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Keeping returns optimal: gain control exerted through sensitivity adjustments in the harbour porpoise auditory system

Meike Linnenschmidt^{1,*}, Kristian Beedholm², Magnus Wahlberg³,
Jakob Højer-Kristensen³ and Paul E. Nachtigall⁴

¹*Institute of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark*

²*Department of Biological Sciences, Aarhus University, C.F. Møllers Allé 3, 8000 Aarhus, Denmark*

³*Fjord&Bælt, Margrethes Plads 1, 5300 Kerteminde, Denmark*

⁴*Hawaii Institute of Marine Biology, University of Hawaii, PO Box 1106, Kailua, HI 96734, USA*

Animals that use echolocation (biosonar) listen to acoustic signals with a large range of intensities, because echo levels vary with the fourth power of the animal's distance to the target. In man-made sonar, engineers apply automatic gain control to stabilize the echo energy levels, thereby rendering them independent of distance to the target. Both toothed whales and bats vary the level of their echolocation clicks to compensate for the distance-related energy loss. By monitoring the auditory brainstem response (ABR) during a psychophysical task, we found that a harbour porpoise (*Phocoena phocoena*), in addition to adjusting the sound level of the outgoing signals up to 5.4 dB, also reduces its ABR threshold by 6 dB when the target distance doubles. This self-induced threshold shift increases the dynamic range of the biosonar system and compensates for half of the variation of energy that is caused by changes in the distance to the target. In combination with an increased source level as a function of target range, this helps the porpoise to maintain a stable echo-evoked ABR amplitude irrespective of target range, and is therefore probably an important tool enabling porpoises to efficiently analyse and classify received echoes.

Keywords: auditory brainstem response; ABR threshold; automatic gain control; dynamic range

1. INTRODUCTION

Echolocation [1] evolved convergently in toothed whales and bats. Both these animal orders use echolocation for foraging and orientation by emitting short, ultrasonic signals and listening for the returning echoes from objects in their environment. Sound travelling through open air or in deep water loses three quarters of the energy for each doubling of the distance to the source owing to spherical spreading [2]. In decibel units, this is saying that the signal decreases by 6 dB per doubling of the distance, or that the sound level is proportional to $-20 \log R$, where R denotes the distance the sound has travelled. The returning echo from a small target suffers the same amount of attenuation. Therefore, in the case of echolocation, if the animals were to stabilize the echo-received level to overcome these distance-related intensity changes, then they would have to compensate by -12 dB for each halving of the distance to the target (R) or, in other words, applying an overall gain of $40 \log R$. This could be performed by reducing the outgoing signal level, by reducing the auditory sensitivity or by a combination of both. Maintaining a stable echo level may be important for optimal neural processing both in terms of estimating the echo delay and detecting the spectral

content changes introduced by whatever caused the echo. For example, if the animal always produced sounds of a constant level, then the returning echoes from close-by objects could potentially activate all or most available auditory neurons, and thereby render feature discrimination based on spectral content difficult or impossible, whereas echoes from distant objects might be too weak to be detected. In humans, it has been shown that, for a range of levels covering 60 dB, spectral discrimination deteriorates with increasing stimulus level [3].

It has been shown that sonar signals of toothed whales [4–9] and bats [10–12] do exhibit a reduction in source level as the echolocator approaches an object of interest. This is generally referred to as automatic gain control, a term coined for range-dependent receiver sensitivity adjustment in man-made sonar [2]. In toothed whales, this reduction has been quantified to about 6 dB per halving of the range to the target ($20 \log R$). This is sufficient to compensate for only half the energy gained for each halving of distance as the animal approaches the target. Thus, the animal would experience an increasing sound level of the returning echo, if no further range compensation occurred. This incomplete level adjustment has been of great interest in both dolphin and bat studies, and it has been hypothesized that the remaining compensation, if present, must take place in the auditory system. For both toothed whales [13,14] and bats [10,11,15,16], it has been shown that the hearing sensitivity during echolocation can vary as a function of both the size of the

* Author for correspondence (meike@biology.sdu.dk).

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target and the level of the outgoing clicks, but it remains to be seen how changes in the hearing abilities are related to target range.

Hearing can be studied electrophysiologically by non-invasively measuring the auditory brainstem response (ABR) [17,18], which has been used extensively to address many aspects of auditory processing in cetaceans [19–22]. One can record the ABR elicited by transient acoustic stimuli with contact electrodes on the body surface and average these time-locked to the stimulus onset to reduce the influence of independent additive noise. This enables the detection of even the very weak bioelectric signals within the neural and electromagnetic background noise. The ABR is a time-local signal lasting a few milliseconds (figure 1*b*), reflecting neural activity in different centres of the auditory brainstem [17,21]. Within certain limits, the ABR amplitude is positively correlated with the stimulus level and thus presumably with the received level experienced by the animal [17,22]. Smaller cetaceans can be trained to station in a hoop below the water surface while equipped with suction cup electrodes (figure 1*a*; electronic supplementary material, figure S1, figure S2 and movie S1) and are thus ideal study subjects for ABR measurements during active echolocation. Our study was kept as similar as possible to previous studies with a false killer whale (*Pseudorca crassidens*) [13] and a bottlenose dolphin (*Tursiops truncatus*) [14] to make the results directly comparable. However, unlike these earlier studies, we did not use a specific trigger level for the sound recordings. Instead, we recorded all echolocation clicks, including those too weak to elicit an echo-evoked ABR to the cylinder for off-line analysis. Harbour porpoises (*Phocoena phocoena*) are much smaller than the animals used in the previous studies, and provide a greater signal-to-noise ratio (S/N) of the ABR recordings owing to the shorter distance between the surface electrodes and the brainstem [22].

Our study shows that the porpoise biosonar is a flexible system using gain control that is adjustable to the echolocation task at hand.

2. MATERIAL AND METHODS

(a) *Animal and experimental environment*

At the time of the experiment, the male harbour porpoise was about 15 years old, 143 cm long and weighed 42 kg. It was initially accidentally caught in a pond net at the age of approximately 2 years in 1997 and has been kept in a semi-natural net enclosure, currently accompanied by three females. The large net enclosure was divided into a smaller and a larger pool, measured about 34 × 17 m (with a depth between 3 and 5 m), and was located in a little harbour at the opening to a small fjord at Fjord&Bælt in Kerteminde, Denmark. The physical parameters of the brackish water were dominated by an estuary water circulation between the open sea and the narrow fjord. The tide was less than 0.5 m, but shifting wind velocities and directions produced variable water surface levels, and strong currents through the narrow harbour. During experimental sessions in the large pool, the three females were kept in the smaller pool to minimize distraction and maximize focus on the experiment for the male porpoise.

(b) *Experimental setup and procedure*

The porpoise was trained to position itself with the ventral side of its head in a rubber tube hoop (diameter: 34 cm)

centred 0.8 m below the surface. An opaque rectangular plastic screen (76 × 105 cm) of less than 1 mm thickness at 30 cm distance to the hoop prevented the animal from using visual cues during the trials. Echolocation viewing time was controlled by an acoustical shield (−30 dB, 54 × 54 cm) of 1 cm neoprene foam between two 2 mm aluminium plates. A response paddle (7 × 10 cm cylinder made of foam) was located below the surface on the left side above the hoop. All parts of the set-up were attached to an aluminium ladder reaching across the pontoon and continuing 1.44 m out over the water surface (electronic supplementary material, figures S1 and S3). The trainer and researcher were positioned on the pontoon with less than 1 m distance to the ladder on either side of it. Suction cup electrodes were attached to the animal's body surface to record its far-field electrical activity, which was recorded continuously.

A hollow aluminium cylinder (target strength −18 dB; electronic supplementary material, figure S2) was presented at 2, 4 or 8 m distance to the hoop centred 0.8 m below surface in a random order 50 per cent of the time. The acoustic shield was raised for 5 s, controlled by a light–time device, to allow the animal free access for echolocation. If the cylinder was presented, and the animal detected it (go trial), then it had to leave the hoop and touch the response paddle. If the cylinder was not present (no-go trial), then the animal had to stay in the hoop after the acoustic shield was lowered. If the animal's response was correct, then the trainer shortly blew a dog whistle (5 kHz) before rewarding the animal with fish. To signal an incorrect answer, the trainer splashed with his hand in the water and the animal returned to the trainer without receiving a reward.

Usually, two sessions per day were carried out before noon. A session lasted for 10 and 20 min. Data were always collected during a set of 20 trials following a Gellermann [24] schedule; in a set of 10 trials, the cylinder was present or absent equally often in a random order while no more than three subsequent trials had the same cylinder status. Typically, up to six warm-up trials were carried out to give the animal a chance to adjust its hoop behaviour to the present water-current status, to check the animal's motivation, and to ensure the functionality of the set-up and the technical equipment. Cool-down trials were carried out only if the animal made a mistake on the last trial of the session, in order to not finish on a negative note, or if technical difficulties during the 20 trials prompted a repeat of one or more trials in order to assure an equal number of go and no-go trials in each session. On one day, we used only one distance and up to two sessions. A total of 30 sessions (10 at each distance) were performed. Certain criteria were followed to exclude external cues to the animal of cylinder status per trial (electronic supplementary material, methods).

(c) *Electrophysiological and acoustic recordings*

Electrophysiological potentials were measured from the animal as the differentially recorded ABRs using two EEG silver disc electrodes (diameter: 10 mm) submerged into latex suction cups (diameter: 40 mm). The active electrode was placed with its centre at the dorsal head surface 2 cm behind the blowhole and 4 cm to the left of the midline. The reference electrode was fixed to the back of the animal about 10 cm below the anterior end of the dorsal fin on the right side, while the ground electrode contacted the brackish water immediately above the reference electrode. This configuration of electrodes was chosen as it gave the best

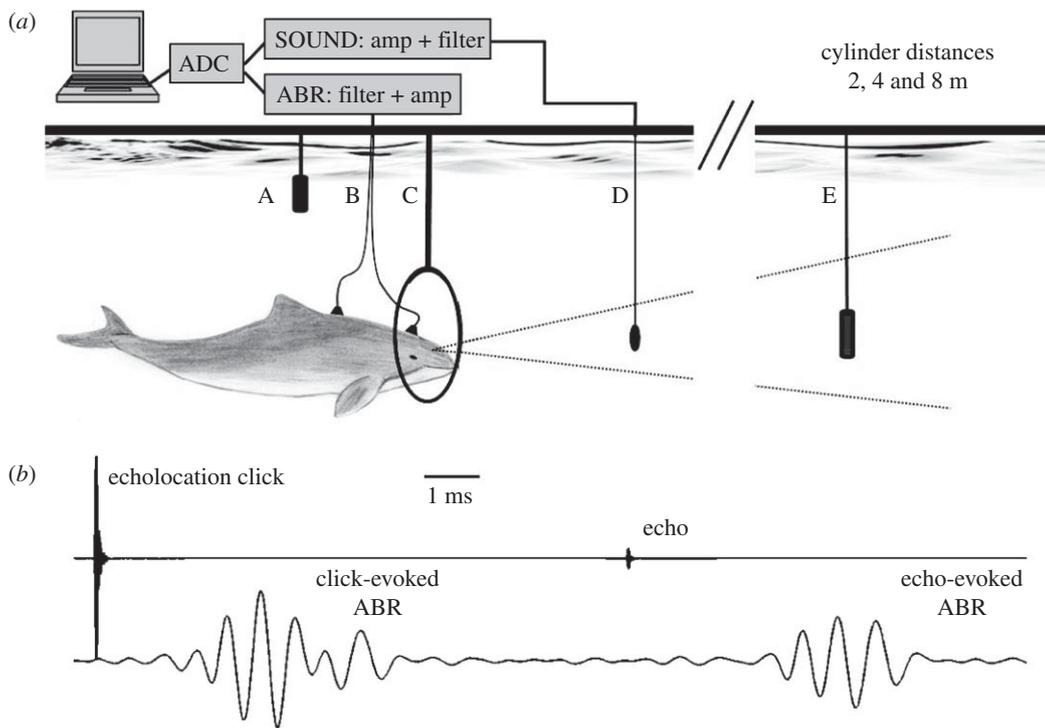


Figure 1. Schematic of the experimental set-up and example of acoustic and ABR data (electronic supplementary material, figure S1, figure S3 and movie S1). (a) A response paddle (A) is near the surface. The recording units for auditory brainstem response (ABR) with suction cup electrodes attached to the animal's body surface (B) and echolocation clicks (SOUND) are connected through an analogue-to-digital converter (ADC) to a laptop. The animal is positioned in a hoop (C) 1 m below surface. The hydrophone (D) is at 1 m and the aluminium cylinder (diameter 37.85 mm, length 127 mm; electronic supplementary material, figure S2) at 2, 4 or 8 m distance to the hoop. The dotted lines represent the -3 dB beam width of 16° by the harbour porpoise [23] and 'amp' stands for amplifier. (b) The echo recorded 0.8 m from the target was 18 dB lower than the sound that impinged on it. The grey trace shows an example of an echolocation click and the echo as returning from the target at 8 m distance together with the corresponding click-evoked ABR and echo-evoked ABR (average of approx. 1000 signals) below.

S/N in the set-up at hand. The conductivity between skin and electrodes was increased using electrode gel. The electrode signal was differentially amplified using a custom-built amplifier (80 dB gain) with a built-in fourth-order band-pass filter between 300 Hz and 10 kHz. To prevent any health risk to the animal, an optical divider (ISO 100 amplifier, Burr-Brown) with an additional gain of 20 dB was inserted between the preamplifier and the recording unit. To achieve the necessary alignment of the ABR trace to the echolocation clicks, both electrophysiological and acoustic data were digitized by the same multi-purpose acquisition board (NI USB-6251, National Instruments) at a rate of 500 kHz, and stored as WAV files. Sound was recorded by a B&K 8103 hydrophone (Brüel & Kjær) 0.8 m below the surface 1 m from the hoop in front of the animal's head. The animal, hydrophone and target were aligned as shown in the electronic supplementary material, figures S3–S5. Acoustical signals were amplified by 52 dB (hydrophone amplifier HA01A, Etec Aps.) and high-pass-filtered (fourth order, -3 dB cut-off frequency of 10 kHz). Recordings were manually started and terminated by the researcher when the animal positioned itself in or left the hoop, respectively. All recording software was custom written to this project in LABVIEW (v. 10.0.1).

(d) Data analysis

Data from the sessions having identical target distance were pooled into three datasets, one for each distance. The ABR traces were band-pass-filtered around 1.5 kHz (second

order, Butterworth, -3 dB points at 300 Hz and 4 kHz), which maximized the S/N. In addition, an artefactual single-frequency spectral component that occurred around 4 kHz was suppressed using a Fourier transform filter, setting the spectral level to the mean of the neighbouring samples but keeping the phase value. The sound traces were band-pass-filtered (second order, Butterworth, -3 dB cut-off frequencies of 100–160 kHz) and the Hilbert envelope was calculated from the magnitude of the analytical signal to determine the peak amplitude [25]. The ABR signal was time-aligned using the occurrence of the clicks in the acoustic channel as a time marker. The ABRs were binned according to source levels and then averaged within each bin. Bins consisted of 64 ABRs and neighbouring bins were sliding Hann-weighted with a 75 per cent overlap. Averaged ABRs were plotted against averaged source level or the average-calculated echo-received level within each bin. To be consistent in the evaluation of the ABR amplitude, we measured the peak absolute value of the largest deflection that was not influenced by responses to echoes from the hydrophone at 1 m in a 600 μ s window. All analyses were carried out in custom-written MATLAB scripts (The MathWorks; version R2010a).

3. RESULTS

The ABR in a harbour porpoise was measured during an echolocation detection task of an aluminium cylinder presented at distances of 2, 4 and 8 m from the animal.

Table 1 shows the psychophysical performance by the animal. The responses are split into four categories: FA (false alarm; meaning that the animal erroneously indicates the presence of a cylinder in absence trials), MISS (meaning that the animal erroneously indicates the absence of the cylinder while it is present), CR (correct rejection; meaning that the animal is correctly indicating that no cylinder was present), and HIT (meaning that the animal is correctly indicating the presence of the cylinder). The cylinder was present on half of the 600 go/no-go trials. The animal responded correctly 590 times. Out of ten incorrect answers, the animal missed the presence of the cylinder only once and made nine false alarms. The animal conducted 200 trials at each distance and performed the task with an overall FA rate of 3 per cent.

The animal used echolocation clicks with peak levels ranging more than 45 dB (from <123 to 168 dB re 1 μ Pa) at all three distances (figure 2a). For all three target ranges, the largest proportion of clicks was found within the upper half of the source-level distribution. The average source level decreased by about 3 dB per halving of the distance: 156.1, 153.5 and 150.2 dB (re 1 μ Pa at 1 m peak) for 8, 4 and 2 m target range, respectively. The peaks of the source level distributions were at 161.8, 156.2 and 152.7 dB for the three ranges, respectively, corresponding to a reduction of up to 5.6 dB per doubling of the target range.

The click-evoked ABR waveforms are shown in figure 3. The waveforms were sorted into source-level bins with equal numbers of clicks (64) in each average. The time axis is adjusted, so that the click is emitted at time zero. Figure 3a–b shows the click-evoked ABR data for echolocation ranges of 2, 4 and 8 m, respectively. In all cases, the ABR is represented by three dominant oscillations, typical for cetacean ABRs [18–22]. They probably represent coherent neural activity in the major nuclei of the auditory system, such as the cochlear nucleus, superior olive and inferior colliculus in the brainstem [21,22]. The peak amplitudes of the click-evoked ABRs as a function of source level are shown in figure 2b. These data are derived from figure 3, and therefore the interval between each measurement of the curves is directly dependent on the number of clicks obtained within each interval of source levels. Thus, the click-evoked ABR amplitude data in figure 2b are more detailed at higher source levels compared with lower ones. At the largest target range of 8 m, the click-evoked ABR amplitudes were independent of the source level. At the 4 m detection range, the click-evoked ABR amplitudes were also independent of source level, but they were, in general, somewhat smaller, except above 160 dB, where they exceeded the values for 8 m. The click-evoked ABR amplitudes for the 2 m trials were generally of lower amplitude than for identical click levels emitted during the trials with larger target range. A drastic change in the click-evoked ABR amplitudes as a function of source level occurred for the 2 m trials over a stretch of about 30 dB in source level variation (135–165 dB re 1 μ Pa). Here, the click-evoked ABR amplitudes varied about four times in amplitude with a positive trend. For source levels below 135 dB re 1 μ Pa, the click-evoked ABR amplitudes for this target range increased with decreasing source level until reaching amplitudes close to the one found for the highest source levels.

Table 1. The performance of cylinder detection of a harbour porpoise during 600 trials. FA, false alarm; CR, correct rejection. The meaning of FA, MISS, CR and HIT are explained in the text.

distance (m)/detection category	FA	MISS	CR	HIT
2	3	1	97	99
4	0	0	100	100
8	6	0	94	100
total	9	1	291	299
FA/MISS rate (%)	3.0	0.3	97.0	99.7

The echo-evoked ABR waveforms to the cylinder echo are shown as a function of echo-received level, target range and time relative to click production in figure 4a. As for the click-evoked ABR, the waveform shows the typical three peaks of a cetacean ABR [18–22]. The echo-received levels decrease by 12 dB for each doubling of distance for the same source levels. If no gain control took place, then the echo-evoked ABR amplitudes should become considerably lower with each doubling of the distance to the target for a given source level. A number of emitted clicks had source levels so low that the echoes elicited only a weak or undetectable echo-evoked ABR. The corresponding echo-evoked ABR amplitudes, as a function of echo-received level, are illustrated in figure 4b. For all three echolocation ranges, it is evident that the echo-evoked ABR amplitudes were largest for the higher echo-received levels and decreased with decreasing echo-received level. There was a sharp drop-off towards lower echo-evoked ABR amplitudes until they were not distinguishable from the noise floor. This drop-off is related to the auditory sensitivity of the animal [22]. In the present study, it shifted towards higher echo-received levels by approximately 6 dB for each halving of the distance (from 2 to 4 m and from 4 to 8 m) for the same echo-evoked ABR amplitude.

4. DISCUSSION

The harbour porpoise performed the psychophysical detection task at a false alarm rate of 3 per cent. The carefully designed and monitored standard psychophysical design enabled us to draw conclusions about the animal's use of echolocation and its attention to the task [26]. The low fraction of misses and false alarms in the overall performance demonstrated that the animal did pay keen attention to the presence or absence of the cylinder at all three distances. The experiment was designed to prevent any other sensory cues for the animal besides echolocation to detect the cylinder, which is important for the discussion that follows.

During the trials, the echolocation click level of the animal reduced on average by about 3–5.6 dB, depending on the measure used, when halving the distance to the cylinder (figure 2a). These level reductions are of the same order of magnitude as values that have been published for small free-swimming toothed whales, which reduced their sonar signal levels by up to about 6 dB (within a couple of decibels of variation) per halving of the echolocation distance when closing in on an object [4–9]. The results from a previous study of the same animal as the one used in this study

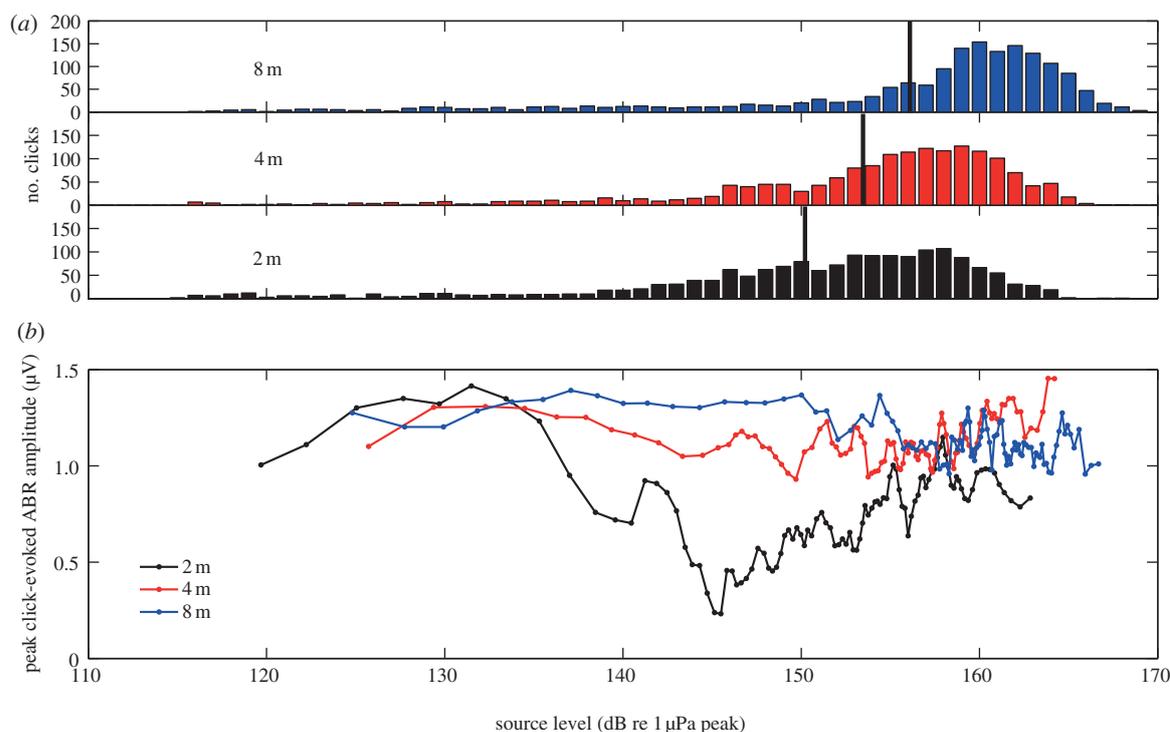


Figure 2. Source-level distributions and click-evoked ABR amplitudes for target distances of 2, 4 and 8 m. (a) Number of clicks produced for each echolocation distance as a function of source level. The black vertical lines represent the mean for all clicks recorded at each distance. (b) Peak click-evoked ABR amplitudes as a function of source level with the target at three different distances. Data from Hann-weighted averages of 64 clicks with neighbouring averages overlapping each other by 48 measurements (figure 3). Data suggest that the hearing sensitivity increases (larger click-evoked ABR amplitudes) when the cylinder is further away and the returning echo level weaker. Figures S3–S5 in the electronic supplementary material support the alignment of the setup and give evidence for the accurate calculations of source levels and correct correlation between click-evoked ABR amplitudes and source levels.

showed that the signal level changed by 4.5–6 dB when either doubling the repetition rate of signal emissions [27] or halving the distance while closing in on an object [9]. A false killer whale [28] and a bottlenose dolphin [14], which both performed the same echolocation task under controlled and similar conditions to our experiment, modified their sonar click levels by 3 dB when halving the distance to the cylinder with a target strength comparable with that in our study (-18 dB). Both these species [14,29] used a larger reduction in source level as a function of range when performing a similar task using a smaller cylinder. In these studies, the source level seemed to depend on a combination of distance and size. The further the echolocation distance and the smaller the cylinder, the more closely the level adjustments reached a reduction of 6 dB when halving the distance to the cylinder. These variations in the source-level adjustments depending on the target size, found in both the field and laboratory data, may either be caused by measurement inaccuracies or by actual variations in the individual animal's hearing response to different echolocation tasks (e.g. perhaps depending on how difficult the task is).

The averaged click-evoked ABRs and echo-evoked ABRs to the cylinder had generally a very good S/N, and the ABR waveforms resembled previously published descriptions [18–22]. The click-evoked ABR amplitudes to echolocation clicks emitted at the same level decreased with decreasing echolocation range (figures 2b and 3). This was in contrast to our expectations, as echolocation clicks of similar source level should elicit similar

click-evoked ABR amplitudes independent of the task, if the hearing system functioned without any active control of any kind. On the contrary, these data show that the click-evoked ABR amplitude was dependent on the target range, so that the click-evoked ABR amplitude was not only a function of the received level but also under the control of the animal. One possible active control at the level of neural activity elicited by the outer hair cells in the cochlea might explain these results [30]. At high source levels, the click-evoked ABR amplitudes reached nearly equal values independent of target distance, which probably shows a saturation of the neural stimulus, and therefore that no control by the animal was possible.

In the previous study, a false killer whale did not show any distance-related variations in the click-evoked ABR when the cylinder had target strength comparable with the one used in our study of a harbour porpoise. Only when the target strength was reduced did the false killer whale demonstrate a click-evoked ABR amplitude variation to echolocation clicks of similar level, depending on target range, to what was found in the harbour porpoise. The reduction in target strength by resizing the object for the false killer whale in effect also reduced the returning echo strength, just as increasing the distance did in the current harbour porpoise experiment. Therefore, both species have control over how loudly they heard the echolocation clicks, but demonstrate this under different experimental conditions.

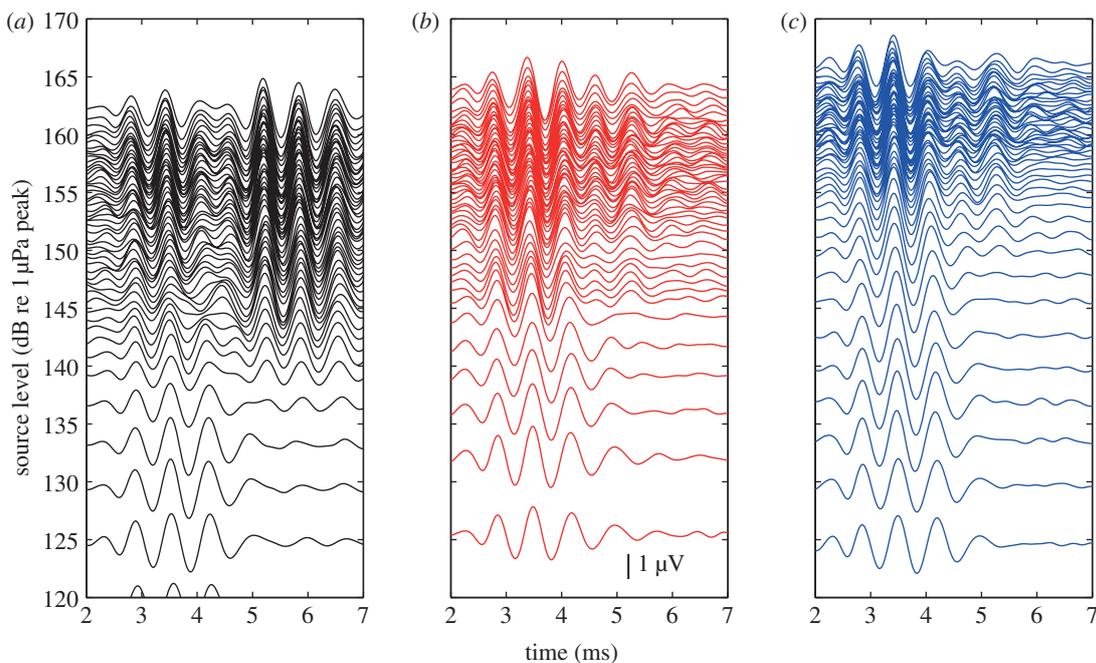


Figure 3. Waveform of click-evoked auditory brainstem responses (ABRs) for target ranges of (a) 2, (b) 4 and (c) 8 m. Click-evoked ABRs as a function of the time elapsed since click production at time zero. Each line represents a Hann-weighted average of 64 click-evoked ABRs plotted at the corresponding emitted source level on the y-axis. Neighbouring lines overlap each other by 48 measurements. In all subplots, the click-evoked ABR is detected as three consecutive oscillations at a delay of roughly 2.5 ms after the emission of the click. At approximately 4.5 ms delay, there is in (b) and (c) (not visible in (a)) a two-cycle oscillation, which is much weaker than the click-evoked ABR, however, and probably represents the ABR to a sound reflection of the small hydrophone at 1 m distance. In (a), the echo-evoked ABR to the cylinder echo already starts to show at a delay of 5 ms with three consecutive oscillations. The ABR to the sound reflection of the hydrophone is not visible, because the click-evoked ABR and the echo-evoked ABR are too close to each other in time and suppress the ABR to the hydrophone.

When observing the echo-evoked ABRs to the cylinders, the animal's control of the ABR to acoustic stimuli works differently than for the click-evoked ABRs. The echo-evoked ABR amplitudes to the cylinder echoes were similar to the shorter target ranges, but much weaker for the largest range in the harbour porpoise (figure 4). This is different from the false killer whale, which had constant echo-evoked ABR amplitudes to the cylinder echoes independent of target distance [13,28], and the bottlenose dolphin showing increasing echo-evoked ABR amplitudes for the cylinder echoes with increased target range [14]. Thus, in these three studies, there seem to be three different ways in which the returning echoes are analysed by the auditory system. The physics of the situation dictate that the amplitude of an echo attenuates by 12 dB for each doubling of the distance for a constant source level. This has carefully been checked for the echoes of the cylinder of this study with a directional transducer emitting high-frequency narrowband signals. Therefore, the echo-evoked ABRs should also decrease with larger target ranges, if there were no mechanisms to alter the hearing abilities of the animal while performing biosonar.

One of the mechanisms that may influence these delay-dependent changes in hearing sensitivity is the gradual release from forward masking [31], as proposed by Supin and co-workers [13,28,32]. From existing data, it seems that the level of forward masking may be different in the different species, thereby affecting the delay-dependent echo-evoked ABR amplitudes in different

ways. The amount of forward masking varies with the level, time and frequency content of the echolocation click [30]. One reason could be the different source levels used by the three species during the detection task. The porpoise used much weaker signals (129–174 dB re 1 μ Pa peak-to-peak) than the false killer whale and the bottlenose dolphin (160–215 dB re 1 μ Pa peak-to-peak), and therefore probably experienced forward masking to a lower extent. This is assuming that the difference in received sound level at the site of the inner ear and the source level is similar for all three species, which may or may not be true. If this is the case, then the neural response in the dephininds may always be fully (or almost fully) saturated when exposed to their loud echolocation clicks. The lower source levels in the harbour porpoise, together with the additional deliberate control over the sensitivity of its auditory system when the detection range is short, could reduce forward masking to such a low level that it allows for more graded click-evoked ABR amplitudes over a range of different source levels (figures 2b and 3). This may also explain why the echo-evoked ABR levels have amplitudes less affected by forward masking, and possibly also other actively controlled mechanisms, compared with what seems to be the case for delphinids.

In this study, we were able to estimate the ABR threshold for the returning echo of the cylinder at all three distances (figure 4). The three curves in figure 4b are not aligned, which we would expect them to be if no automatic gain control in the hearing system was

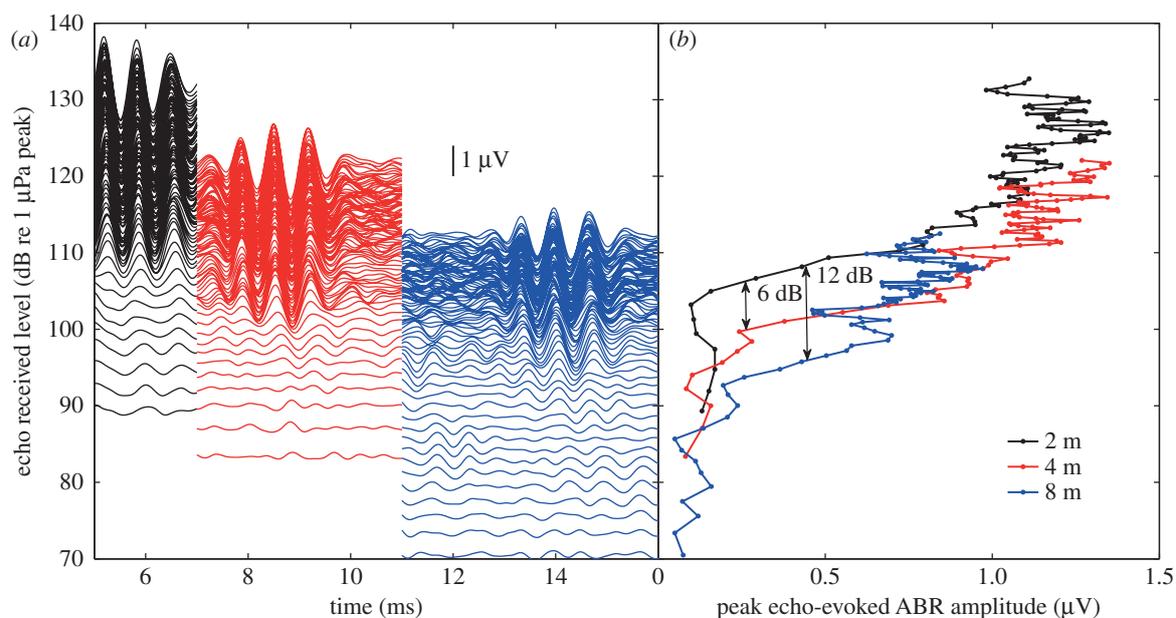


Figure 4. Waveform and amplitude of echo-evoked ABRs. (a) Echo-evoked ABRs as a function of the time elapsed since click production at time zero. The target distances are indicated above the x -axis. Black, red and blue represent the responses to echoes from the cylinder at 2, 4 and 8 m distance, respectively, as calculated from the speed of sound in water (1.5 m ms^{-1}). Each line represents a Hann-weighted average of 64 clicks plotted at the average echo-received level value on the y -axis. Neighbouring lines overlap each other by 48 measurements. (b) Peak echo-evoked ABR amplitudes as a function of the average echo-received level. The arrows indicated with 6 and 12 dB are graphical illustrations of the ABR threshold shift in relation to doubling the echolocation range.

taking place. The displacement of the echo level given similar echo-evoked ABR amplitudes for closer targets is 6 dB per halving of the echolocation range, which suggests that the auditory system is less sensitive at the closer ranges. From the above-mentioned discussion, we can conclude that this effect is not caused by forward masking as much as by a general reduction in hearing sensitivity during the reception of both outgoing click and echo. This change in ABR threshold probably occurs only when the animal's attention is focused directly on the detection task. In a previous experiment, the same porpoise was trained to station in front of a target simulator playing back incoming signals with a controlled delay and reduced, but fixed, level [33]. When the echo delay was varied, there was no sign of any adjustment in the porpoise hearing sensitivity to the echolocation click as measured with ABR. Nevertheless, the animal was not asked to make a decision or solve any task associated with the artificial echoes, and consequently was not required to focus on them.

The present study demonstrates simultaneous control over emitted signal level and the ABR amplitude of an echolocating animal. The results show that porpoises tend to reduce both the signal source level and hearing sensitivity as they approach the target. The effect in the auditory system seems to be caused by an overall reduction in the sensitivity of hearing during echolocation, affecting both the outgoing click and the returning echo, rather than forward masking from the outgoing click on the echo, as observed in the other delphinid studies. Together with previous investigations of other species of toothed whales, as well as bats, this indicates that hearing during echolocation is a much more dynamic process than has previously been thought. There is also a large difference in the animals' hearing, depending on

whether the animal is attending to a target. Therefore, conclusions drawn from psychophysical data on echolocation performance must be treated with great care, as the animals' hearing abilities may be greatly affected not only by whether the animal has been actively echolocating during the trials, but also by how difficult the echolocation detection or discrimination task is.

The fact that harbour porpoises can vary the experienced level of acoustic stimuli depending on the echolocation task has implications not only for our understanding of vertebrate hearing in general, but also more specifically for conservation biology of these animals. These data force us to re-evaluate how harbour porpoises and other cetaceans detect, interact with and sometimes are caught by fishing nets. Close to an object of interest, the reduction in source level and the increase in ABR threshold suggest that it will be more difficult for the porpoise to detect other objects in the vicinity compared with when the animal is focusing on objects further away. This indicates that it takes very involved considerations to make any estimation of, for example, the ranges at which a porpoise can detect fishing nets, and that any such numbers in the published literature should be examined extremely carefully and critically.

5. CONCLUSION

Our study shows a 3–5.4 dB reduction of the emitted signal intensities and simultaneously a 6 dB decrease in the auditory sensitivity for each halving of the distance between the porpoise and the target, meaning the animal exerts deliberate gain control on the transmitting and receiving side of its biosonar to stabilize the echo level independent of distance. This implies that the

porpoise biosonar is a flexible system using gain control that is adjustable to the echolocation task at hand.

Echolocation is the ideal sensory modality for the study of general principles of perception owing to the level of attention and control of outgoing as well as returning signals. These findings point to the possibility of actively adjusted sensory thresholds at a central level, which is important for understanding the role of attention on perceptual processes not only in hearing but for all sensory modalities. The data show that the animal compensates for the distance-dependent echo energy loss by simultaneously varying its ABR threshold and the emitted signal strength. Thus, the ABR threshold is flexible and not constant, as is commonly assumed. The ABR threshold depends substantially on the target distance and the attention of the animal while performing the echolocation task. This verifies that a harbour porpoise is able to vary the dynamic range of its biosonar not only on the transmitter but also the receiver side. These findings open up the opportunity for further studies on how toothed whales and other vertebrates can modify their hearing abilities depending on the difficulties of the detection task and the attention of the test subject.

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