The envelopes of clicks were obtained from a click detector and used to trigger the simulated echo. The threshold for triggering was set to 132 dB re. 1 μ Pa pRMS (peak equivalent root mean square¹²) at the hydrophone. A digital delay channel was used to generate the desired delays. The amplitude was set with a digitally controlled attenuator. The amplified simulated echo was projected from a Sonar Products HS150 hydrophone at the backside of the pontoon bridge, 2.3 m in front of the listening post (Fig. 1).

The trigger signal for the simulated echo from the generator also served to trigger a 16 or 32 ms recording period containing the ABR, the potential difference between the two electrodes on the porpoise amplified by 110 dB. The recording period containing the ABR was sampled at 250 or 500 ksamples/s with a 12 bit dynamic range (National Instruments, DAQCard-6062E), averaged on line and saved after 64 presentations. The extreme over sampling eliminated the risk of high frequency interference from diverse sources showing up as aliased components within the frequency band of interest. The averaged traces were digitally filtered off-line between 500–2200 Hz, the frequency band where the ABR signal had the most energy, and the peak of the absolute amplitude was registered.

In experiment 1, the amplitude of the simulated echo at the listening post was held constant at 128 dB re. 1 μ Pa pRMS while the delay between the porpoise click and simulated echo was changed, representing changing distances to the simulated target. In experiment 2, the amplitude of the simulated echo was reduced by 9 dB per doubling of delay or somewhat less than expected from spherical spreading losses; -12 dB per doubling of distance. A perfect auditory AGC mechanism should compensate with $+12$ dB per doubling of distance, so by using 9 dB, the amplitude of the ABR response should *increase* with increasing delay. The peak ABR

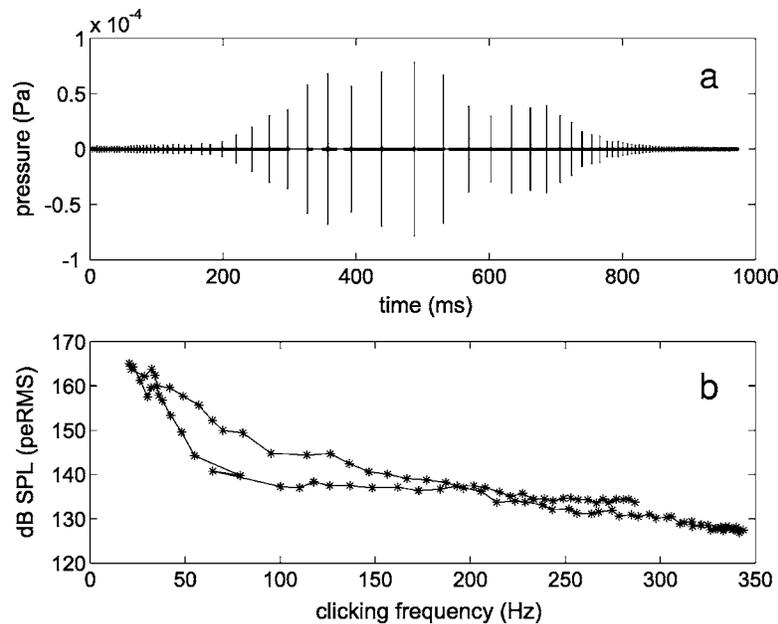


Fig. 2. Example of Eigil's echolocation behavior while on station. (a) Raw sample data recorded in slightly less than one second while Eigil focused his attention in the direction of the simulated target (documented by simultaneous video recordings-Mm. 1.). Click amplitudes are clearly negatively correlated with click rate. In (b) this relationship is documented further by plotting peak amplitude against the click rate defined as the reciprocal of the time to the preceding click.

levels in experiment 2 were compared to the peak ABR levels recorded at different amplitudes, but at a constant delay of 8.5 ms, which is the average of all delays tested in experiment 2. Two sessions on the same day with 5 trials each were used to gather data for experiment 1 and one session on another day with 5 trials was used for data gathering in experiment 2.

3. Results

Figure 2 shows part of a typical echolocation series while Eigil is on station. He spontaneously alternates between high intensity, low rate clicks and low intensity, high rate clicks several times during a trial. Only high intensity signals triggered simulated echoes. He is rewarded for remaining on station and not for producing sonar clicks.

[Mm. 1. Eigil at station, sonar clicks via a detector (562 KB).]

The results of experiments 1 and 2 are shown in the form of waterfall plots [Figs. 3(a) and 3(b)]. Each trace is displaced upwards by amounts proportional to the delay of the phantom target. In experiment 1 (constant echo levels) ABR peak amplitudes [Fig. 3(a)] show no obvious changes as the delay increased. Also, the ABR elicited by the echolocation pulse is constant in amplitude [first ABR in each trace in Fig. 3(a)]. In experiment 2 (decreasing echo levels with increased delay) ABR peak amplitudes [Fig. 3(b)] decrease with increasing delay, where as the amplitudes of the ABR elicited by the outgoing clicks remain unchanged. The ABR amplitudes to the emission in experiment 2 [Fig. 3(b)] are larger at all stimulus delays than those in experiment 1 [Fig. 3(a)]. This may reflect a higher average outgoing click level in these trials, or it may reflect day-to-day variations in ABR amplitude. Figure 4 compares peak ABR amplitudes at various stimulus levels with a constant delay of 8.5 ms, the average delay in experiment 2, to ABR amplitudes obtained from experiment 2 [Fig. 3(b)]. The slope of 17.8 nV/dB, obtained

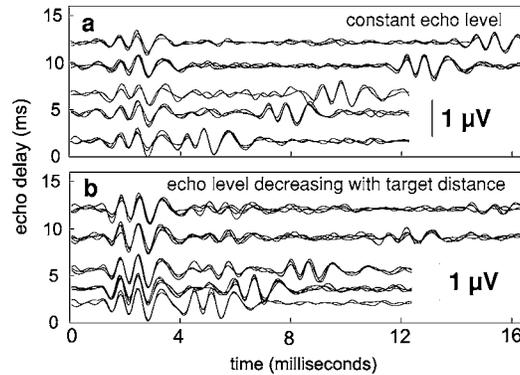


Fig. 3. ABR waveforms as a function of simulated echo delay. The y-axis indicates the delay for the simulated echo (2, 3.5, 5.5, 9, 12 ms). The vertical bar in the lower right-hand corner refers to ABR traces. Each trace is the average bioelectrical response to 64 stimulations. The first ABR deflection in each trace results from the outgoing porpoise click. In (a) the received level was held constant at 128 dB re. 1 μ Pa peRMS. Data were gathered from 5 trials in 2 sessions on one day. In (b) the echo stimulus levels were attenuated by 9 dB for a doubling of stimulus delay, approximating spherical spreading losses. Data were collected from 5 trials in 1 session.

when amplitudes decline with increased delay [see Fig. 3(b)], is not significantly different ($P < 0.57$) from the slope of 16.3 nV/dB obtained when the stimulus intensity was varied, but stimulus delay kept constant.

4. Conclusions

These results strongly suggest that this harbor porpoise possesses no automatic gain control (AGC), at least at the levels of the middle ear or the brainstem.

Had there been an active AGC mechanism in the first experiment, the response to the echo should have increased in amplitude with increasing delay, since a compensation for spreading losses would have allowed more sound energy to enter the hearing system with increasing delay. This did not happen [Fig. 3(a)].

In the second experiment where -9 dB was used for a doubling of delay, a perfect AGC mechanism in the sonar receiver would have given slightly increasing ABRs for increasing delays. This did not happen [Fig. 3(b)]. An incomplete AGC mechanism would have resulted in a regression coefficient between received echo level and ABR response that was lower than what we found when the echo delay was held constant, but echo amplitude varied (Fig. 4, filled circles). However, these slopes were not significantly different.

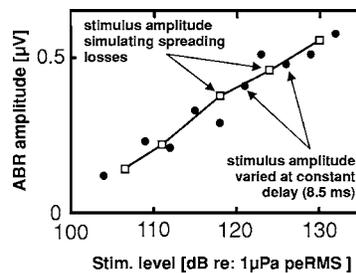


Fig. 4. Influence of echo level on peak ABR amplitude with and without accompanying delay changes. The peaks of the average data in Fig. 3(b) (one average value for each delay) are plotted against the received level in dB re. 1 μ Pa, peRMS (open squares, \square). For comparison, the closed circles \bullet show the peak ABR values at various stimulus levels, but with a constant delay of 8.5 ms, the average delay for the results shown in Fig. 3(b).

One explanation for the marked difference to the results of Supin *et al.*^{2,3} would be that the false killer whale adjusted the transmitted level as to keep the received echo at a constant amplitude and thus saturating the ABR to the outgoing click, obscuring the amplitude increase. But this scenario is unlikely, since the test animal produced very similar sounds at all delays.³ In this respect the false killer whale's echolocation behavior differs from that recorded from free-ranging dolphins, where the transmitted click level is adjusted to the delay of the target by 6 dB per doubling of distance.^{13,14} We did not address the question of an AGC mechanism achieved by controlling the outgoing sonar click level since Eigil varies the click level almost continuously while on station (Fig. 2).

Another explanation might involve attention. In our experiments there was no reward associated with the echo, as was the case in the experiments of Supin *et al.*,^{2,3} where the false killer whale performed a detection experiment.

Yet another possibility is that there might be a difference between the two species of odontocetes in this respect. If this were in fact the case, it might be explained by differences in source levels used by the two species. We never observed click levels above 180 dB re. 1 μ Pa pRMS from Eigil. It therefore might be argued that protection of the inner ear through some kind of middle ear mechanism is less likely in the smaller species than in the larger, louder toothed whales.

These questions could be resolvable if (1) the simulated echo experiments were performed with the false killer whale and/or (2) the harbor porpoise was trained to perform in a detection experiment³ while the ABR recordings were made. We are currently planning the latter of these experiments.

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References and links

- ¹A. Y. Supin, V. V. Popov, and A. M. Mass, *The Sensory Physiology of Aquatic Mammals* (Kluwer Academic, London, 2001).
- ²A. Y. Supin, P. E. Nachtigall, W. W. L. Au, and M. Breese, "The interaction of outgoing echolocation pulses and echoes in the false killer whale's auditory system: Evoked-potential study," *J. Acoust. Soc. Am.* **115**, 3218–3225 (2004).
- ³A. Y. Supin, P. E. Nachtigall, W. W. L. Au, and M. Breese, "Invariance of evoked-potential echo-responses to target strength and distance in an echolocating false killer whale," *J. Acoust. Soc. Am.* **117**, 3928–3935 (2005).
- ⁴S. A. Kick, and J. A. Simmons, "Automatic gain control in the bats sonar receiver and the neuroethology of echolocation," *J. Neurosci.* **4**, 2725–2737 (1984).
- ⁵J. A. Simmons, A. J. Moffat, and W. M. Masters, "Sonar gain control and echo detection thresholds in the echolocating bat, *Eptesicus fuscus*," *J. Acoust. Soc. Am.* **91**, 1150–1168 (1992).
- ⁶D. J. Hartley, "Stabilization of perceived echo amplitudes in echolocating bats. I. Echo detection and automatic gain control in the big brown bat, *Eptesicus fuscus*, and the fishing bat, *Noctilio leporinus*," *J. Acoust. Soc. Am.* **91**, 1120–1132 (1992a).
- ⁷D. J. Hartley, "Stabilization of perceived echo amplitudes in echolocating bats. II. The acoustic behavior of the big brown bat, *Eptesicus fuscus*, when tracking moving prey," *J. Acoust. Soc. Am.* **91**, 1133–1149 (1992b).
- ⁸O. W. Henson, "The activity and function of the middle-ear muscles in echo-locating bats," *J. Physiol. (London)* **180**, 871–887 (1965).
- ⁹N. Suga, and P. Schlegel, "Neural attenuation of responses to emitted sounds in echolocating bats," *Science* **177**, 82–84 (1972).
- ¹⁰S. H. Ridgway, D. A. Carder, T. Kamolnick, R. R. Smith, C. E. Schlundt, and W. R. Elsberry, "Hearing and whistling in the deep sea: depth influences whistle spectra but does not attenuate hearing by white whales (*Delphinapterus leucas*) (Odontocete, Cetacea)," *J. Exp. Biol.* **204**, 3829–3841 (2001).
- ¹¹M. P. Olivieri, "What can be learned from one of nature's most advanced biosonar: Discussion on Bottlenose dolphins echolocation waveforms with respect to echolocation tasks in shallow water," *J. Acoust. Soc. Am.* **111**, 2371 (2002).

- ¹²D. R. Stapells, T. W. Picton, and A. D. Smith, "Normal hearing thresholds for clicks," *J. Acoust. Soc. Am.* **72**, 74–79 (1982).
- ¹³M. H. Rasmussen, L. A. Miller, and W. W. L. Au, "Source levels of clicks from free-ranging white-beaked dolphins (*Lagenorhynchus albirostris* Gray 1846) recorded in Icelandic waters," *J. Acoust. Soc. Am.* **111**, 1122–1125 (2002).
- ¹⁴W. W. L. Au and K. J. Benoit-Bird, "Automatic gain control in the echolocation system of dolphins," *Nature* (London) **423**, 861–863 (2003).