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Audiogram Variability in Normal Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

In odontocetes, underwater audiograms have been obtained mostly in one or two individuals in a species. A representative number of animals should be investigated to document variability. In the present study, an attempt has been made to estimate the audiogram mean and scatter among normal bottlenose dolphins (*Tursiops truncatus*). Measurements were made in dolphins captured in the wild and kept in captivity for three to five months, using auditory evoked potential (AEP) technique (envelope-following response [EFR]) to measure underwater hearing thresholds. Fourteen subjects, 11 males and 3 females, provisionally from 3 to 15 years old, were investigated. Hearing thresholds were measured at frequencies from 8 to 152 kHz with ¼-octave steps. All the subjects had qualitatively similar audiograms, except one. The averaged audiogram featured the best sensitivity (the threshold below 50 dB re 1 µPa) at 45 kHz. Thresholds rose slowly to lower frequencies (up to 65 dB at 8 kHz) and steeply at higher frequencies (up to 97 dB at 152 kHz). Inter-individual standard deviations varied, depending on frequency, from 4.4 to 11.7 dB, mostly not more than 10 dB. One animal featured a significant hearing loss with increased thresholds at frequencies above 54 kHz. An analytical formula for a standard audiogram is suggested based on these data.

Key Words: odontocetes, bottlenose dolphin, *Tursiops truncatus*, audiogram, auditory evoked potentials, hearing loss

Introduction

The auditory system of odontocetes (toothed whales, dolphins, and porpoises) is known for unique capabilities with respect to sensitivity and frequency range. Traditionally, characteristics of the auditory system of odontocetes were studied using psychophysical techniques. After a pioneering study of Johnson (1967), who presented a detailed audiogram (threshold vs frequency function) of a bottlenose dolphin (*Tursiops truncatus*), either complete or partial audiograms of almost a dozen odontocete species were obtained: the harbor porpoise (*Phocoena phocoena*) (Andersen, 1970; Kastelein et al., 2002), killer whale (*Orcinus orca*) (Hall & Johnson, 1971; Bain & Dalhiem, 1994; Szymanski et al., 1999), Amazon river dolphin (*Inia geoffrensis*) (Jacobs & Hall, 1972), beluga whale (*Delphinapterus leucas*) (White et al., 1978; Awbrey et al., 1988; Johnson, 1992; Finneran et al., 2005), Pacific bottlenose dolphin (*Tursiops gilli*) (Ljungblad et al., 1982), false killer whale (*Pseudorca crassidens*) (Thomas et al., 1988), Chinese river dolphin (*Lipotes vexillifer*) (Wang et al., 1992), Risso's dolphin (*Grampus griseus*) (Nachtigall et al., 1995), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) (Tremel et al., 1998), tucuxi dolphin (*Sotalia fluviatilis*) (Sauerland & Dehnhardt, 1998), and striped dolphin (*Stenella coeruleoalba*) (Kastelein et al., 2003).

In addition to psychophysical methods, the auditory evoked potential (AEP) method has become widely usable for studying the hearing abilities of odontocetes. An advantage of this technique is that it does not require long preliminary training nor a cooperative subject. Initially used with odontocetes through an intracranial recording technique (Bullock et al., 1968; Bullock & Ridgway, 1972; Popov et al., 1986), lately this method was adopted for non-invasive investigation of odontocetes (Ridgway et al., 1981; Popov & Supin, 1985). With the use of the AEP method, audiograms were obtained in a number of odontocete species: the harbor porpoise (Popov et al., 1986), bottlenose dolphin (Popov & Supin, 1990a), beluga whale (Popov & Supin, 1987; Klishin et al., 2000), common dolphin (*Delphinus delphis*) (Popov & Klishin, 1998), Amazon river dolphin (Popov & Supin, 1990b), killer whale (Szymanski et al., 1999), Pacific white-sided dolphin (Au et al., 2003), striped dolphin (André et al., 2003), and the finless porpoise (*Neophocaena phocaenoides*) (Popov et al., 2005).

Most of those studies, both psychophysical and AEP, were performed using not more than one or two, sometimes three subjects. A small number of subjects is regular for investigation of cetaceans because in captivity these animals are rather rare and expensive. Real knowledge of hearing abilities of a species is not possible, however, without investigation of a sufficient number of individuals to assess both the mean and inter-individual variation of the measured parameters. For comparison, audiometric standards for humans are based on measurements of at least many dozens of individuals (see review in Fay, 1988; Yost, 1994)

In the present study, we tried to fill gaps to a certain extent. The goal of the study was to obtain audiograms in a large number of individuals of one and the same odontocete species—the bottlenose dolphin. Among odontocetes, this species is one of the most widely used for experimental studies, including bioacoustical studies, so knowledge of hearing abilities of this species seemed important. For such measurements, the AEP method was much more adequate than the psychophysical one because of the inability to carefully train animals that are kept in captivity a short period of time. Therefore, via the use of the AEP method, we obtained audiograms for these bottlenose dolphins through the catch-and-release program.

Materials and Methods

Subjects, Facilities, and Experimental Design

Experimental subjects were 14 Black Sea bottlenose dolphins (*Tursiops truncatus ponticus*), 11 males and 3 females, captured in the Black Sea during the summer seasons of 2004 and 2005 and kept in captivity by a catch-and-release program for short periods of time. Exact age of the animals was not known, but experienced veterinarians provisionally estimated them as 3- to 15-y-old. The animals were kept 3 to 5 mo in the Utrish Marine Station of the Russian Academy of Sciences, Black Sea coast, Russia. They were housed in a pool (9 × 4 × 1.2 m) filled with sea water. The care and use of all the animals was performed under the *Guidelines of the Russian Ministry of Science and Education* for the use of animals in biomedical research.

During the experiment, the animal was taken from the home pool and placed on a stretcher in a plastic bath (4 × 0.6 × 0.6 m) filled with sea water in such a manner that the dorsal surface of the head with the blowhole remained above the water surface. The walls and bottom of the bath and the water surface in front of the animal's head were covered by sound-absorbing material (rubber with cone-shaped closed air cavities) to reduce sound reflections and to make the stimulus sound field more uniform.

AEP Recordings

For non-invasive evoked-potential recording, suction-cup electrodes were used consisting of a 15-mm stainless-steel disk mounted within a 60-mm silicon suction cup. The active electrode was fixed at the dolphin's head surface, 5 cm behind the blowhole, above the water surface. The reference electrode was fixed at the dorsal or pectoral fin. The electrodes were connected by shielded cables to the input of a custom-made EEG amplifier that provided 88-dB gain within a frequency range of 200 to 5,000 Hz, as defined at -3 dB points of 6-dB/oct slopes. The amplified signal was digitized and collected using an NI-6040E data acquisition board (National Instruments) utilizing a sampling rate of 16 kHz and an acquisition window of 25 ms. To extract the signal from noise, the digitized signal was coherently averaged (1,000 sweeps averaged) using triggering from the stimulus onset.

Sound Signals

Sound signals were digitally synthesized at an update rate of 500 kHz and converted digital-to-analog by the same E-6040 board, amplified, attenuated, and played through a B&K 8104 transducer. The transducer was positioned at a distance of 1 m in front of the animal's head, near the front wall of the bath. The play-back channel was calibrated both before and after the experiments by positioning a calibrated receiving hydrophone (B&K 8103) at the same location as the animal's head.

The sound signals were 20-ms long trains of tone pips (Figure 1A). Each pip was enveloped by one 0.25-ms cycle of the cosine function; pip rate was 1,000 Hz. These parameters of modulation were chosen since amplitude-modulated (in particular, sinusoidally modulated) sounds of modulation rate around 1,000 Hz are effective to produce a robust, rhythmic AEP response (Supin et al., 2001) in odontocetes; using rather short tone pips instead of sinusoidally modulated tones resulted in a wider stimulus spectrum (Figure 1B), which is favorable to make the stimulus more effective to produce the response. Carrier frequencies of stimuli varied from 8 to 152 kHz, separated by ⅛-oct steps. These frequency values, rounded to 0.1 kHz, were taken as follows: 8.0, 9.5, 11.2, 13.5, 16.0, 19.0, 22.5, 27.0, 32.0, 38.0, 45.0, 54.0, 64.0, 76.0, 90.0, 108.0, 128.0, and 152.0 kHz. The stimuli were presented at a rate of 10 s^{-1}. Intensity of these stimuli is specified below in sound-pressure rms measures throughout all the burst

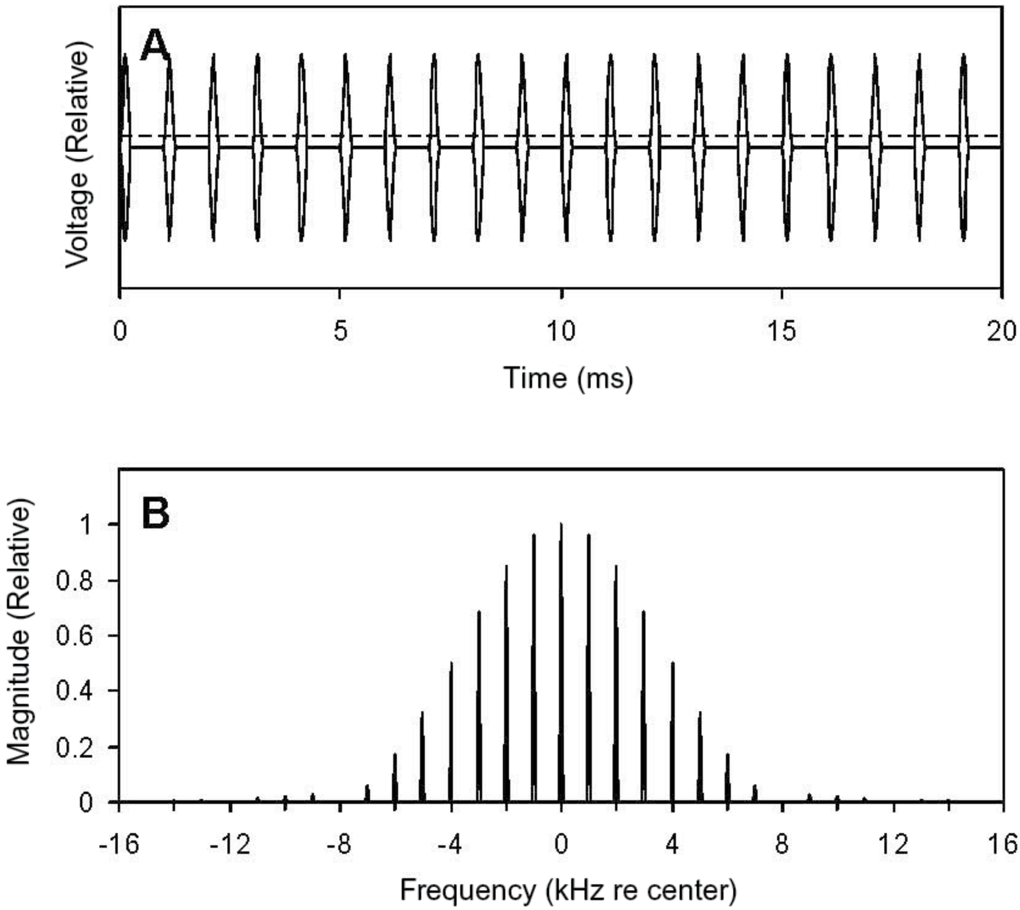

Figure 1. Pip-train stimulus used for threshold determination; A. signal envelope—horizontal dashed line shows the sound pressure rms value of the entire burst; B. signal frequency spectrum—frequency is specified in kHz relative to the carrier frequency. Spectrum magnitude is specified in relative units.

duration. Note that for this particular waveform, the rms value is ~ 0.22 (-13.3 dB) re pip peak (see Figure 1).

Even though the walls of the bath were covered with sound-attenuating material, some sound reflections from the bath walls and water surface were inevitable, thus resulting in interference patterns in the small enclosed space. To assess the influence of these interference patterns on the stimulus parameters, sounds were monitored by a B&K 8103 hydrophone near the animal's head. The monitoring showed that despite the sound reflections within the bath, the real modulation depth of the stimuli remained not less than 70 to 80%, and local sound levels varied by not more than 5 dB.

Threshold Evaluation and Audiogram Derivation

For threshold evaluation, stimulus level was decreased from obviously supra-threshold to sub-threshold values. A 16-ms part of the rhythmic evoked-potential response to the stimulus, from 6 to 22 ms, was Fourier transformed to obtain its frequency spectrum. The magnitude of the 1-kHz peak was plotted as a function of stimulus intensity, and an oblique near-threshold part of the plot was approximated by a straight regression line (the criteria for selection of a range for straight-line approximation were explained in more detail by Supin et al., 2001). The intersection of this line with the zero-amplitude level was adopted as a threshold estimate. This threshold-determination procedure was repeated at different carrier frequencies. The resulting threshold vs frequency function represented the audiogram.

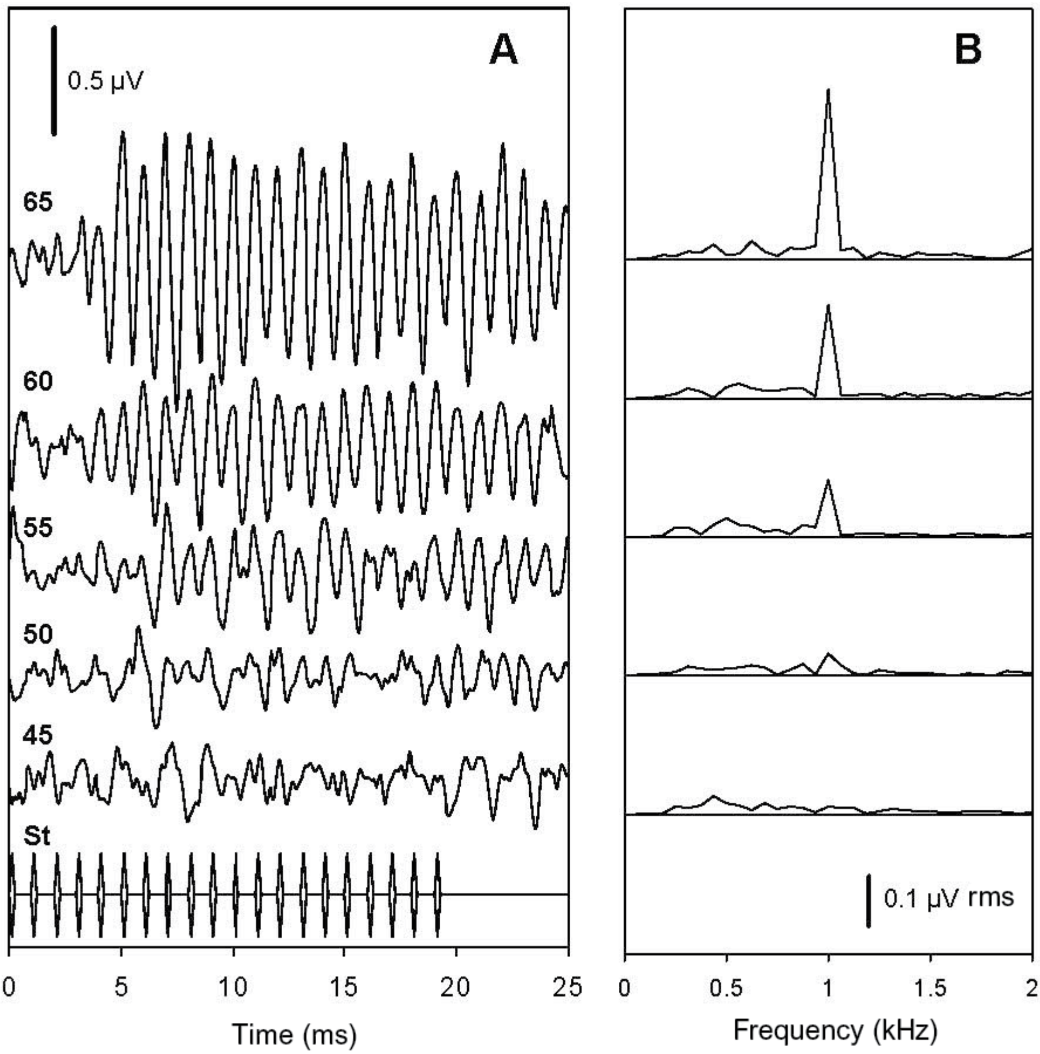

Figure 2. A. examples of EFR to pip-train stimuli of various intensities; stimulus 90 kHz, intensities from 65 to 45 dB rms re 1µPa as indicated; St – stimulus envelope. B. frequency spectra of responses presented in (A), analysis window from 6 to 22 ms after beginning the record.

Results

AEP Waveform and Threshold Determination

Rhythmic pip trains evoked robust, rhythmic responses, which followed the pip rate (i.e., the envelope-following response [EFR]). Typical EFR records are exemplified in Figure 2A. Both the start and end of the response appeared with a few ms lag relative to the stimulus. This lag provided a good opportunity to check artifact contamination of records. The response-free initial part of the records showed clearly that the records were not contaminated with electromagnetic artifacts; as well, the response persistence until about 5 ms after the stimulus ended showed the physiological nature of the response.

The responses were intensity dependent, as Figure 2 exemplifies, at stimulus intensities from 65 to 45 dB re 1 µPa. With intensity decrease, the responses decreased until it disappeared in noise.

Frequency spectra of the records presented in Figure 2A are shown in Figure 2B. These spectra were obtained by Fourier transform of a part of the record, from 6 to 22 ms. This 16-ms window contained a major part of the EFR record but did not contain the latency and the initial transient part of the response. At stimulus intensities above 50 dB, all the spectra featured a definite peak at the stimulus pip rate of 1 kHz. At the intensity of 50 dB, this peak was comparable with the spectrum noise level, but still detectable, and at the intensity of 45 dB, it completely disappeared.

Figure 3 demonstrates the threshold determination procedure. The magnitude of the 1-kHz peak of the response spectrum was taken as an estimate of the response magnitude and plotted against the stimulus level. The near-threshold part of the plot featuring obvious dependence on intensity, from 50 to 65 dB, was approximated by a straight regression line; the point at 45 dB was not included in the approximation range because of an obvious absence of a response. The obtained regression line crossed the zero-amplitude level at a point of 48.6 dB. This value was accepted as the threshold estimate.

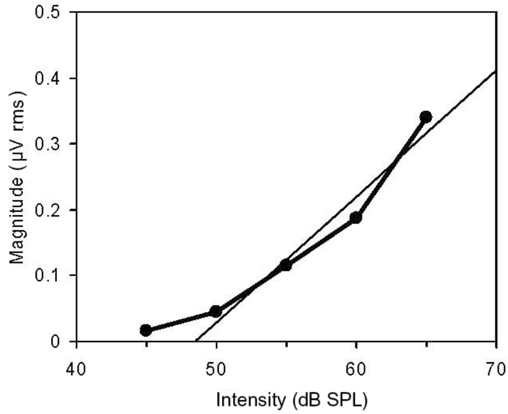

Figure 3. An example of threshold determination using the regression-line technique, with the same sample as in Figure 2; response magnitude (rms value of 1-kHz spectrum component) is plotted as a function of stimulus intensity. The regression line is drawn through points 50 to 65 dB, crossing the zero level at 48.6 dB.

Audiograms

Using the same procedure, thresholds were determined at a variety of sound frequencies, from 8 to 152 kHz, in all investigated animals. The majority of the audiograms were obtained with ¼-oct steps in the frequency; however, in some cases, because of the limited time available for experimentation, a low-frequency part of the audiogram was obtained with ½-oct steps (Table 1). In the majority of the subjects, conditions at the facility and care for the animals allowed only one complete measurement run, except for Subjects #1 (three runs), 2, 6, 10, and 12 (two runs each). For these five subjects, the mean of the three or two runs, respectively, was taken as the audiogram. For all other subjects, the sole available thresholds vs frequency function was taken as the audiogram.

All audiograms collected in the manner described above are summarized in Figure 4A. They grouped to a rather compact family, although inter-individual scatter at some frequencies was as

Table 1. Audiometric data for 14 individual bottlenose dolphins using auditory evoked potential methods; thresholds are presented in dB rms re 1µPa.

Frequency (kHz)	Subjects													
	#1	#2	#3	#4	#5	#6	#7	#8	#9	#10	#11	#12	#13	#14
8.0	74.4	61.9	75.9	--	--	81.8	--	66.6	--	51.5	63.8	61.1	60.8	57.5
9.5	75.5	58.5	--	--	--	--	--	--	--	50.6	67.7	50.1	69.7	65.9
11.2	66.5	58.6	81.4	77.8	--	75.8	--	66.6	64.7	50.7	67.1	50.15	57.1	67.2
13.5	69.7	58.7	--	--	--	--	--	--	--	60.5	75.1	44.3	58.8	62.7
16.0	60.5	--	55.4	67.6	65.8	51.5	--	64.9	49.3	61.8	71.7	41.7	61.2	62.0
19.0	60.3	53.9	--	--	--	--	--	--	--	65.5	66.4	42.9	52.3	51.7
22.5	61.1	57.6	51.7	52.9	58.8	61.0	67.0	60.0	56.4	61.4	56.3	43.5	46.2	56.2
27.0	57.6	54.4	--	--	--	--	--	--	--	62.1	53.2	48.9	45.7	53.8
32.0	55.9	58.9	58.2	55.6	56.4	57.8	--	52.3	52.7	54.9	61.0	46.2	51.3	47.8
38.0	52.8	58.2	45.4	50.3	65.1	57.2	60.9	41.5	45.6	48.2	57.9	46.7	44.1	46.4
45.0	51.7	58.8	44.4	54.8	58.0	56.0	50.1	45.0	45.2	47.4	50.8	49.6	45.5	47.3
54.0	53.9	55.5	43.7	54.4	54.7	53.1		52.6	49.9	47.8	50.1	50.7	41.2	42.2
64.0	54.0	73.3	46.9	49.4	61.0	58.1	58.2	54.1	47.3	54.9	53.2	48.4	47.6	52.1
76.0	52.2	76.4	47.2	49.0	64.4	60.7	60.2	--	49.4	57.0	52.0	53.1	47.9	56.1
90.0	52.3	83.0	53.6	61.0	65.6	64.4	65.1	--	52.1	61.4	55.6	61.6	54.2	57.7
108.0	55.9	93.4	53.3	64.5	72.7	69.6	61.4	68.1	57.9	65.0	60.3	62.4	56.9	61.7
128.0	69.4	99.5	63.8	79.3	68.8	76.6	75.3	--	67.6	70.0	65.7	69.8	68.7	70.3
152.0	102.9	113.0	100.0	83.9	89.7	83.5	100.0	99.6	97.2	100.5	99.7	99.0	94.9	101.9

much as ± 15 dB. The only obvious deviation from this family was audiogram #2, which featured a significant increase of thresholds at high frequencies above 54 kHz. Therefore, we adopted all the individual audiograms, except #2, as a basis to calculate the mean normal audiogram and normal inter-individual variation. The audiogram #2 was adopted as a deviation from the norm.

The inter-individual mean, standard deviation (SD), and standard error of mean (SE) obtained from all (except #2) of the individual audiograms are presented in Figure 4B. The mean audiogram featured the lowest threshold (slightly below 50 dB re 1 μPa) at a frequency of 45 kHz. Thresholds rose slowly to lower frequencies (up to 65 dB at 8 kHz) and steeply to higher frequencies (up to 97 dB at 152 kHz). Inter-individual standard deviations varied, depending on frequency, from 4.4 to 11.7 dB, mostly not more than 10 dB.

Age-Dependence of Hearing Sensitivity

To compare audiograms of subjects of different ages, we used two criteria: (1) the best sensitivity estimated as a mean of six threshold values at frequencies from 32 to 76 kHz (i.e., in the frequency region of the lowest thresholds), and (2) cutoff frequency estimated as a frequency such that the threshold reached a level of 80 dB re 1μPa (i.e., about 30 dB above the lowest mean threshold).

Dependence of these two estimates on the subject's age is presented in Figures 5A and 5B, respectively. Except for subject #2 (the dot additionally marked by a circle), the plots did not show a definite dependence on age for all subjects. For the best-sensitivity values, the regression line drawn by all points (except that of the subject #2) ran at a level around 50 dB and had a very small slope of 0.36 ± 0.30 dB/y. For the cutoff values, the regression line drawn also excluding the point for subject #2, ran at a level of 135 to 140 kHz and also had a very small slope of 0.53 ± 0.32 kHz/y. The difference from zero was not statistically significant for both the slopes. Thus, the majority (except one) of the investigated animals did not display a noticeable dependence of hearing

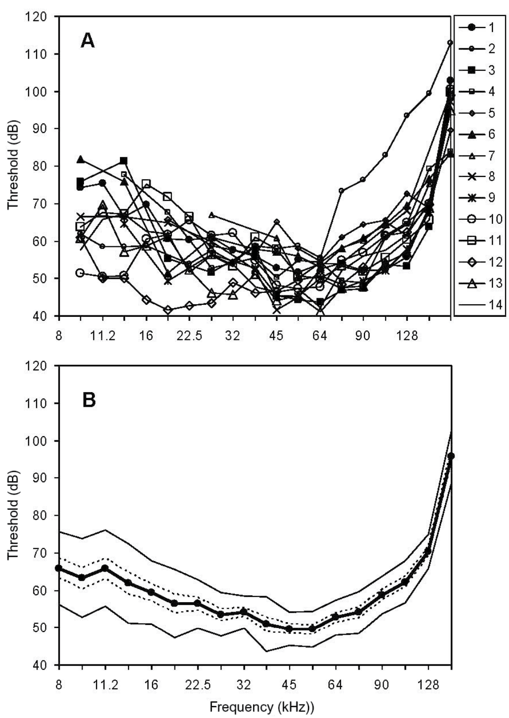

Figure 4. A. individual audiograms of 14 bottlenose dolphins; subject identification numbers are indicated in the legend. B. the averaged audiogram of 13 subjects, #1 and #3 to #14 (solid line with dot symbols); thin lines – standard deviation area, dashed lines – standard error area.

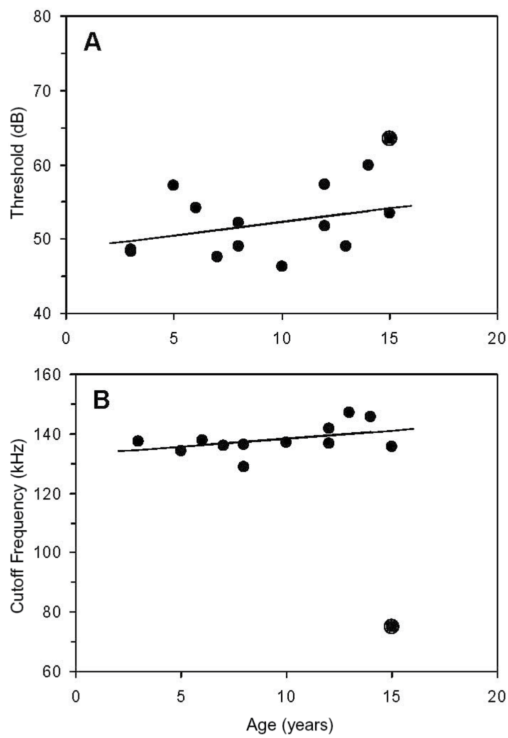

Figure 5. Hearing parameters' dependence on age; A. mean threshold within a frequency range from 32 to 76 kHz. B. cutoff frequency at a level of 80 dB re 1 μPa. Dots – data for individual subjects, straight lines – regression line drawn through 13 of 14 presented dots, except the dot for subject #2 (marked by circles).

characteristics by age. On the other hand, the age of the only animal (#2) that had a noticeable hearing loss (the 80-dB cutoff frequency at 74 kHz, contrary to 135 to 140 kHz in others) was estimated at about 15 y (i.e., at the upper boundary of the age range).

Discussion

Features of the Audiograms and Applicability of the Averaged Audiogram as a Standard

General features of the audiograms of bottlenose dolphins have been described already in a few investigations, both psychophysical and AEP (see "Introduction"). The audiograms presented herein agree well with those descriptions and feature the same key properties: a wide frequency range (above 150 kHz), the best sensitivity at rather high frequencies (tens of kHz), a steep increase of thresholds above the optimal frequency, and a slow increase below the optimal frequency.

It is noteworthy that the audiograms obtained herein with the use of the AEP method featured very low thresholds. In many audiograms, the best thresholds were as low as 40 dB, and the lowest point of the averaged audiogram was near 50 dB re 1 µPa ($6.5 \cdot 10^{-14}$ W/m^2). These values are of the same order as the lowest thresholds found in psychophysical measurements (Johnson, 1967). This result shows that the AEP method is appropriate for audiometric measurements in odontocetes, and thresholds obtained with this method can be used to elaborate a standard audiogram.

Therefore, we suggest adopting the averaged audiogram presented above as a standard audiogram for the bottlenose dolphin. More precisely speaking, this standard is valid for the investigated subspecies, the Black Sea bottlenose dolphin. A question remains open—that is, to what extent this standard is valid for other subspecies of the species *T. truncatus*. As a first approximation, the inter-subspecies differences of hearing abilities may be neglected. Validity of this assumption can be checked when similar measurements in other subspecies become available.

Analytical Expression for the Normal Audiogram

If an audiogram is adopted as a standard of normal hearing, it may be helpful to approximate it by a certain simple analytical function. Such approximation makes comparison of any particular result with the standard easier. Best of all is the use of a function which manifests the real physiological processes determining the dependence of threshold on sound frequency. Unfortunately, it is hardly possible at the present level of knowledge, and, even if it were possible, the analytical expression might be too complicated. For practical purposes, however, an empirically adjusted function, arbitrarily chosen and as simple as possible, can be used.

We suggest approximating the low-frequency branch of the audiogram (below the lowest-threshold point) by a linear function:

$$T_l(g) = a(g - m) + b\,,$$

and the high-frequency branch (above the lowest-threshold point) by an exponential function:

$$T_h(g) = \exp[c(g - m)] + b\,,$$

where, T is threshold in dB; g is the octave measure of frequency; m is the octave-specified position of the minimum-threshold point on the frequency scale (i.e., the term $[g - m]$ is the deviation from the minimum-threshold frequency); a and c are constants determining the steepness of the low- and high-frequency branches, respectively; and b is a constant determining the shift of both branches along the ordinate scale. A function combining both the low- and high-frequency branches of the audiogram may be merely expressed as

$$T(g) = \max[T_l(g); T_h(g)].$$

We adjusted all these constants to reach the best fitting of the analytical expression to the averaged audiogram according to the least-mean-square criterion. The best fitting was achieved at a = -6.9 dB/oct, b = 48.9 dB re 1µPa, c = 2.24 ln (dB/oct), m = 5.55 oct, and g is expressed in octaves re 1 kHz. The obtained analytical function is shown in Figure 6 along with the averaged audiogram and its SE area. The figure demonstrates that the function really fits the experimental data and runs mostly within the SE area. Thus, we suggest to adopt a function

$$T = \max\{-6.9(g - 5.5);\ \exp[2.24(g - 5.5)]\} + 48.9\,,$$

(specifying g in octaves re 1 kHz and T in dB re 1 µPa) as an analytical approximation of the normal audiogram of bottlenose dolphins. Of course, the precision of constant specification used above does not mean that the normal audiogram is really derived so precisely. For practical use, rounded constant values as a = -7 dB/oct, b = 50 dB, c = 2.2 ln (dB/oct), and m = 5.5 oct may be satisfactory. This rounding does not influence significantly the

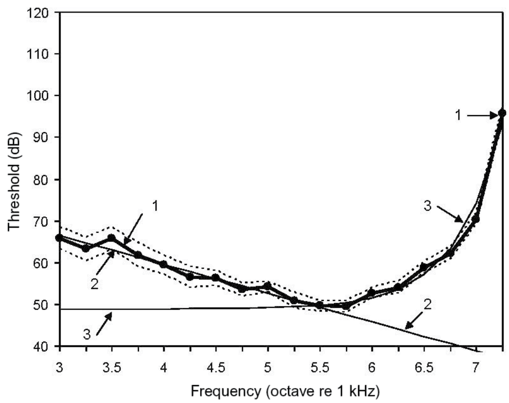

Figure 6. Analytical approximation of the averaged audiogram; 1 (solid line with dot symbols). experimental averaged audiogram (dashed lines – the standard error area), 2. linear function approximating the low-frequency branch, and 3. exponential function approximating the high-frequency branch.

predicted threshold values. Moreover, the approximation function used herein was chosen arbitrarily as a first step. It does not exclude that a variety of other functions may be suggested for approximation of the normal audiogram.

Hearing Loss in Dolphins

Recently, there were reports that a significant hearing loss, mostly in high frequencies, is not rare in odontocetes (e.g., belugas, bottlenose dolphins, and a false killer whale) kept in captivity over a long period of time (Finneran et al., 2003, 2005; Houser & Finneran, 2005; Yuen et al., 2005). Presumably, it was associated with their age that was up to a few decades.

In our study, only one of the subjects (#2) featured noticeable deviation from all others: it had a significant threshold increase at frequencies above 54 kHz. Thirteen of 14 subjects featured audiograms which did not deviate very much from one another, so all of them could be considered as normal within a certain scatter range. Since all the subjects were not kept in captivity for very long, they can be considered to be representatives of a wild population.

Thus, in regards to hearing loss, there was a significant difference between the long-kept captive animals mentioned above and the briefly kept animals (presumably representatives of a wild population) investigated herein. At least a few potential reasons may be considered as responsible for this difference: (1) subjects investigated herein were not old enough (probably not older than 15 y) to feature a significant hearing loss; (2) significant hearing loss in captive populations was associated with some conditions of being kept in captivity (e.g., the diet, medical treatment, etc.); and (3) animals with significant hearing loss had less ability to survive in the wild and were eliminated from the investigated population.

At present, we do not have enough data to decide which of these reasons is really responsible for the difference between the investigated long-kept and briefly kept populations. The fact that the only animal featuring a noticeable hearing loss was rather old (about 15 y) indicated a possibility of age-induced loss, but it cannot be adopted as evidence since other subjects of similar ages had normal hearing. The influence of environmental conditions on hearing can be estimated only as a result of specially designed investigations. It is obvious that such investigations must be carried-out for establishing noise standards for keeping cetaceans in captivity and for establishing age-dependent standards of normal hearing.

Acknowledgments

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