# Audiogram of a formerly stranded long-finned pilot whale (*Globicephala melas*) measured using auditory evoked potentials

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## SUMMARY

**Long-finned pilot whales are highly social odontocetes found in temperate and subpolar regions. This species is particularly known for its interaction with fisheries as well as its mass strandings. Recent tagging work has provided some information about pilot whales in the wild but, even though they have been successfully kept in captivity, little is known about their sensory capabilities. This study investigates the hearing abilities of a rehabilitated 2 year old male long-finned pilot whale. A complete audiogram was collected using auditory evoked potential techniques that included measurements of nine frequencies from 4 to 100 kHz presented as sinusoidally amplitude-modulated tones. The results indicated that the region of best hearing was between 11.2 and 50 kHz and the subject had relatively poor high frequency hearing compared with other odontocete species. This study emphasizes the importance of collecting basic hearing measurements from new species, understanding diagnostic life histories as well as continuously increasing the sample size of audiometry measurements within and between odontocete species as animals become available.**

Key words: long-finned pilot whale, hearing, auditory evoked potentials, acoustics, marine mammals.

## INTRODUCTION

Pilot whales have a tendency to follow conspecific 'pilot' leaders, which may explain their common name and also make them particularly vulnerable to drive fisheries and mass stranding events (Kritzler, 1952; Fehring and Wells, 1976; Ellis, 1982). Long-finned pilot whales (*Globicephala melas* Traill 1809) inhabit the deep waters of the North Atlantic and feed on squid and other prey normally found down to 600 m (Baird et al., 2002; Aguilar Soto et al., 2008). They do not usually dive as deeply as other pelagic odontocete cetaceans such as beaked whales or sperm whales (Heide-Jorgensen et al., 2002). Long-finned pilot whales are very similar to the short-finned pilot whale (*Globicephala macrorhynchus*) and differ primarily by the habitats they occupy, the long-finned pilot whale being found primarily in subpolar oceanic regions while the short-finned pilot whale is found in tropical and subtropical regions. Both species are classified as Data Deficient on the IUCN Redlist and have been included in the 2005 Atlantic pelagic longline take reduction team initiated under the Marine Mammal Protection Act. Early reports (Sergeant, 1962) on pilot whales indicated that they were excellent animals for taxonomic studies because they are 'common, widely distributed and prone to strand in herds' (p. 412). Both male and female long-finned pilot whales can reach over 6 m in length, appear black with a lighter color blaze in the chest area, and have a distinct and exaggerated bulbous melon (Olsen, 2009) that primarily grows post-partum (Sergeant, 1962). An infant pilot whale, prior to growing the distinctively large melon, may resemble a false killer whale. While recording and analysis of the acoustic signals of the pilot whale have been carried out for over 40 years (Scheville, 1964; Busnel and Dziedzic, 1966), and the whales are assumed to echolocate (Evans, 1973), hearing studies have not been attempted despite the

fact that they have long been kept successfully in captivity (Kritzler, 1952; Brown and Norris, 1956; Brown, 1960; Bowers and Henderson, 1972). Hearing among members of the subfamily *Globicephalinae* such as false killer whales, pilot whales, melon-headed whales, pygmy killer whales and Risso's dolphins have not been extensively studied. Two studies on the hearing of single adult false killer whales demonstrated high frequency hearing up to 100 kHz (Thomas et al., 1988) for a fully adult animal along with the development of presbycusis with increased age and a lowering of the upper frequency thresholds to near 30 kHz in an older animal (Yuen et al., 2005). A study of an infant Risso's dolphin indicated high frequency hearing up to 150 kHz (Nachtigall et al., 2005) with an apparent similar loss of hearing in an older animal with upper frequency limits just below 100 kHz (Nachtigall et al., 1995). The hearing of the pygmy killer whale, melon-headed whale and pilot whale has not yet been measured.

Most young odontocetes hear frequencies over 100 kHz (Nachtigall et al., 2000; Houser and Finneran, 2006) and may lose their high frequency hearing with age (Ridgway and Carder, 1997). While behavioral experiments remain the ideal method of evaluating hearing and measuring audiograms, more rapid measurements can be obtained using the envelope following response (EFR) auditory evoked potential (AEP) procedure (Supin et al., 2001), which measures the brain waves in response to patterned sounds (Nachtigall et al., 2007). Behavioral experiments require captive trained animals and up to a year to complete, while AEP experiments can be conducted rapidly. AEP measurements can even be gathered effectively with catch-and-release experiments, during temporary capture and measurement on board a boat (Nachtigall et al., 2008), and only require 90 min to complete an audiogram. Fortunately, the AEP experiments provide data comparable to that of the behavioral

experiments (Yuen et al., 2005; Houser and Finneran, 2006) and can be used with animals that are not fully trained or adapted to laboratory and captive environments.

Estimation of the hearing parameters of a species or population is best done using a large sample size in a quiet laboratory environment. Unfortunately these experimental conditions are rarely available when dealing with cetaceans. While the quiet laboratory environment with many test subjects is the ideal baseline setting for determining species hearing thresholds, most marine mammals' audiograms, particularly odontocetes, have been estimated from single animals measured in environments of opportunity. Recently most of these hearing measurements have been conducted rapidly using AEPs (Nachtigall et al., 2007). Species or population hearing estimates and variability must be estimated from individual animal data gathered separately, with factors such as age, health and medical record taken into account.

The current study involved a 2 year old male long-finned pilot whale (*Globicephala melas*) that was rescued from a stranding near the beach of Nazaré, North of Lisbon, Portugal on 27th August, 2006. The animal was very young, not yet weaned, and in poor health. The whale was first treated at the Sociedade Portuguesa de Vida Selvagem (SPVS) facility in Quiaios – Figueira da Foz; then transferred to the Lisbon Zoo in November 2006 where veterinary treatment continued. Through an extraordinary effort from the zoo staff, the animal's health stabilized and the animal began eating solid fish and squid after about a year. The subject was subsequently trained to remain still at the surface while frequencies between 4 and 100 kHz were presented and the audiogram was measured using the AEP EFR procedure.

## MATERIALS AND METHODS
### Subject
During its rehabilitation, the whale was trained to station, gate, target control, slide-out and bow; the medical training involved blood and gastric sampling, chuffing for blowhole samples and ultrasound measurements. During the time of the study, the animal also participated in the zoo's dolphin public presentations three times per day performing bows and a beaching at the end of each show. The subject was further trained to remain still at the surface and accept soft latex suction cup attachments in order to examine its hearing using AEP (Fig. 1). Hearing tests were conducted from 27th April to 3rd May, 2009 in the holding pool of the main show area of Lisbon Zoo (Fig. 2A) at quiet times between, before and after the daily dolphin presentations.

### Tank and background noise levels
The back pool of the Lisbon Zoo dolphinarium measured 10 m × 36.5 m (Fig. 2A) and 6 m deep, and was filled with artificial sea water. Water pumps were located over 100 m from the dolphinarium providing a quiet environment with limited ambient noise. It was assumed that the background noise measurements would be very similar between pools. Background noise measurements taken prior to the hearing measurements revealed a quiet background noise environment. A Reson TC-4032 hydrophone (–170 dB re 1 V/mPa; Slangerup, Denmark) was used to measure the ambient noise of the experimental pool. One minute files were recorded on a Microtrack II 2 channel digital recorder (M-Audio, Irwindale, CA, USA) with a sampling rate of 96 kHz. One channel had a 15 dB gain while the other channel had no gain to compensate for alienated signals. Files were then transferred to a laptop and 10 files of 1 s each were extracted using Adobe Audition 3.0, analyzed and averaged using a customized Matlab algorithm.



Fig. 1. Experimental set-up with the animal wearing electrodes embedded in latex suction cups. The subject remained at the surface 1 m away from the hydrophone placed 30 cm below the surface.

### Acoustic stimulus generation and presentation
Both acoustic stimulation and electrophysiological measurements were collected using the system described by Taylor and colleagues (Taylor et al., 2007), which has been used both with captive animals (Mooney et al., 2008) and during capture–release experiments (Nachtigall et al., 2007). At the beginning of each session, the animal was positioned at the water surface parallel to the side of the pool and approximately 50 cm away from the tank wall. Three latex suction cups were positioned on the back of the animal and the acoustic stimulation was presented in front of the subject 1 m away from its auditory meati (Fig. 1). Two hydrophones were used to present the acoustic stimulation: an ITC-1032 (Santa Barbara, CA, USA) for frequencies between 4 and 50 kHz and a Reson TC-4013 for frequencies above 50 kHz. Because of the curvature of the experimental pool, the hydrophones were positioned approximately 1 m away from the tank wall in order to be in front of the animal at a 30 cm depth. Each hydrophone was calibrated prior to the hearing measurements.

For the audiogram measurements, sound stimuli were sinusoidally amplitude modulated (SAM) tone bursts. The tones were digitally synthesized using a customized Labview program and a National Instruments PCMIA-6062 E DAQ card (Austin, TX, USA) implemented in a laptop. The tone bursts were 19 ms in duration followed by 30 ms of silence so that the acoustic stimuli were presented at a rate of $20\,\mathrm{ms^{-1}}$. The tones were modulated at a rate of 1000 Hz based on the modulation rate transfer function obtained with other species and the update rate was 256 kHz for frequencies below 50 kHz and 512 kHz for carrier frequencies above 50 kHz. Output voltages were measured as peak-to-peak voltage ($V_{\mathrm{p-p}}$) using a Tektronix TPS 2014 oscilloscope (Beaverton, OR, USA). The measured voltages were then converted to peak-equivalent root mean square (r.m.s.) voltage by subtracting 15 dB. This peak-equivalent r.m.s. voltage was then used to calculate the sound pressure level (SPL) for each individual frequency (Mooney et al., 2008). SPLs were then varied using a Hewlett-Packard (Palo Alto, CA, USA) P-350D attenuator which could attenuate in 1 and 10 dB steps.

### Electrophysiology
The animal's response to the acoustic stimulus was recorded using three Grass 10 mm gold EEG electrodes (West Warwick, RI, USA)
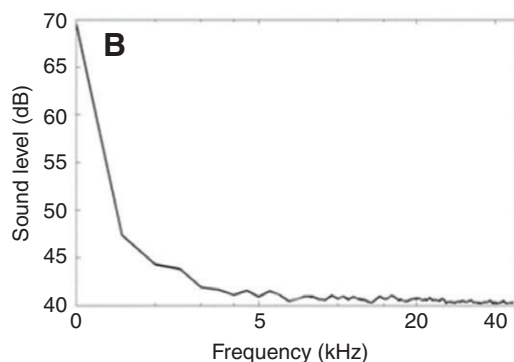
Fig. 2. (A) Experimental pool in the back of the main show pool at Lisbon Zoo (indicated by the arrow). (B) Tank background noise calculated with a 1024 point fast Fourier transform (FFT) and collected with a Reson TC-4032 hydrophone with a 96 kHz sampling rate. Sound levels are expressed in dB $1 \mu Pa^2 \, Hz^{-1}$.

embedded in latex suction cups. The active electrode was positioned 3–5 cm posterior to the blowhole of the subject, the second electrode on the back and the third one acted as a ground and was positioned on the dorsal fin of the animal (Fig. 1). The three sensors were connected to a Grass CP-511 bio-amplifier where the signal was amplified 10,000 times and filtered from 300 to 3000 Hz. The response was filtered again with a Krohn-Hite 3384 by-pass filter (Brockton, MA, USA) with the same settings. Using the same card that generated the acoustic stimulus, the brain response was then digitized at 16 kHz and transferred to the same laptop computer. A record consisted in collecting and averaging 1000 responses that were 26 ms each in duration and triggered with the acoustic stimulus played to the animal.

### Audiogram threshold determination and data analysis

A total of 16 sessions were required to complete the experiment, each session lasting 30–45 min. A session usually consisted of collecting thresholds for two frequencies and each threshold was measured at least once. A threshold was evaluated using data obtained from an average of seven trials or records for each of the nine stimulus frequencies. The SPL for the first trial was selected according to previous odontocete audiograms (Thomas et al., 1988; Nachtigall et al., 2005; Nachtigall et al., 2008) and was usually 10–20 dB above the published thresholds. The SPL was then varied in 5–10 dB steps until no evoked potential was observed for at least two trials (Fig. 3). Previous work has shown that SAM tone bursts generate an EFR. For each frequency and SPL, a 256 point fast Fourier transform (FFT) was performed on a 16 ms window of the corresponding EFR. Each FFT provided a frequency spectrum and the peak response at 1000 Hz (Fig. 4A) was used to estimate the response of the subject to the acoustic stimulation. For each frequency, the peak responses at 1000 Hz were plotted against the corresponding SPL. A linear regression addressing the data points was extended to calculate the hypothetical zero value which would be used to predict the threshold (Fig. 4B). An absolute threshold could not be obtained with AEP because of the inherent biological electrical noise; nevertheless comparisons between behavioral and auditory brainstem response (ABR) techniques have shown that the two techniques yield similar results (Yuen et al., 2005).

### RESULTS

The deep waters of the experimental pool of the Lisbon Zoo dolphinarium provided a quiet environment for the hearing measurements. Most of the ambient noise above 2000 Hz was below 40 dB (Fig. 2B) and below the sensitivity of the recording equipment, and represented an excellent environment for absolute hearing measurements (Au et al., 2002).

The EFR obtained from the animal followed the typical response obtained with other species (Nachtigall et al., 2005; Popov et al., 2005; Mooney et al., 2008) with a delay of 4–6 ms which corresponded to the latency of the neurophysiological response. When the sound stimulus SPL was well above the threshold level, a completely formed response was recorded and as the SPL decreased, the response disappeared in the ambient biological noise. Fig. 3 shows the EFR response to a SAM tone with a 32 kHz center frequency. At 90 dB, the EFR was complete and closely
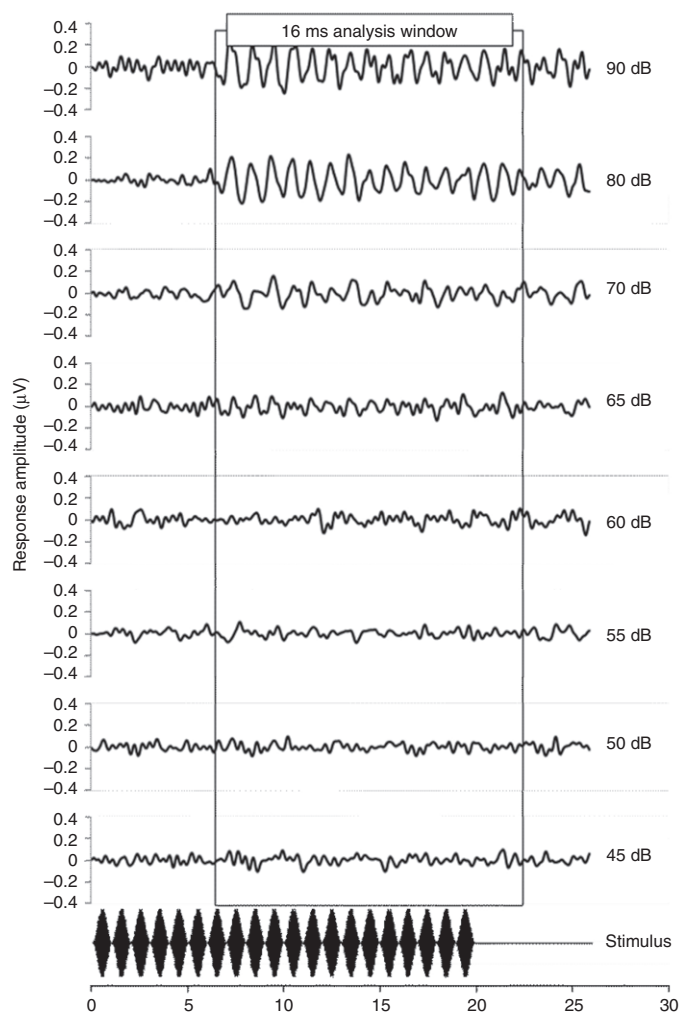


Fig. 3. Sinusoidal envelope of stimulus and envelope following response (EFR) to threshold of 32 kHz tone from 90 to 45 dB re. 1 μPa.
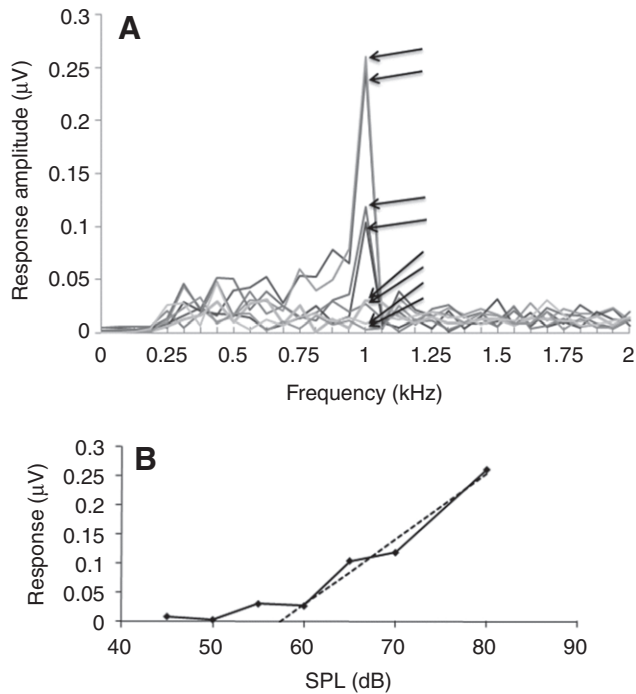
Fig. 4. (A) FFT of the EFR amplitudes of a long-finned pilot whale. Response (µV r.m.s.) is to a sinusoidal amplitude-modulated (SAM) tone with a 32 kHz carrier frequency and a 1 kHz modulation rate. (B) Plot of the EFR response amplitude *versus* sound pressure level (SPL) for the 32 kHz SAM tones (solid line, diamonds) and the linear regression (broken line) calculated. The threshold for 32 kHz corresponded to the intersection of the regression line with the hypothetical zero response value. The linear regression was based on points from 60 to 80 dB. The response was calculated here to be at 57 dB re 1 µPa.



Fig. 5. Audiogram of the pilot whale stationing at the surface using auditory evoked potential (AEP) techniques.

followed the envelope of the acoustic stimulus; however, the EFR started becoming less visible at approximately 65 dB and was completely indiscernible from the ambient noise at 60 dB. The FFT of the signal indicated similar results where the amplitude of the EFR peak at 1000 Hz increased with SPL (Fig. 4A). The linear regression indicated that the threshold for that specific frequency was similar to both the EFR and the FFT and was calculated to be at 57 dB (Fig. 4B).

The complete audiogram (Fig. 5) had the common U-shape found in mammals and was overall similar to other odontocete audiograms (Johnson, 1967; Thomas et al., 1988; Szymanski et al., 1999; Kastelein et al., 2002; Yuen et al., 2005) with a steep slope in the high frequency region and a more leveled slope in the lower frequencies. The region of best hearing was found to be between 11.2 and 50 kHz with thresholds below 70 dB (Table 1). The best hearing was found at 40 kHz with a 53.1 dB threshold. Overall threshold measurements had low values mainly because of the low ambient noise of the pool where the measurements were conducted. The slope of the thresholds became very steep above 50 kHz and the poorest sensitivity was measured at both ends of the frequency spectrum with 77 dB at 4 kHz and 124 dB at 100 kHz.

## DISCUSSION

The hearing measurements obtained with this *G. melas* indicate that the animal had overall hearing abilities similar to those of other odontocete species. The U-shaped audiogram with a region of best hearing up to 50 kHz and threshold values in the 50 dB range
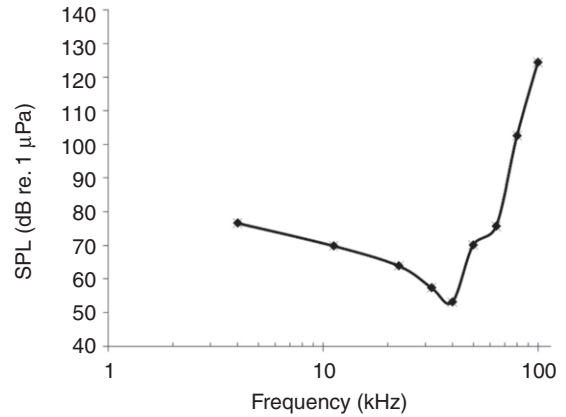
emphasize the quality of threshold measurements in a quiet environment. The high frequency hearing region was found to be relatively poor compared with the hearing capabilities of other toothed whales that can hear up to 150 kHz (Johnson, 1967; Nachtigall et al., 2005; Popov et al., 2005). Although these results represent the first audiogram for this species, one should interpret these data carefully. For most odontocetes, only one or two audiograms are available per species (Nachtigall et al., 2000). Extensive work with *Tursiops truncatus* has shown that intraspecific variations in hearing measurements exist and are often related to the age of the subjects. Popov and colleagues measured the hearing capabilities of 14 *T. truncatus* and showed that thresholds between individuals varied with frequency (Popov et al., 2007). In addition, the authors showed that one animal exhibited significant high frequency hearing loss above 50 kHz. Houser and coworkers noted these types of variations while measuring hearing sensitivity in captive *T. truncatus gilli* individuals (Houser et al., 2008). While it is important to obtain baseline hearing information, it is also fundamental – when possible – to quantify variability within and between species. The Risso's dolphin audiogram was first obtained by Nachtigall and colleagues (Nachtigall et al., 1995) and was collected with a relatively old individual, using standard behavioral techniques; the results indicated good hearing up to 80 kHz. Nachtigall and colleagues collected hearing measurements with a neonate *Grampus griseus* which had excellent hearing up to 150 kHz (Nachtigall et al., 2005). In addition, reports of deaf odontocetes have been recorded and emphasize that hearing abilities can vary greatly between individuals (Ridgway and Carder, 1997; André et al., 2003). Research conducted on groups of genetically

Table 1. Auditory evoked potential (AEP) thresholds for each frequency tested

| Frequency (kHz) | AEP threshold dB re. 1 µPa |
|---|---|
| 4 | 76.7 |
| 11.2 | 69.8 |
| 22.5 | 63.9 |
| 32 | 57.4 |
| 40 | 53.1 |
| 50 | 70.2 |
| 64 | 75.7 |
| 80 | 102.6 |
| 100 | 124.4 |

homogeneous mice and guinea pigs has shown that the response to acoustic injury varies greatly between individuals (Maison and Liberman, 2000; Yoshida and Liberman, 2000). Thus, even with a controlled noise environment and a genetically homogeneous subject pool, interanimal auditory differences persist. These results reiterate how important it is to remain cautious while extrapolating population or species hearing ranges from measurements of a single individual.

Many factors are known to cause high frequency hearing loss. Presbycusis, or the loss of hearing with aging, is usually characterized with a broadband loss of hearing across the entire frequency range, although this loss might be greater in higher frequencies (Demeester et al., 2009). Given the young age of the subject of this experiment, it seems very unlikely that presbycusis was a factor in the interpretation of this audiogram. Environmental noise has also been shown to be involved in the loss of high frequency hearing. Given the low background noise measured at the facility, it seems again unlikely that it could have caused the relatively poor high frequency hearing of the experimental subject. It should be noted, however, that the causes of the stranding were unknown and that background noise measurements of the facility where the animal was first rehabilitated were not collected. The observed audiogram can potentially be due to an event that caused high frequency hearing loss that occurred prior to the animal's stranding.

Two more parsimonious explanations can be proposed to account for the relatively poor high frequency hearing. First, the species *G. melas* might not have good high frequency hearing compared with other odontocete species. In fact, the audiogram is not dissimilar to the hearing sensitivities recorded from *Pseudorca crassidens* (Thomas et al., 1988). Thus, the present results might reflect adequately this species' audiogram. Pilot whales can be up to 6 m long and it has been shown that larger mammals tend to produce lower frequency sound (Heffner and Heffner, 1983; Wang et al., 1995). Whistle and click frequency spectra have been collected with free-ranging *G. melas* and have shown that this species produces sounds usually lower in frequency than those of other smaller odontocetes (Steiner, 1981; Weilgart and Whitehead, 1990). No outgoing echolocation clicks produced by the subject were collected during the experiment and the zoo staff noted that during its rehabilitation the subject was overall acoustically silent compared with the four bottlenose dolphins housed in the same facility. Thus, the hypothesis that the hearing measurements of this subject are representative of the species cannot be completely excluded.

The second hypothesis is supported by the medical records of the animal which indicated that during its initial rehabilitation, the pilot whale was administered ototoxic drugs including the aminoglycoside antibiotics gentamycin and netilmicin, which are known to frequently cause hearing impairment in humans (Bernard et al., 1979; Brummett et al., 1978). In addition, during the first stages of its rehabilitation, the pilot whale subject was administered several other potentially ototoxic medicines thus increasing the probability that the different drugs had a combined effect on the hearing of the subject (Harpur, 1982). High frequency hearing loss is known to be one of the primary effects of ototoxic medicines well before the appearance of other symptoms such as tinnitus – also known as ear buzzing – and other broadband hearing loss (Tange et al., 1985; Fausti et al., 1992). Previous work by Finneran and colleagues compared the hearing sensitivities of two captive beluga whales and showed that one individual had high frequency hearing loss above 37 kHz (Finneran et al., 2005). Both animals were born in captivity and they had similar life histories; however, the animal with high

frequency hearing loss was administered with the aminoglycoside antibiotic amikacin, and this was concluded to be the likely cause of the observed differences in hearing ranges.

In addition to hearing loss, ototoxic medicines are known to cause tinnitus, distorted hearing, a feeling of fullness in the ears as well as dizziness or vertigo, which can be measured in human patients but are difficult to quantify in animal subjects. The implications of such side effects of ototoxic medicine must be taken into account especially in the case of temporary rehabilitation. A loss of high frequency hearing might result in a decrease of echolocation performance as well as a lowering of foraging abilities.

These results show limited high frequency hearing but do not demonstrate high frequency hearing loss because no measurements were collected prior to administering the drugs. This study provides basic information regarding the hearing capabilities of the long-finned pilot whale *G. melas*, but the extrapolation to all long-finned pilot whales and their close relatives the short-finned pilot whales must be tempered by the possibility of potential effects of ototoxic medicine on hearing abilities.

## LIST OF ABBREVIATIONS

| | |
|---|---|
| ABR | auditory brainstem response |
| AEP | auditory evoked potentials |
| EFR | envelope following response |
| FFT | fast Fourier transform |
| r.m.s. | root mean square |
| SAM | sinusoidally amplitude modulated |
| SPL | sound pressure level |

## REFERENCES

**Aguilar Soto, N., Johnson, M. P., Madsen, P. T., Díaz, F., Domínguez, I., Brito, A. and Tyack, P.** (2008). Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J. Anim. Ecol.* **77**, 936-947.

**André, M., Supin, A. Ya., Delory, E., Kamminga, C. and Degollada, E.** (2003). Evidence of deafness in a striped dolphin (*Stenella coeruleoalba*). *Aquat. Mamm.* **29**, 3-8.

**Au, W. W. L., Lemonds, D. W., Vlachos, S., Nachtigall, P. E. and Roiblat, H. L.** (2002). Atlantic bottlenose dolphin (*Tursiops truncatus*) hearing thresholds for brief broadband signals. *J. Comp. Psychol.* **116**, 151-157.

**Baird, R. W., Borsani, J. F., Hanson, M. B. and Tyack, P. L.** (2002). Diving and night-time behavior of long-finned pilot whales in the Ligurian Sea. *Mar. Ecol. Prog. Ser.* **237**, 301-305.

**Bernard, A., Pechere, J.-C. and Jequier, J.-C.** (1979). Detection of Tobramycin and Netilmicin-induced ototoxicity in guinea pigs with evoked action potentials. *J. Infect. Dis.* **139**, 418-423.

**Bowers, C. A. and Henderson, R. S.** (1972). *Project Deep OPS: Deep Object Recovery with Pilot and Killer Whales.* San Diego, CA: Naval Undersea Center.

**Brown, D. H.** (1960). Behavior of a captive pacific pilot whale. *J. Mammal.* **41**, 342-349.

**Brown, D. H. and Norris, K. S.** (1956). Observations of captive and wild cetaceans. *J. Mammal.* **37**, 311-326.

**Brummett, R. E., Fox, K. E., Brown, R. T. and Himes, D. L.** (1978). Comparative ototoxic liability of Netilmicin and Gentamicin. *Arch. Otolaryngol.* **104**, 579-584.

**Busnel, R. G. and Dziedzic, A.** (1966). Acoustic signals of the pilot whale (*Globicephala melaena*) and of the porpoises (*Delphinus delphis* and *Phocoena phocoena*). In *Whales, Dolphins and Porpoises* (ed. K. S. Norris), pp. 607-646. Berkeley: University of California Press.

**Demeester, K., van Wieringen, A., Hendrickx, J., Topsakal, V., Fransen, E., van Laer, L., van Camp, G. and Van de Heyning, P.** (2009). Audiometric shape and presbycusis. *Int. J. Audiol.* **48**, 222-232.

**Ellis, R.** (1982). *Dolphins and Porpoises.* New York: Alfred A. Knopf.

**Evans, W. E.** (1973). Echolocation by marine delphinids and one species of fresh-water dolphin. *J. Acoust. Soc. Am.* **54**, 191-199.

**Fausti, S. A., Henry, J. A., Schaffer, H. I., Olson, D. J., Frey, R. H. and McDonald, W. J.** (1992). High-frequency audiometric monitoring for early detection of aminoglycoside ototoxicity. *J. Infect. Dis.* **165**, 1026-1032.

**Fehring, W. K. and Wells, R. S.** (1976). A series of strandings by a single herd of pilot whales on the west coast of Florida. *J. Mammal.* **57**, 191-194.

**Finneran, J. J., Carder, D. A. and Dear, R.** (2005). Pure tone audiograms and possible aminoglycoside-induced hearing loss in belugas (*Delphinapterus leucas*). *J. Acoust. Soc. Am.* **117**, 3936-3943.

**Harpur, E. S.** (1982). The pharmacology of ototoxic drugs. *Br. J. Audiol.* **16**, 81-93.

**Heffner, R. S. and Heffner, H. E.** (1983). Hearing in large mammals: horses (*Equus caballus*) and cattle (*Bos taurus*). *Behav. Neurosci.* **97**, 299-309.

**Heide-Jorgensen, M. P., Bloch, D., Stefansson, E., Mikkelsen, B., Ofstad, L. H. and Dietz, R.** (2002). Diving behaviour of long-finned pilot whales *Globicephala melas* around the Faroe Islands. *Wildl. Biol.* **8**, 307-313.

**Houser, D. S. and Finneran, J. J.** (2006). A comparison of underwater hearing sensitivity in bottlenose dolphins (*Tursiops truncatus*) determined by electrophysiological and behavioral methods. *J. Acoust. Soc. Am.* **120**, 1713-1722.

**Houser, D. S., Gomez-Rubio, A. and Finneran, J. J.** (2008). Evoked potential audiometry of 13 Pacific bottlenose dolphins (*Tursiops truncatus gilli*). *Mar. Mamm. Sci.* **24**, 28-41.

**Johnson, S. C.** (1967). Sound detection thresholds in marine mammals. In *Marine Bioacoustics* (ed. W. N. Tavolga), pp. 247-260. New York: Pergamon Press.

**Kastelein, R., Bunskoek, P., Hagedoorn, M., Au, W. W. L. and de-Haan, D.** (2002). Audiogram of a harbor porpoise (*Phocoena phocoena*) measured with narrow-band frequency-modulated signals. *J. Acoust. Soc. Am.* **112**, 334-344.

**Kritzler, H.** (1952). Observations on the pilot whale in captivity. *J. Mammal.* **33**, 312-334.

**Maison, S. F. and Liberman, M. C.** (2000). Predicting vulnerability to acoustic injury with a non-invasive assay of olivocochlear reflex strength. *J. Neurosci.* **20**, 4701-4707.

**Mooney, T. A., Nachtigall, P. E., Castellote, M., Taylor, K. A., Pacini, A. F. and Esteban, J.-A.** (2008). Hearing pathways and directional sensitivity of the beluga whale *Delphinapterus leucas*. *J. Exp. Mar. Biol. Ecol.* **362**, 108-116.

**Nachtigall, P. E., Au, W. W. L., Pawloski, J. L. and Moore, P. W. B.** (1995). Risso's dolphin hearing thresholds in Kaneohe Bay, Hawaii. In *Sensory Systems of Aquatic Mammals* (ed. R. A. Kastelein, J. A. Thomas and P. E. Nachtigall), pp. 49-55. Woerden, The Netherlands: DeSpil.

**Nachtigall, P. E., Lemonds, D. W. and Roitblat, H. L.** (2000). Psychoacoustic studies of whale and dolphin hearing. In *Hearing by Whales* (ed. W. W. L. Au, A. N. Popper and R. J. Fay), pp. 330-364. New York: Springer-Verlag.

**Nachtigall, P. E., Yuen, M. E., Mooney, T. A. and Taylor, K. A.** (2005). Hearing measurements from a stranded infant Risso's dolphin (*Grampus griseus*). *J. Exp. Biol.* **208**, 4181-4188.

**Nachtigall, P. E., Mooney, T. A., Taylor, K. A. and Yuen, M. L.** (2007). Hearing and auditory evoked potential methods applied to odontocete cetaceans. *Aquat. Mamm.* **33**, 6-13.

**Nachtigall, P. E., Mooney, T. A., Taylor, K. A., Miller, L. A., Rasmussen, M. H., Akamatsu, T., Teilman, J., Linnenschmidt, M. and Vikingsson, G. A.** (2008). Shipboard measurements of the hearing of the white-beaked dolphin, Lagenorhynchus albirostris. *J. Exp. Biol.* **211**, 642-647.

**Olsen, P. A.** (2009). Pilot whales. In *Encyclopedia of Marine Mammals,* 2nd edn (ed. B. W. P. F. Perrin and J. G. M. Thewissen), pp. 847-852. New York: Academic Press.

**Popov, V. V., Supin, A. Ya., Wang, D., Wang, K., Xlao, J. and Li, S.** (2005). Evoked-potential audiogram of the Yangtze finless porpoise *Neophocaena phocaenoides asiaeorientalis* (L). *J. Acoust. Soc. Am.* **117**, 2728-2731.

**Popov, V. V., Supin, A. Ya., Pletenko, M. G. and Tarakanov, M. B.** (2007). Audiogram variability in normal bottlenose dolphins (*Tursiops truncatus*). *Aquat. Mamm.* **33**, 24-33.

**Ridgway, S. H. and Carder, D. A.** (1997). Hearing deficits measured in some *Tursiops truncatus* and the discovery of a deaf/mute dolphin. *J. Acoust. Soc. Am.* **101**, 590-594.

**Scheville, W. E.** (1964). Under water sounds of cetaceans. In *Marine Bio-Acoustics* (ed. W. N. Tavolga), pp. 307-316. New York: Pergammon Press.

**Sergeant, D. E.** (1962). On the external characters of the blackfish or pilot whales (genus *Globicephala*). *J. Mammal.* **43**, 395-413.

**Steiner, W. W.** (1981). Species-specific differences in pure tonal whistle vocalizations of five Western North Atlantic dolphin species. *Behav. Ecol. Sociobiol.* **9**, 241-246.

**Supin, A. Y., Popov, V. V. and Mass, A. M.** (2001). *The Sensory Physiology of Aquatic Mammals*. Boston: Klumer Academic Publisher.

**Szymanski, M. D., Supin, A. Ya., Brain, D. E. and Henry, K. R.** (1999). Killer whale (*Orcinus Orca*) hearing: auditory brainstem response and behavioral audiograms. *J. Acoust. Soc. Am.* **106**, 1134-1141.

**Tange, R. A., Dreschler, W. A. and van der Hulst, R. J.** (1985). The importance of high-tone audiometry in monitoring for ototoxicity. *Arch. Otolaryngol.* **242**, 77-81.

**Taylor, K. A., Nachtigall, P. E., Mooney, T. A., Supin, A. Ya. and Yuen, M. M. L.** (2007). A portable system for the evaluation of the auditory capabilities of marine mammals. *Aquat. Mamm.* **33**, 93-99.

**Thomas, J. A., Chun, N., Au, W. and Pugh, K.** (1988). Underwater audiogram of a false killer whale (*Pseudorca crassidens*). *J. Acoust. Soc. Am.* **84**, 936-940.

**Wang, D., Würsig, B. G. and William, E. E.** (1995). Comparisons of whistles among seven odontocete species. In *Sensory Systems of Aquatic Mammals* (ed. R. A. Kastelein, J. A. Thomas and P. E. Nachtigall), pp. 299-324. Woerdem, Netherlands: Spil Publishers.

**Weilgart, L. S. and Whitehead, H.** (1990). Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behav. Ecol. Sociobiol.* **26**, 399-402.

**Yoshida, N. and Liberman, M. C.** (2000). Sound conditioning reduces noise-induced permanent threshold shift in mice. *Hear. Res.* **148**, 213-219.

**Yuen, M. E., Nachtigall, P. E., Supin, A. Ya. and Breese, M.** (2005). Behavioral and auditory evoked potential audiograms of a false killer whale (*Pseudorca crassidens*). *J. Acoust. Soc. Am.* **118**, 2688-2695.