Polar bear *Ursus maritimus* hearing measured with auditory evoked potentials

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Summary

While there has been recent concern about the effects of sound on marine mammals, including polar bears, there are no data available measuring the hearing of any bear. The in-air hearing of three polar bears was measured using evoked auditory potentials obtained while tone pips were played to three individually anaesthetized bears at the Kolmården Djurpark. Hearing was tested in half-octave steps from 1 to 22.5 kHz. Measurements were not obtainable at 1 kHz and best sensitivity was found in the range from 11.2–22.5 kHz. Considering the tone pips were short and background noise measurements were available, absolute measurements were estimated based on an assumed mammalian integration time of 300 ms. These data show sensitive hearing in the polar bear over a wide frequency range and should cause those concerned with the introduction of anthropogenic noise into the polar bear's environment to operate with caution.

Key words: bear hearing, polar bear, evoked potential.

Introduction

Recent concern about the effects of anthropogenic noise on the well-being of marine mammals (National Research Council, 1994; National Research Council, 2000; National Research Council, 2003; National Research Council, 2005) has prompted a great deal of work on the hearing of aquatic and semi-aquatic mammalian species (Au et al., 2000; Wartzok and Ketten, 1999; Richardson et al., 1995; Tyack et al., 2006; Nachtigall et al., 2005). The polar bear *Ursus maritimus* is the only bear species classified as a marine mammal (Rice, 1998), but there has been no audiometric examination of their hearing. According to the most comprehensive review of animal hearing studies (Fay, 1988), and a search of the literature published since, in fact no measurements have been completed on the hearing of any bear.

One way to estimate the hearing of a species is to examine the calls of its prey and its response to those calls. Ringed seals *Phoca hispida* and bearded seals *Erignathus barbatus* are prominent in the diet of polar bears (Stirling, 2002). In some areas, the predator–prey relationship between ringed seals and polar bears is so interrelated that a count of the population of one of them can indicate the population level of the other (Stirling and Øritsland, 1995). Polar bears' preferred prey items are the newborn pups and subadults (Stirling and McEwan, 1975), and they primarily hunt seals in areas of moving pack ice, which include known important locations of seal birth lairs (Smith, 1980).

Four types of vocalizations made by ringed seals can be heard at all times of day in the Arctic spring: (1) low-pitched barks, (2) high pitched yelps, (3) low and high pitched growls and (4) short descending chirps (Stirling, 1973). Sonograms of the recorded sounds indicated that most of the energy was relatively low frequency below 2 kHz, with some harmonics up to 8 kHz.

The behavioral responses of polar bears to the calls of ringed seals recorded under water and then presented to the bears in air were measured (Cushing et al., 1988), and elicited similar responses from two recently captured bears. The bears erected their ears, lifted their heads, visually scanned the room and then began sniffing. As the ringed seal calls continued to be played the bears became active, paced their cage, groaned and chuffed, then pawed and chewed at their cage bars. All of these behaviors were observed only rarely in the baseline behavioral examinations prior to the presentation of ringed seal sounds, indicating that the bears responded to their primary prey's underwater vocalizations, presented in air, in a manner that indicated some importance of in-air hearing in detecting and locating their under-ice prey. Cushing's observations suggest that if polar bears could hear the underwater vocalizations of the ringed seals they might use seal vocalizations as a method to locate their favorite prey. It has also been noted (Stirling and Thomas, 2003) that the distinct trills of bearded seals might also provide a prominent cue for polar bear localization of these animals. A

measurement of bear hearing would assist in the quantification of this sensory system during foraging behavior.

Polar bears are distributed throughout the Arctic in 19 populations, comprising an estimated total of 20 000–25 000 bears (Marine Mammal Commission, 2006). There is increasing concern now over the effects of climate changes and human activities in the Arctic on current polar bear populations (Amstrup, 1993; Schrope, 2001). In particular, human activity may potentially impact the behavior of polar bears through the introduction of sound into an environment in which, until recently, anthropogenic noise was almost completely absent (Stirling, 1990). The effects of anthropogenic noise can best be predicted if a baseline of bear hearing capabilities is first established, and this requires hearing measurement.

The hearing of large marine mammals has typically been measured with trained captive animals using psychophysical techniques (Nachtigall et al., 2000). Polar bears are large and aggressive, even in controlled environments, so traditional behavioral audiometry is difficult to perform. Therefore, obtaining data on the hearing capabilities of polar bears presents a challenge. There have been a number of recent measurements of large mammal hearing using auditory evoked potential (AEP) audiometry (Supin et al., 2001; Yuen et al., 2005; Nachtigall et al., 2005) and this technique is used in the present study to determine the hearing sensitivity of polar bears. This AEP procedure can be used successfully, even when animals are anesthetized, so when three polar bears had to be anesthetized for veterinary examination in Kolmården Djurpark (Sweden), we used the opportunity to examine their ability to hear in air.

Materials and methods

Subjects

The subjects were three polar bears *Ursus maritimus*, two females (Mirsha, 26 years old, 270 kg body mass; Ilka, 12 years old, 290 kg body mass) and one male (Nordman, 12 years old, 420 kg body mass), housed in Kolmården Zoo, Sweden.

Experimental, facilities, procedure, and anesthesia

During experimentation, each animal was isolated in an indoor secure enclosure and was anaesthetized by using a combination of Zalopine® (medetomidin-HCl, 10 mg ml^{-1}; Orion Pharma, Orion Corp., Espoo, Finland), 3.5–5 mg total initial dose per animal, and Zoletil® forte vet (tiletamin-HCl+zolazepam-HCl, Virbac S.A. BP 27, 06511 Carros CEDEX, France), 350–600 mg total initial dose per animal, delivered with a 3 ml blowdart (Dan-Inject ApS, Sellerup Skovvej 116, DK-7080 Børkop, Denmark) into the lower front leg. Combinations of these drugs are successfully used to anesthetize and temporarily immobilize a variety of large mammals, including grizzly bears (Reynolds and Verhoef, 2000), brown bears, gray wolves (Arnemo, 2006) and koalas (Unwin, 2004). Their effects on mammalian hearing *per se* have not been previously established.

Background noise monitoring

Ideally audiometry is conducted within very low-noise background conditions like those found in a sound-proof booth. As is common with most marine mammal hearing studies (Nachtigall et al., 2000; Kastak et al., 2005) these conditions were unavailable and therefore all the measurements were carried out in a background of low ambient noise. Control of background noise level was handled by monitoring and noise was measured next to the animal's head using a Bruel and Kjaer 2231 sound level meter (Nærum, Denmark) within a frequency range of 0.125–32 kHz. In order to estimate the noise spectral compositions, 100-ms samples of the noise taken from the analog output of the sound level meter were digitized at a sampling rate of 64 kHz by a DAQ-6062E data acquisition card (National Instruments, http://www.ni.com) installed in a standard laptop computer, stored in computer memory, and Fourier-transformed off-line.

Stimuli

The sound stimuli to be heard and measured were short tone pips of a carrier sinusoid frequency enveloped by a one-cycle cosine function (Fig. 1A) specifically designed to optimize hearing measures using auditory evoked potentials. The carrier frequencies varied from 1 to 22.5 kHz by half-octave steps, i.e. 1, 1.4, 2, 2.8, 4, 5.6, 8, 11.2, 16 and 22.5 kHz. The envelope cycle duration was 5.6 times longer than the carrier cycle but was not longer than 2 ms. The frequency spectrum of this waveform is presented in Fig. 1B. With the used envelope duration, the pip frequency bandwidth (at a level of 0.5 of the spectrum magnitude, i.e. –6 dB) in octave measure was $\log_2[(1+1/5.6)/(1–1/5.6)]=0.52$, i.e. almost exactly a half-octave, except for the pips of the lowest frequencies (1–2 kHz), which were 2 ms long and, respectively, ±0.5 kHz wide. Stimuli were digitally synthesized at a sampling rate of 128 kHz, digital-to-analog converted by the DAQ-6062E card, amplified, attenuated, and played through a high-frequency piezoelectric speaker ('tweeter') positioned at a distance of 25 cm from the right ear of the animal, the speaker axis being directed to the ear (Fig. 2). Frequency response irregularity of the speaker was up to 30 dB within a range from 1–22.5 kHz, but not more than 10 dB within any half-octave band except at the lowest part of the frequency range (1–2 kHz) where it reached 16 dB/octave. However, even at the steepest frequency–response irregularity, the acoustic signal spectrum shifted by not more than 6% (0.08 octave) relative to the electric signal (Fig. 1B). Stimulus intensity was measured by a calibrated microphone positioned at the speaker axis at the distance of 25 cm.

Evoked-potential recording

The brain-evoked potentials were recorded using subcutaneous custom-made stainless steel needle 0.5 mm electrodes. The active electrode was positioned at the head vertex, and the reference electrode was placed on the neck along with a ground electrode, as shown in Fig. 2. All the needle electrodes were inserted just under the skin surface. The
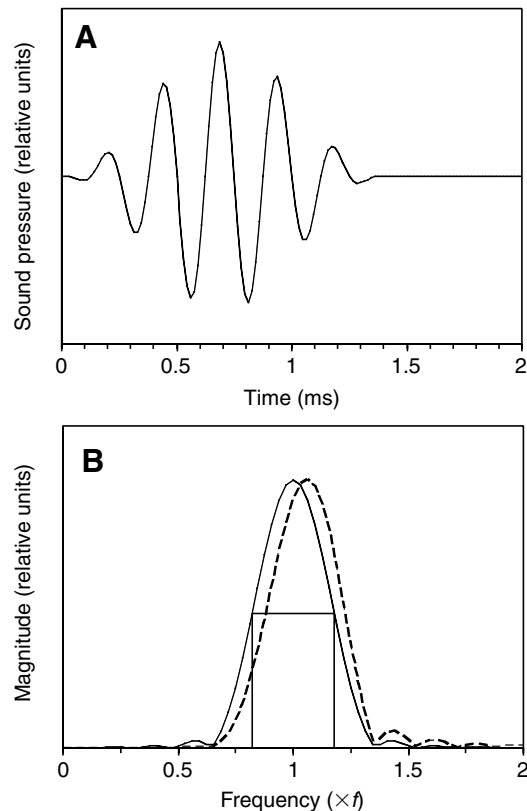
Fig. 1. (A) Stimulus waveform (the example is a 4-kHz signal). (B) Frequency spectra of the stimulus. Solid line, electrical signal; broken line, reproduction with frequency–response irregularity of the speaker 16 dB/octave; frequency is presented in multiples of the carrier frequency *f*. Straight lines in B show the spectrum width at a level of 0.5 (–3 dB) *re* maximum.

signals from the electrodes were amplified by a custom-made balance amplifier (gain 25 000, passband 200–5000 Hz at a –3 dB level) and digitized at a sampling rate of 16 kHz by the DAQ-6062E data acquisition card. To extract the AEP from noise, 1000× 15 ms samples were averaged by a custom-written program based on LabVIEW (National Instruments) technology.

Threshold evaluation

To find a hearing threshold at each carrier frequency, AEPs were recorded in response to stimuli of intensities decreased by 5 dB steps, starting with an intensity provoking a well-developed response and continuing to a level incapable of provoking an AEP detectable in noise. In order to better extract an AEP waveform from the background physiological electrical noise and quantitatively estimate its amplitude, cross-correlation analysis was used (Supin et al., 2001). Cross-correlation functions (CCF)

between the evaluated record and a standard AEP waveform were computed, using a definite AEP to a high-intensity stimulus of the same frequency as a standard. A CCF was computed for a 10 ms window of the original record, from 2.5 to 12.5 ms after the stimulus, and within a lag range of ±2 ms. The magnitude of the CCF peak was specified in terms of the root mean squared (RMS) of the searched-for waveform within a 10 ms analyzed window. The CCF peak magnitudes were plotted as a function of stimulus intensity expressed in dB and were approximated by straight regression lines. The intersections of the regression lines with the zero-magnitude levels were accepted as the threshold estimates.

Results

Ambient noise parameters

The overall ambient noise level in the experimental enclosure, as measured in a frequency band from 0.125 to 32 kHz, fluctuated from 62 to 72 dB. Within a major part of the spectrum frequency range, from 0.25 to 32 kHz, its frequency spectrum density (in terms of power per Hz) decreased with frequency at a rate of around 6 dB/octave; being presented in terms of power per octave, the spectrum decreased with frequency at a rate of around 3 dB/octave. For comparison with typical hearing thresholds, it was reasonable to present the noise level in bands of the same width as the sound stimuli, i.e. in half-octave bands. Being measured as SPL values in half-octave bands (Fig. 3), the noise level within the investigated frequency range varied from 44.5–54.5 dB SPL around 1 kHz to 34–44 dB SPL around 22.5 kHz. This area of noise level fluctuation is approximated by the delimiting straight lines in Fig. 3.

Auditory evoked potential waveform and properties

Examples of AEP to tone pips of varying intensity are presented in Fig. 4A. The AEP waveform was a sequence of
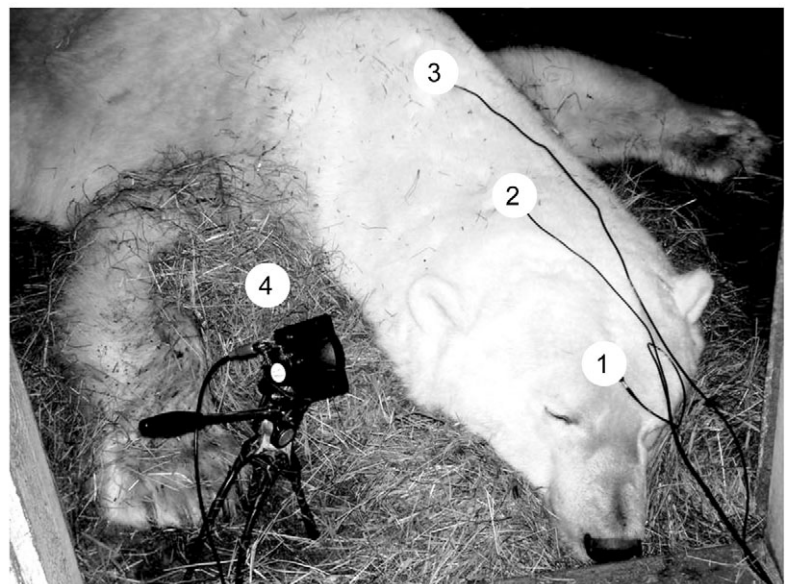

Fig. 2. Experimental set-up. 1, active electrode; 2, reference electrode; 3, grounding; 4, speaker.
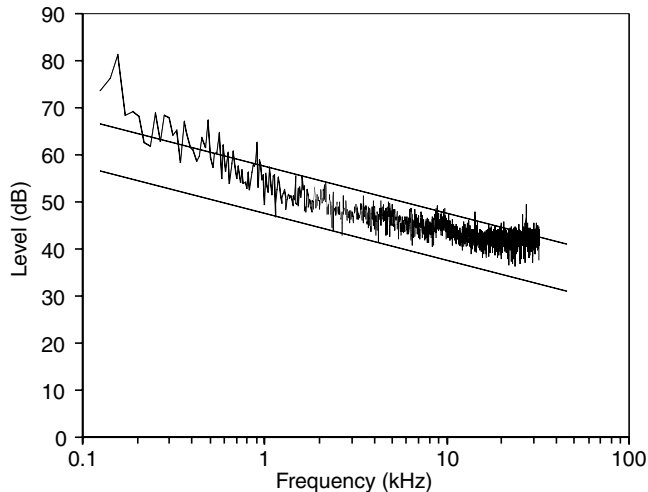
Fig. 3. Frequency spectrum of the ambient noise. Spectrum power is specified in SPL of half-octave bands. The straight lines with a slope of –3 dB/octave approximate the limits of noise fluctuation corresponding to overall noise levels of 62 and 72 dB SPL.

alternating positive and negative waves with onset latency from around 3 ms at high stimulus intensities to around 3.5 ms at low stimulus intensities. At high intensities, the waveform included up to 5 positive–negative cycles lasting 8–9 ms; at lower intensities not all of these waves were detectable.

The AEP amplitude was intensity-dependent. However, in general it was rather low. Even at the highest available intensities (110 dB in Fig. 4), the AEP amplitude did not exceed 0.5 μV. At lower intensities, the amplitude was even less. Therefore, although as low background noise at around 30 nV RMS was achieved in the records, a detection of low-amplitude AEPs in noise was problematic.

AEP thresholds

Examples of cross-correlation functions (CCF) between the low-amplitude AEP waveforms (presented in Fig. 4A) and a standard AEP waveform are shown in Fig. 4B. For computation, the AEP waveform evoked by the highest intensity (110 dB) of the same frequency was used as a standard. All the exemplified CCFs had a positive peak at or near the zero lag. Peak magnitude diminished with decreasing intensity, thus reflecting the diminishing AEP amplitude. The CCF peak position at the lag scale was also intensity dependent: its delay increased as the intensity decrease, thus reflecting the increase of the AEP latency.

To find the AEP threshold, CCF peak magnitudes (marked by dots in Fig. 4) were used as evaluates of the AEP amplitude. The CCF peak magnitudes were plotted as a function of stimulus intensity expressed in dB (Fig. 5). In a near-threshold intensity range, these functions could be satisfactorily approximated by straight regression lines (r^2=0.94 in Fig. 5). The intersection of the regression line with the zero-magnitude level was accepted as a threshold estimate. In the example presented in Fig. 5, this estimate was 68.3 dB.
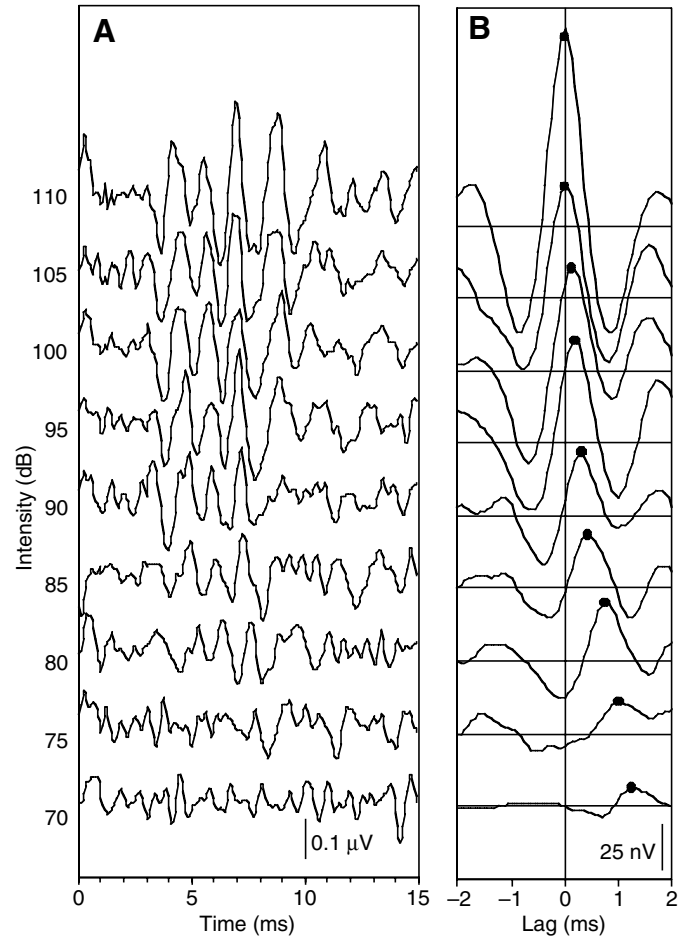

Fig. 4. (A) Examples of auditory evoked potential (AEP) waveforms to stimuli of 4 kHz carrier frequency at various intensities (dB SPL). (B) Cross-correlation functions (CCFs) between the corresponding waveforms and a standard AEP waveform obtained at high (110 dB) stimulus intensity. CCFs are calibrated in RMS values within a 10-ms window. Dots in B show CCF peak positions.

Using this technique of threshold evaluation, AEP thresholds were measured at frequencies ranging from 1 to 22.5 kHz in half-octave steps. However, at the frequency of 1 kHz AEP the response amplitude was not large enough, even at the highest available intensity, to draw the regression line. So the audiograms (thresholds as a function of sound frequency) were only obtained at frequencies from 1.4 kHz and higher. The audiograms obtained for the three subjects are presented in Fig. 6A. An averaged audiogram is presented in Fig. 6B.

Discussion

Basic thresholds

Because of the difficulty in obtaining subjects, many marine mammal hearing audiograms have been obtained from a single individual subject (Nachtigall et al., 2000). It is difficult to estimate how well a species hears from a single subject because there is always individual variability,
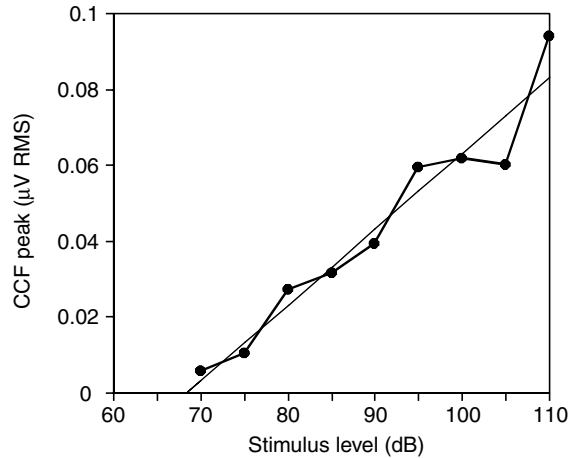
Fig. 5. An example of AEP magnitude (specified as peak CCF value) dependence on stimulus intensity. The same measurements as in Fig. 3 (4-kHz carrier frequency). The straight line is the regression line for the data within a range of 70–110 dB (r^2=0.94).

regardless of the species (Yost, 1994). Although there was some data scatter and inter-individual variation among the thresholds of the three bears, this variation mostly did not exceed 10 dB at any given threshold and some were remarkably uniform like that obtained at 4 kHz (Fig. 6) – all three bears showed a threshold near 70 dB. These thresholds can be compared, for example, to similar thresholds measured in noise within a sound-proof booth for two semiaquatic carnivores, a California sea lion and a Northern Elephant seal (Southall et al., 2003). The sea lion and northern elephant seal presented with 4 kHz masking tones of 35 and 40 dB showed thresholds of 60 dB and 63.5 dB, respectively, somewhat similar to the polar bear mean threshold of 70 dB at 4 kHz obtained in fluctuating noise conditions around 40–50 dB (Fig. 3).

Correction of the data for temporal summation and comparison with the ambient noise

As indicated earlier, we did not have the opportunity to measure the bear hearing in a sound-proof booth. All the measurements were done in a background of ambient noise. So the question arose as to whether the obtained thresholds were real absolute hearing thresholds or thresholds masked by ambient noise. To answer the question, the obtained thresholds had to be compared to the background noise level.

The critical band widths in bears are unknown. However, it can be supposed that they are on the same order as those of other mammals, i.e. 10–20% of the central frequency (0.14–0.26 octave). This is of course less than the stimulus bandwidth of 0.5 octave used herein. In this situation, a direct comparison between the stimulus and noise is possible using the noise intensity in bands of the same width as the stimulus bandwidth (half-octave bands), because a critical band extracts one and the same fraction of energy from both the 0.5-octave stimulus and a 0.5-octave band of noise.
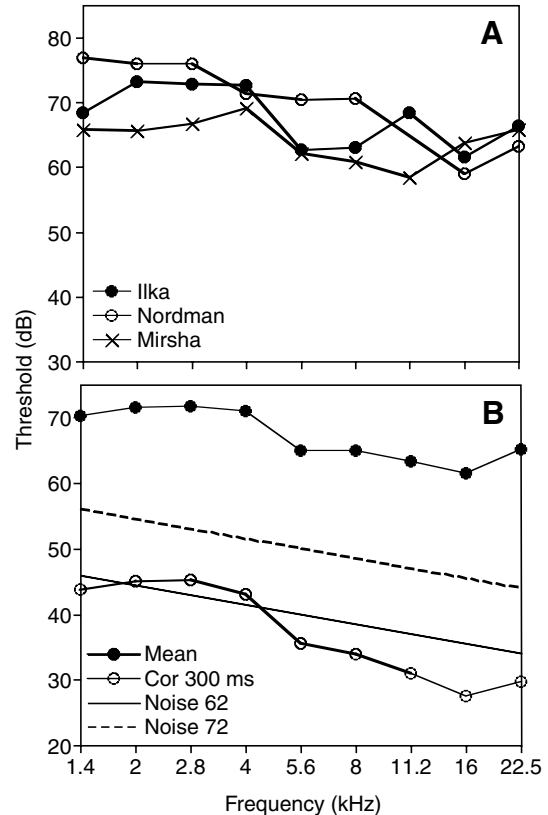

Fig. 6. (A) Individual audiograms for the three polar bears in the ambient noise conditions. (B) The inter-individual averaged audiogram (mean), its correction for a 300 ms temporal summation (corr 300 ms), and limits of ambient noise fluctuations corresponding to overall noise levels of 62 and 72 dB (noise 62 and noise 72).

For a correct comparison, however, one must take into consideration that the stimuli were short pips, probably shorter than the limit of temporal summation in the bear's auditory system, whereas the background noise was not limited in duration. Therefore, a correction had to be done for incomplete temporal summation of the stimuli. The temporal summation limit has, of course, never been measured in bears because the hearing of bears has never been measured (Fay, 1988), but in the majority of mammals that have been investigated, including carnivores, the temporal summation limit is normally between 100 and 1000 ms (Fay, 1988). So by analogy, a similar limit may be expected in bears. We assume a conservative intermediate value of 300 ms as a temporal summation limit. Our stimuli were cosine enveloped, i.e. the envelope was defined as: $0.5[1-\cos(2\pi t/T)]$, where t is time and T is the cosine cycle duration. For this envelope form, the equivalent rectangular duration (ERD) is:

$$\mathrm{ERD} = \int_{t=0}^{t=1} \{0.5\,[1-\cos(2\pi t/T)]\}^2\,\mathrm{d}t = 0.375T\ .$$

The cosine cycle duration T lasted from 2 ms (at frequencies of 1.4–2.8 kHz) to 0.25 ms (at 22.5 kHz), so the stimulus ERD

varied from 0.75 to 0.094 ms, respectively. Thus applying the temporal summation limit of 300 ms, the correction should be from 26 dB (for a 0.75 ms stimulus) to 35 dB (for a 0.094 ms stimulus). The resulting corrected thresholds for a temporal summation limit of 300 ms are shown in Fig. 6B along with the original averaged thresholds. Of course, we do not know whether the temporal summation limit in the bear was really 300 ms; however, if it ranged between 100 and 1000 ms, the correction would not differ by more than ±5 dB.

Significance of the threshold data

A major part of the threshold-*vs*-frequency function corrected for temporal summation is at or near the lower boundary of the area of the ambient noise (Fig. 6). These thresholds are therefore logically masked thresholds in the ambient noise rather than real absolute hearing thresholds. Thus, we cannot state that we obtained a real absolute threshold audiogram of the polar bear. But, our inability to find absolute thresholds does not mean the data presented above were not informative; most marine mammals hearing studies have been conducted in the presence of background noise. And, the absolute thresholds of hearing cannot be higher than the masked thresholds, thus the obtained data indicate that the absolute thresholds of hearing of polar bears are certainly below these levels. Thus, we can conclude that the bear hearing sensitivity is rather good within a range of 11.2–22.5 kHz: absolute thresholds are lower than 27–30 dB. Absolute thresholds without a noise background have not been published or estimated for pinnipeds, but absolute sensitivities at levels very similar to the polar bear are likely based on the masked hearing thresholds shown for the animals in Southall et al.'s work (Southall et al., 2003).

It is important to note that the bear thresholds are also rather low within a rather wide frequency range, up to the highest tested frequency of 22.5 kHz where the threshold is below 30 dB. So the frequency range of the polar bear's hearing is wider than this frequency, i.e. wider than in humans, which is less than 20 kHz (for a review, see Yost, 1994). Thus we can state that polar bears possess an acute and wide-frequency-range hearing ability. Given the relatively low frequencies of the measured vocalizations produced by seals (Stirling, 1973) and heard by the bears in air (Cushing et al., 1988), we had no *a priori* reason based on foraging and the calls of their prey to expect that the bears would hear such a wide range of frequencies, but they did. Perhaps there is simply an overall advantage in the use of high frequencies for auditory localization. An awareness of the polar bear's acute and relatively wide-frequency hearing should cause people to operate with caution where there may be an impact of anthropogenic noise on polar bears. Certainly these results call for additional research on the high frequency hearing of all bears.

Two questions come to mind when evaluating these evoked potential data as true hearing data: (1) are evoked potential thresholds the same as those obtained when an animal is perceiving the sounds and reporting them, and (2) are measurements obtained from a bear anesthetized with Zalopine® and Zoletil® a true indication of its hearing abilities? The definition of hearing usually requires some sort of perception on the part of an animal or human, and thus in the strictest sense auditory-evoked potential studies do not directly measure hearing (Stevens, 1970). Recent work, however, directly measuring hearing on whales and dolphins and comparing traditional behavioral and AEP procedures, has shown that the methods produce directly comparable results (Yuen et al., 2005; Houser and Finneran, 2006). If these findings can also be applied to the polar bear, then it seems reasonable to assume that the AEP measures have at least given a clear first measure of polar bear hearing. The data indicate that polar bears hear very well, particularly in the range between 11.2 and 22.5 kHz. If Zalopine® and Zoletil® disrupted the ability to measure auditory evoked potentials, these sorts of data would not have been obtained.

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