Killer whale (*Orcinus orca*) hearing: Auditory brainstem response and behavioral audiograms

Michael D. Szymanski[a)]
University of California Davis, Psychology Department, Davis, California 95616

David E. Bain
Marine World Foundation, Vallejo, California 94589

Kent Kiehl
University of British Columbia, Department of Psychiatry, 2255 Wesbrook Mall, Vancouver, British Columbia V6T 2A1, Canada

Scott Pennington, Scott Wong, and Kenneth R. Henry
University of California Davis, Psychology Department, Davis, California 95616

(Received 8 September 1998; revised 12 April 1999; accepted 5 May 1999)

Killer whale (*Orcinus orca*) audiograms were measured using behavioral responses and auditory evoked potentials (AEPs) from two trained adult females. The mean auditory brainstem response (ABR) audiogram to tones between 1 and 100 kHz was 12 dB (*re* 1 μPa) less sensitive than behavioral audiograms from the same individuals (±8 dB). The ABR and behavioral audiogram curves had shapes that were generally consistent and had the best threshold agreement (5 dB) in the most sensitive range 18–42 kHz, and the least (22 dB) at higher frequencies 60–100 kHz. The most sensitive frequency in the mean *Orcinus* audiogram was 20 kHz (36 dB), a frequency lower than many other odontocetes, but one that matches peak spectral energy reported for wild killer whale echolocation clicks. A previously reported audiogram of a male *Orcinus* had greatest sensitivity in this range (15 kHz, ~35 dB). Both whales reliably responded to 100-kHz tones (95 dB), and one whale to a 120-kHz tone, a variation from an earlier reported high-frequency limit of 32 kHz for a male *Orcinus*. Despite smaller amplitude ABRs than smaller delphinids, the results demonstrated that ABR audiometry can provide a useful suprathreshold estimate of hearing range in toothed whales. *© 1999 Acoustical Society of America.* [S0001-4966(99)04408-2]

PACS numbers: 43.80.Lb, 43.80.Nd [WWLA]

INTRODUCTION

Members of the toothed whale family *delphinidae* have an auditory system with excellent high-frequency hearing, broad range, and high temporal resolution (rev. Au, 1993). Unusually sensitive high-frequency hearing to at least 100 kHz is a characteristic of most delphinids studied to date and can be explained in part by the selection for echolocation in these marine mammals. *Orcinus orca*, the largest delphinid species, echolocates (Diercks *et al.*, 1971), is cosmopolitan in distribution, and communicates with pulsed calls, whistles, and clicks (Dalheim and Awbrey, 1982; Ford, 1989; Barrett-Lennard, Ford, and Heise, 1996).

In a behavioral study of *Orcinus* hearing, Hall and Johnson (1972) found that a single male had a high frequency audiogram cutoff at 32 kHz, which is inconsistent with other odontocete audiograms that typically extend to 100 kHz and higher (rev. Au, 1993). More recent data from Orcinus indicated killer whales can respond to pure tones up to 120 kHz, although complete audiograms have not yet been reported (Bain, 1992; Bain and Dalheim, 1994; Szymanski *et al.*, 1995b).

Behavioral audiograms have been collected from nine odontocete species: bottlenose dolphin *Tursiops truncatus* (Johnson, 1967); harbor porpoise *Phocoena phocoena* (Anderson, 1970); common dolphin *Delphinus delphis* (Belkovich and Solntseva, 1970); *Orcinus* (Hall and Johnson, 1972); Amazon river dolphin *Inia geoffrensis* (Jacobs and Hall, 1972), beluga *Delphinapterus leucas* (White *et al.*, 1978; Awbrey *et al.*, 1988), false killer whale *Pseudorca crassidens* (Thomas *et al.*, 1988), tucuxi *Sotalia fluviatilis guianensis* (Sauerland and Dehnhardt, 1998), and Pacific white-sided dolphin *Lagenorhynchus obliquidens* (Remmel *et al.*, 1998). In these studies upper frequency limit ranges from 100 to 150 kHz, if Hall and Johnson's (1972) *Orcinus* data are not included. All species tested to date, including larger species such as *Delphinapterus* (White *et al.*, 1978) and *Pseudorca* (Thomas *et al.*, 1988), reportedly have high-frequency hearing to at least 100 kHz.

The auditory brainstem response (ABR) audiogram is an alternative to behavioral hearing tests and originally was examined in cetaceans by Bullock *et al.* (1968), Ladygina and Supin (1970), and Bullock and Ridgway (1972), all studies which used intracranial methods. Ridgway *et al.* (1981) demonstrated that dolphin ABRs could be recorded extracranially in awake, calmly behaving animals. The original noninvasive recording technique has been modified and extended (Popov and Supin, 1985, 1990a, 1990b; Dolphin *et al.*, 1995a,

---

[a)] Author to whom correspondence should be addressed; current address: University of California San Francisco, Department of Radiology, Biomagnetic Imaging Laboratory, S-362, 513 Parnassus Ave., San Francisco, CA 94143-0628.

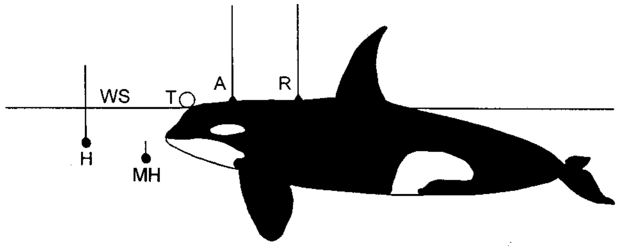

FIG. 1. The recording session position of the whale in the ABR audiogram paradigm. H—hydrophone, MH—monitoring hydrophone, WS—water surface, T—target, A—active electrode, R—reference electrode. Not to scale.

1995b; Szymanski *et al.*, 1995a, 1998). Odontocete ABRs have been recorded from six species, including: *Tursiops* (Bullock *et al.*, 1968), *Phocoena* (Bibikov, 1992), *Sotalia, Inia, Delphinapterus* (Popov and Supin, 1990b), and a neonatal sperm whale (Carder and Ridgway, 1991). Evoked potential audiograms have been collected mostly from smaller species.

Findings from ABR audiometry have been consistent with behavioral measures of hearing in toothed dolphins and whales. But there are not any published reports that have compared the evoked potential and behavioral audiograms from the same individuals. Recent recordings of the killer whale ABR (Szymanski *et al.*, 1998) suggested that ABR and behavioral audiograms could be compared in the same individual whales. Our study was conducted to compare the ABR and behavioral audiograms of two trained female killer whales.

I. MATERIAL AND METHODS

A. Subjects

Two adult female killer whales were tested, both had previously participated in behavioral (Bain and Dalheim, 1994) and evoked potential experiments (Szymanski *et al.*, 1995a, 1995b, 1998). One whale, ''Yaka,'' was 26–28 years old at the time of the study and originally was collected from the Northern resident A5 pod off the coast of British Columbia in 1969. The other whale, ''Vigga,'' was 16–18 years old during the study and was taken from Icelandic waters in 1980.

B. ABR experimental conditions

Evoked potential experiments were conducted at Marine World Africa USA, an oceanarium and animal park in Vallejo, California between 1995 and 1996. The test pool, filled with sea water, was about 4 m deep and 15 m in diameter. The whales were trained to remain stationary alongside the tank wall with the apex of the melon of their head at a target and their blowholes breaking the water surface. A transducer was submerged 1 m below the surface and 1 m from the whale's rostrum (Fig. 1). Slight movements occurred during testing, but if the whale moved off target more than 10 cm the trial was called off.

C. ABR stimuli

Cosine-gated tone bursts were digitally generated and attenuated with 12-bit resolution using Modular Instruments, Incorporated (MI^2) equipment. The projector was an International Transducer Corporation (ITC) spherical hydrophone model (ITC) 1042, 3.5 cm in diameter. Frequencies were tested in a random order at: 1, 2, 4, 8, 12, 16, 20, 32, 45, 60, 80, and 100 kHz. Tone burst duration was 1 ms at 1 and 2 kHz, and 0.5 ms at all other frequencies. The monitoring hydrophone was a Sea Systems model 1000r, which was positioned about 0.5 m lateral to the whale, 1 m below the surface, in line with the lower jaw at the approximate level of the pan bone, the presumed primary sound channel in delphinids (Fig. 1) (Brill *et al.*, 1988). Stimuli were calibrated daily at the frequencies being tested before the whale was in position. The monitoring hydrophone was placed at the approximate site where the whale's pan bone would be located and spectral content and intensity levels were measured. The signal level also was calibrated with the whale in position and found to fluctuate between 6–10 dB *re* 1 μPa (Fig. 2). In behavioral experiments, conducted in 1991–1993, an LC32 was used as a projecting hydrophone and a Brüel and Kjær 8105 as a monitoring hydrophone.

D. Stimuli presentation

A modified descending and ascending method of limits was used. Tone bursts were presented at 30/s, in blocks of 350 stimuli. Tone burst intensities ranged from 10 to 150 dB *re* 1 μPa, peak-to-peak, and in a given trial were first presented 40 to 60 dB above the previously measured behavioral threshold. The experimenter attenuated the tone burst in 10-dB steps until the ABR response was no longer visually detectable in two consecutive trials. Stimuli were then increased in 5-dB steps until the ABR reappeared. Threshold measures were taken at least two times for each whale at each frequency.

E. ABR threshold determination

Delphinid ABR wave IV (PIII-NIV) (Szymanski *et al.*, 1998), analogous to Jewett's wave V in humans (Ridgway *et al.*, 1981), was used as a dependent measure of threshold. Wave IV was chosen because it had the largest peak-to-peak amplitude and previously has been used for threshold measures in dolphins (Popov and Supin, 1990a, 1990b). Auditory threshold was defined as the minimum amount of stimulus power needed to evoke a response greater than background EEG noise (Elberling and Don, 1987). A peak-to-peak 350 nV PIII-NIV level was chosen because background, averaged EEG noise, on no-tone trials and prestimulus epochs, was about ±150 nV (Fig. 3).

F. Evoked potential recording

When the whale was stationary, a trainer placed two gold Grass EEG electrodes embedded in suction cups on the animal's head. One suction cup electrode was affixed to a point about 17 cm caudal of the blowhole. The second electrode was placed near the dorsal fin about 75 cm caudal of

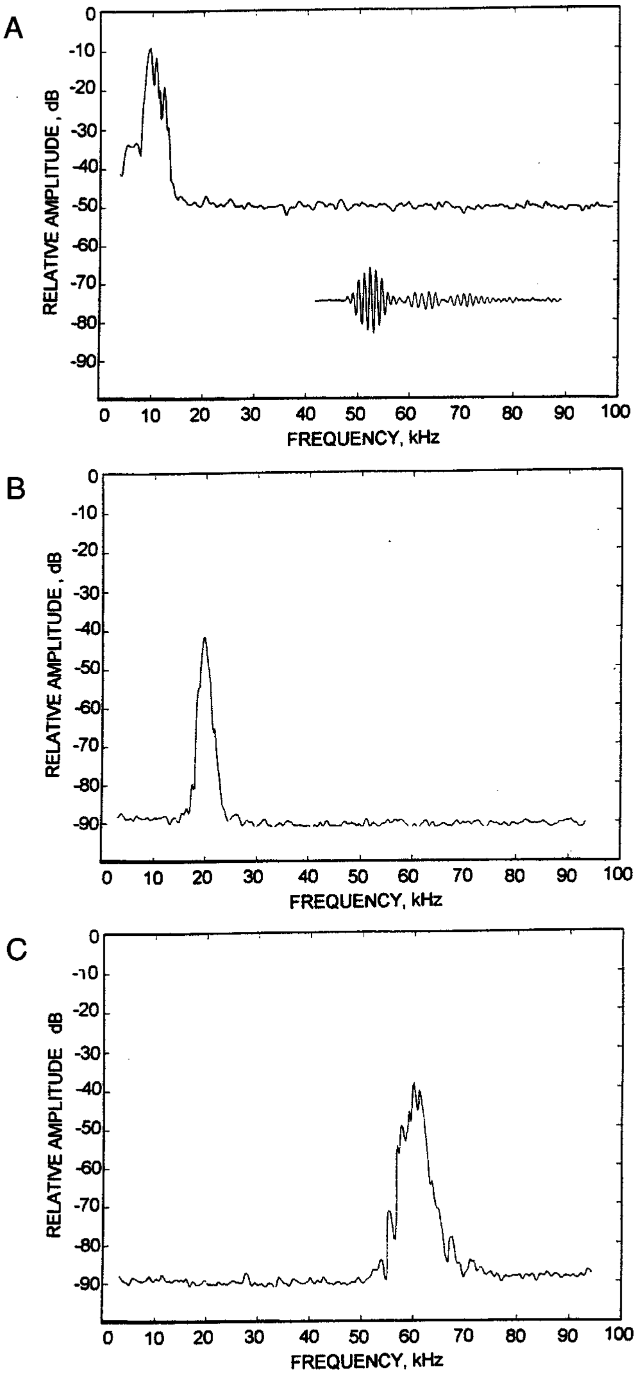

FIG. 2. Sample stimuli power spectrum at three frequencies (a) 10 kHz, (b) 20 kHz, (c) 60 kHz recorded near the whale's head at the lower jaw in approximate line with the pan bone. A 10-kHz stimulus waveform, recorded from the monitoring hydrophone, is shown in the top panel.

the blowhole along the midline. Both electrodes were above the water surface, and their impedance varied between 0.5 and 3 kΩ.

The signal between the two electrodes was differentially amplified 100 000 times through two Grass P15 amplifiers and bandpass-filtered 100 Hz to 3 kHz. The AEPs were averaged in 30-ms epochs from 350 individual responses at 200-kHz sampling rate and stored for off-line analysis. On-line artifact rejection was used and amplitude swings >150 μV were excluded. A total of 350 artifact free traces were required for an average to be included. Each time the whale held a stationary position and the EEG electrodes were attached it was possible to collect two averaged waveforms, a procedure which lasted 2–3 min. Agreement between the two responses was not required. A response was judged acceptable, during later off-line analysis, if it corresponded with another trace collected at the same frequency and intensity in the same recording session.

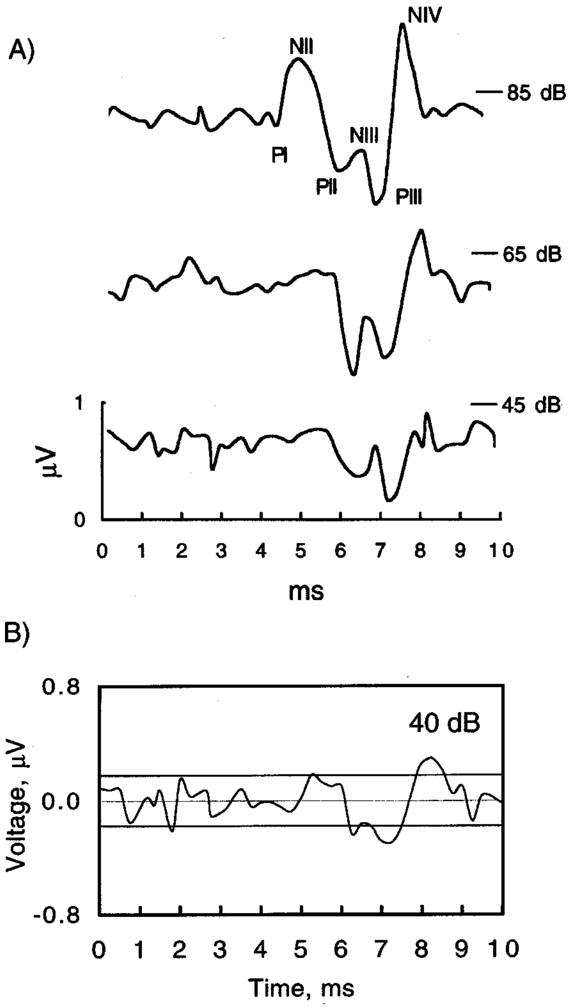

FIG. 3. (a) Representative *Orcinus* ABRs. Main response waves PI to NIV are labeled, negativity at active electrode plotted upward. Examples are *Orcinus* ABRs from ''Yaka'' to 32-kHz tones at three intensities, 85, 65, and 45 dB *re* 1 μPa. Acoustic levels are peak-to-peak measurements. (b) The horizontal lines at ± 0.175 μV illustrate the minimum ABR amplitude used as criteria for wave PII-NIV detection. Auditory threshold in this trial was 40 dB *re* 1 μPa, peak-to-peak.

Then the suction cups were removed, the whale was reinforced with fish and allowed to swim around the pool. Upon returning to the pool area near the trainer, the whale was typically instructed to perform one show or husbandry behavior, reinforced with fish, and then instructed to hold a stationary position for another ABR collection.

G. Behavioral methods

A go/no-go response paradigm was used to test the whales between 1991 and 1993. The whales were trained to station with the apex of the melon against a bar submerged 1 m below the water's surface. After the whale was stationed underwater, a 2-sec tone randomly occurred between 1 to 10 sec and the whale had 4 sec to respond. A false alarm was scored if the whale responded prior to the tone onset, and the trial was repeated. A hit was scored if the whale responded within 4 sec after tone onset, after which the subject was reinforced with whole fish. A miss was scored if the whale responded later than 4 sec after tone onset. If the whale waited for the recall tone, which occurred after a tone presentation and a 4 sec response interval, the animal was reinforced. The reinforcement procedure used was the same as during the whale's husbandry and performance behavior, and food provided during research sessions typically constituted 20%–50% of the whale's daily diet.

There were two motivations for the behavioral paradigm: (1) to increase reinforcement on more than 50% of the trials; and (2) to minimize frustration in the animals. It is obvious that the whale could wait for the recall tone and get reinforced but the animals did not. More fish could be obtained by responding to the tone, i.e., the animal would be reinforced at least 3 sec earlier than if it waited for the recall tone. From an optimal foraging strategy perspective, this would be a better response because it would maximize fish intake.

H. Threshold determination for behavioral audiograms

Sound levels were reduced by 6–8 dB after signals were detected and increased by 6–8 dB after the whale failed to detect the tone. Threshold was defined as two detections at one intensity level, and two failures to detect the tone level below. Behavioral thresholds reported here are the averages of three determinations.

A variety of catch trials were employed. These included no signal presentation, very high or very low frequencies which the transducers could not produce, setting the signal level to 0 V, and disconnecting single components of the sound production system. Personnel were varied to ensure inadvertent cueing did not develop. Also, the whale's behavioral responses were judged by an observer who was blind to signal timing.

II. RESULTS

A. ABR data

Orcinus ABRs recorded to tone bursts resembled AEPs recorded to clicks from the same animals (Szymanski *et al.*, 1998). The waveform resembled the ABR in other delphinids and occurred within 10 ms of tone onset. The largest wave, PIII-NIV (Fig. 3), had a maximum peak-to-peak amplitude of about 1 μV and its maximum amplitude was greatest of the ABR waves. Response amplitude decreased as stimuli were attenuated, with smaller waves typically disappearing into background EEG noise before wave PIII-NIV. The ABR NIV peak latency also increased as stimuli were attenuated as shown in Szymanski *et al.* (1995a). The variability in ABR amplitude is shown in Fig. 4 as input-output function at 32 kHz.

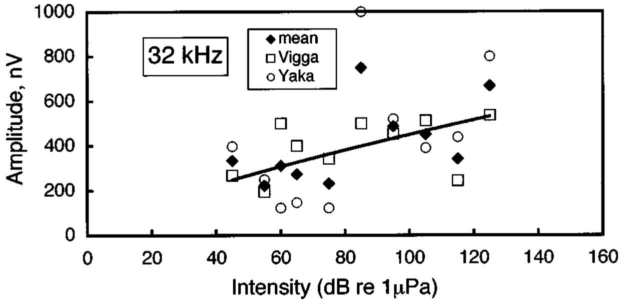

FIG. 4. A representative input-output function showing the relationship between acoustic intensity and ABR amplitude. The line of best fit represents a power function fitted to the mean. The acoustic level is peak-to-peak sound intensity in dB *re* 1 μPa. The output ABR amplitude in nanovolts (nV) is for wave PIII-NIV to 32-kHz tone bursts. Individual whale ABR amplitude data points are the mean of two responses at that intensity. The overall mean is based on four responses at that intensity, two ABR amplitudes from each whale.

B. Audiogram data

Both whales responded behaviorally and electrophysiologically to tones between 1 and 100 kHz. During behavioral trials, one whale responded to 120-kHz tones. The mean audiogram, computed from behavioral and ABR thresholds, was U-shaped and had its most sensitive frequency at 20 kHz (Fig. 5). The most sensitive range, herein defined as 10 dB from the most sensitive frequency (20 kHz at 36 dB [*re* 1 μ Pa]), was between 18 and 42 kHz. The ABR audiogram was about 5 dB less sensitive in this range, which was the area of best agreement between ABR and behavioral audiogram curves. The ABR audiogram was least sensitive at the highest frequencies tested (ABR threshold +41 dB at 100 kHz). In general, the ABR audiogram resembled the curve of the behavioral audiogram, but overall the behavioral audiogram was a mean of 12 dB more sensitive (Table I).

C. Behavioral responses

False alarm rates were less than 5% in catch trials for both whales. The whales' performance on trials that were 20 dB>threshold ($n=160$ trials) were analyzed. The whales did not make any false alarms when tones were 20 dB >threshold, and accuracy was 95% correct.

III. DISCUSSION

A. Audiogram comparisons

The killer whale audiogram resembles the hearing of other delphinids and extends to at least 120 kHz. The maximum sensitivity, +36 dB [*re* 1 μ Pa] at 20 kHz, is the greatest reported for odontocetes and is similar in sensitivity to that reported by Hall and Johnson (1972) (20 kHz, ~35 dB [*re* 1 μPa]). The nearly U-shaped audiogram resembles Hall and Johnson's (1972) data from a single male, except for their high-frequency cutoff of 32 kHz, and the current results of 120 kHz.

In light of Ridgway and Carder's (1993, 1997) findings that a sex difference in high-frequency hearing loss is associated with age in delphinids, it is necessary to consider whether presbycusis in the male *Orcinus* accounted for the current discrepancy in high-frequency hearing. Presbycusis

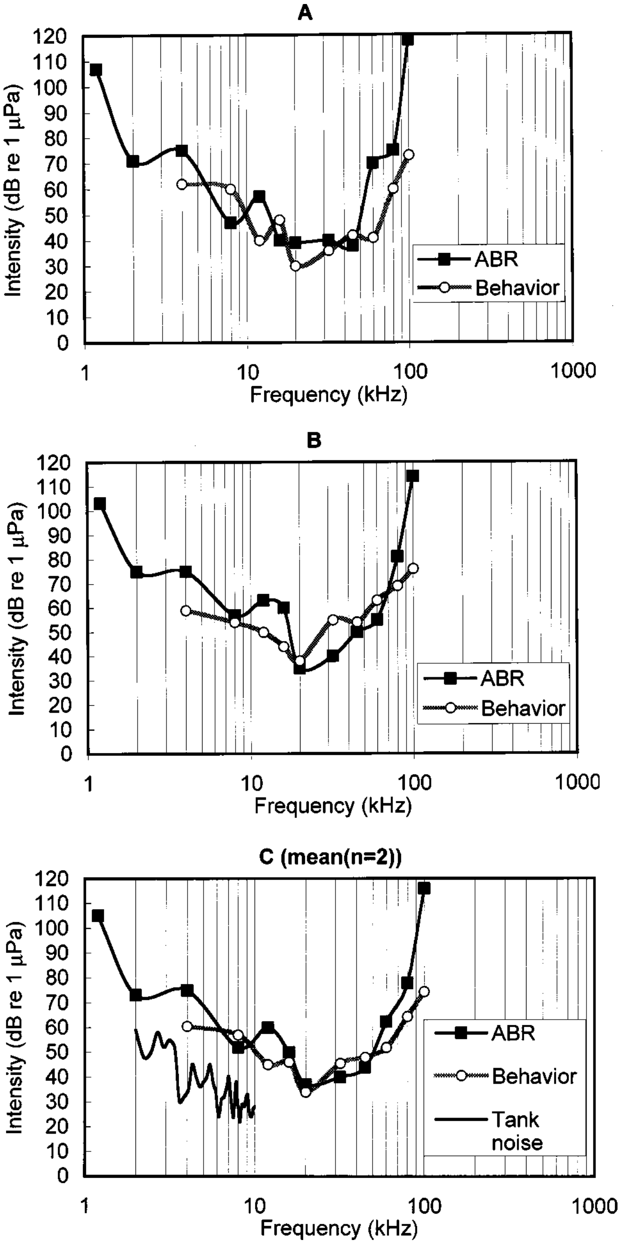

FIG. 5. The ABR and behavioral audiograms for (a) Yaka, and (b) Vigga. (c) Mean of both animals. Tank noise is plotted from a measurement made using an ITC 1042 hydrophone and a Hewlett Packard 3561 Dynamic Signal Analyzer bandwidth 238 Hz.

seems an unlikely explanation, however, because the male tested by Hall and Johnson (1972) was a subadult male captured three years prior to his audiogram measurement. While we can not rule out sex differences in hearing between a young male Orcinus and adult females, it seems unlikely because dramatic sexual dimorphisms in high-frequency audiograms have not been shown in other mammals or observed in other delphinid species.

Other factors that could alternatively explain a hearing loss include genetic and pathogenic disease, and ototoxic drug and noise exposure. It is worth noting, that noise has been used to herd wild marine mammals for capture, and that inner ear damage in wild marine mammals (Bohne *et al.*, 1985; Richardson *et al.*, 1991, 1995) and whales (Ketten, Lien, and Todd, 1993; Ketten *et al.*, 1998) has been attributed to anthropogenic noise from underwater explosive blasts. We were unable to determine whether the whale tested by Hall and Johnson (1972) was exposed to harmful levels of noise in its home range or during its capture. Of course it would be speculative to conclude that noise-induced hearing loss accounted for Hall and Johnson's (1972) subadult male *Orcinus* audiogram high-frequency cutoff of 32 kHz.

TABLE I. Overall mean behavioral and ABR thresholds at each frequency tested. The acoustic level is based on peak-to-peak values. The ABR thresholds are based on four replications (two for each whale) of wave PIII-NIV at a minimum 350 nV peak-to-peak response amplitude.

Frequency in kHz	Behavioral threshold dB *re* 1 μPa RMS	Physiological (ABR) threshold dB *re* 1 μPa Peak-to-Peak
1	*	105
2	*	72
4	61	75
8	57	52
12	45	60
16	46	50
20	34	37
32	46	40
45	48	45
60	52	65
80	65	78
100	75	116

In captivity it is possible that hearing loss could be caused by animal husbandry factors including ototoxic antibiotic treatments and tank noise. Captive odontocetes commonly receive antibiotics, but there is no record that the whale tested by Hall and Johnson was given ototoxic drugs or exposed to damaging levels of tank noise (personal communication, Dan Odell, Sea World, Orlando, FL, 1994). When Hall and Johnson's (1972) audiogram is considered in light of the current data, their results are consistent with a sensorineural high-frequency hearing loss that could have been due to one or more of the above-mentioned factors.

B. ABR and behavioral audiogram differences

The relationship between physiological and behavioral auditory thresholds is dependent upon organismal variables and stimuli characteristics, in addition to electrophysiological recording parameters. Elberling and Don (1987) suggested that the slope of the ABR amplitude function by stimulus intensity, and the magnitude of the averaged EEG background noise are the primary factors responsible for ABR detection and ABR audiogram thresholds. In killer whales, the background bioelectrical noise was greater and ABR signal magnitude less than in other odontocetes (Popov and Supin, 1990b). The small amplitude of the killer whale ABR is one factor that may account for some of the variability between the behavioral and ABR audiograms (Szymanski *et al.*, 1998). Two other contributing factors include: (1) natural variability in responsiveness, both behaviorally and physiologically, which can contribute to sensory threshold differences; and (2) variability in the received signal intensity and signal spectrum near the whale's head and at the whale's acoustic pathway during the ABR experiment.

During ABR collection, the acoustic environment was variable because the whale was at the water surface, a reflective boundary, and near a wall without sound absorption materials. Second, the acoustic path to the delphinid inner ear is a controversial subject. Therefore the hydrophone may not have been in the optimal position (Au and Moore, 1984), and may also have been in the near field. In this experiment we assumed the acoustic path to be via the acoustic window of the mandible, although some researchers have maintained a sound path exists around the external auditory meatus, and further that high- and low-frequency pathways may differ.

A result that merits discussion is the threshold similarity found in ABR and behavioral audiograms to tones of different duration. Thresholds to 1-ms tones in the mean ABR audiogram overall are within 12 dB of behavioral thresholds to tones 2000 times as long, and in the most sensitive region (18–42 kHz) are within 6 dB. In Tursiops, Johnson (1968) found behavioral thresholds decreased 15 to 30 dB with increasing duration over this magnitude. Unfortunately, we did not determine behavioral thresholds to tones of different duration as Johnson did, rather we collected behavioral thresholds to 2-sec tones and ABR thresholds to 0.5- and 1-ms tones, therefore our duration-of-tone burst data are a comparison of behavioral thresholds to electrophysiological thresholds and should not be necessarily consistent with Johnson's findings, in part because the ABR response is primarily an onset response.

In mammals it is common for ABR thresholds to be about 10–30 dB greater than behavioral thresholds (Gorga *et al.*, 1988). But in dolphins, behavioral and ABR thresholds share a greater correspondence (Johnson, 1967; Bullock *et al.*, 1968; Popov and Supin, 1990b). In terrestrial mammals the increased sensitivity of behavioral compared to ABR audiograms can in part be attributed to temporal integration and effective stimuli differences. Effective stimuli for evoking the ABR are brief tone bursts (5–10 ms) with rapid onsets compared to the longer tones (1–2 s) and slower onsets commonly used in behavioral audiometry. Behavioral thresholds typically decrease inversely with tone duration up to about 200 ms, according to data from terrestrial mammals. It is worth noting that dolphins have short temporal integration, about 0.5 ms near threshold, according to behavioral (Moore *et al.*, 1984) and ABR studies (Popov and Supin, 1990a).

Because the ABR is an onset response it seems likely there is little effect of temporal integration on ABR audiogram threshold. Nonetheless, in light of known delphinid specializations for rapid temporal integration, it would be interesting to examine onset effects on ABR thresholds more carefully. When an ABR is generated, the auditory system is responding to a broad band component of the signal and therefore there is some frequency ambiguity. Furthermore, in regard to sensitivity, the ABR and behavioral audiograms here should only be considered an estimate of Orcinus hearing thresholds because the received intensity was likely variable between (6–10 dB). Thus in the current study the ABR audiogram only can provide a rough estimate of hearing sensitivity at a given frequency.

C. Odontocete ABR audiograms: Effects of body and head size

The ABR technique, though less sensitive than behavioral measures when collapsed over all frequencies, provides a reasonable suprathreshold estimate of hearing range in Orcinus (+5 dB in the most sensitive range 18–42 kHz, and +22 dB at higher frequencies 60–100 kHz). The ABR audiogram curve follows the behavioral audiogram and in general corresponds with the shapes of Popov and Supin's (1990b) ABR audiograms from four smaller odontocete species. Our maximum ABR peak-to-peak signal levels, however, were an order of magnitude smaller, 1.2 μV compared to a range of 10 to 20 μV in Popov and Supin's (1990b) results. This difference can be explained by the larger body size of *Orcinus*, which has a brain–body mass ratio of 1:1000, compared to 1:100 in dolphins (Ridgway and Brownson, 1984; Szymanski *et al.*, 1995a; Szymanski *et al.*, 1998). In odontocetes, because ABR amplitude seems to decrease with a lower brain–body mass ratio, these results suggest the ABR may be difficult to collect from larger cetaceans, such as baleen whales, which have a lower brain–body mass ratio than odontocetes.

The most sensitive frequency for Orcinus was 20 kHz, in both behavioral and ABR audiograms. This represents the lowest frequency of best sensitivity known among odontocetes, mean threshold 36 dB [*re* 1 μPa], which is consistent with general mammalian audiometric findings that larger species have more sensitive lower frequency audiograms (Heffner and Heffner, 1982). Among odontocete audiograms the most sensitive frequency varies as a function of species, but within a species the sensitive audiogram region typically corresponds to the typical peak energy in echolocation clicks, e.g., ~20 kHz in orcinus (Hall and Johnson, 1972; Awbrey *et al.*, 1982), ~30 kHz in delphinapterus (White *et al.*, 1978); ~64 kHz in pseudorea (Thomas *et al.*, 1988); ~65 kHz in tursiops (Johnson, 1967; Kamminga and Beitsma, 1990); and ~130 kHz in *phocoena* (Anderson, 1970; Dubrovsky, Krasnov and Titov, 1971; Popov and Supin, 1990a). The killer whale auditory system fits this trend, an obvious selective advantage when orienting or hunting with biosonar clicks and echoes.

Because *Orcinus* hearing has the lowest most sensitive frequency and one of the lowest high-frequency limits among odontocetes, it seems plausible that *Orcinus* auditory function has been constrained by body size, following general mammalian trends. But *Orcinus* also demonstrates remarkably good high-frequency hearing for an animal its size, which reflects its status as an echolocating odontocete in the family delphinidae. The upper limit of hearing, 100 kHz for Orcinus, is more similar to those of other toothed dolphins and whales than has been previously reported.

ACKNOWLEDGMENTS

Support was granted by the U.S. National Academy of Sciences Collaboration in Basic Science and Engineering

Grant to M.D.S. and D.E.B., and Russian Foundation for Basic Research Grant 97-04-48377 to Aleksander Ya. Supin. Support was provided by the Marine World Foundation, its staff, and trainers. The authors thank Dr. Aleksandar Ya. Supin, Dr. Sam H. Ridgway, and three anonymous reviewers for comments on the work. This report is based on Ph.D. research by the first author, and is dedicated to the memory of Yaka, trainer Sonny Allen, and Dr. Ken Norris.

Anderson, S. (**1970**). ‘‘Auditory sensitivity of the harbor porpoise (*Phocoena phocoena*),’’ in *Investigations on Cetacea*, edited by G. Pilleri (Bentili, AG Berne Bumpliz, Berne, Switzerland), Vol. 2, pp. 255–259.

Au, W. W. L. (**1993**). *The Sonar of Dolphins* (Springer Verlag, New York).

Au, W. W. L., and Moore, P. W. B. (**1984**). ‘‘Receiving beam patterns and directivity indices of the Atlantic bottlenose dolphin *Tursiops truncatus*,’’ J. Acoust. Soc. Am. **75**, 255–262.

Awbrey, R. T., Thomas, J. A., Evans, W. E., and Leatherwood, S. (**1982**). ‘‘Ross Sea killer whale vocalizations: Preliminary description and comparison with those of some Northern Hemisphere killer whales,’’ Rep. Int. Whal. Comm. **32**, 667–670.

Awbrey, F. T., Thomas, J. A., and Kastelein, R. A. (**1988**). ‘‘Low frequency underwater hearing sensitivity in belugas (*Delphinapterus leucas*),’’ J. Acoust. Soc. Am. **84**, 2273–2275.

Bain, D. E., and Dalheim, M. E. (**1994**). ‘‘Effects of masking noise on detection thresholds of killer whales,’’ in *Consequences of the Exxon Valdez Oil Spill*, edited by T. Loughlin (Academic, New York), pp. 243–256.

Bain, D. E. (**1992**). ‘‘Hearing abilities of killer whales (*Orcinus orca*),’’ National Marine Mammal Laboratory Contract Report #43ABNF00249 and #43ABNF002500, pp. 1–20.

Barrett-Lennard, L. G., Ford, J. K. B., and Heise, K. A. (**1996**). ‘‘The mixed blessing of echolocation differences in sonar use by fish-eating and mammal-eating killer whales,’’ Anim. Behav. **51**, 553–565.

Belkovich, V. M., and Solntseva, G. N. (**1970**). ‘‘Anatomy and function of the ear in dolphins,’’ J. Comparative Zoo. **2**, 275–282.

Bibikov, N. G. (**1992**). ‘‘Auditory brainstem responses in the harbor porpoise (*Phocoena phocoena*),’’ in *Marine Mammal Sensory Systems*, edited by J. Thomas, R. A. Kastelein, and A. Ya. Supin (Plenum, New York), pp. 197–211.

Bohne, B., Thomas, J., Yohe, E., and Stone, S. (**1985**). ‘‘Examination of potential hearing damage in Weddell seals (*Leptonychotes weddelli*) in McMurdo Sound, Antarctica,’’ Antarctic J. U.S. **20**, 174–176.

Brill, R. L., Sevenich, M. L., Sullivan, T. J., Sustmen, J. D., and Witt, R. E. (**1988**). ‘‘Behavioral evidence for hearing through the lower jaw by an echolocating dolphin (*Tursiops truncatus*),’’ Mar. Mam. Sci. **4**, 223–230.

Bullock, T. H., Grinnell, A. D., Ikezono, E., Kameda, K., Katsuki, Y., Nomoto, M., Sato, O., Suga, N., and Yanagisawa, K. (**1968**). ‘‘Electrophysiological studies of central auditory mechanisms in cetaceans,’’ J. Comp. Physiol. **59**, 117–156.

Bullock, T. H., and Ridgway, S. H. (**1972**). ‘‘Evoked potentials in the central auditory system of alert porpoises to their own and artificial sounds,’’ J. Neurobiol. **3**, 79–99.

Carder, D. A., and Ridgway, S. H. (**1991**). ‘‘Auditory brainstem response in a neonatal sperm whale, Physeter spp.,’’ J. Acoust. Soc. Am. Suppl. 1 **88**, S4.

Dalheim, M. E., and Awbrey, F. (**1982**). ‘‘A classification and comparison of vocalizations of captive killer whales,’’ J. Acoust. Soc. Am. **72**, 661–670.

Diercks, K. J., Trochta, R. T., Greenlaw, C. F., and Evans, W. E. (**1971**). ‘‘Recording and analysis of dolphin echolocation signals,’’ J. Acoust. Soc. Am. **49**, 1729–1732.

Dolphin, W. F. (**1995a**). ‘‘The envelope following response in three species of cetaceans,’’ in *Sensory Systems of Aquatic Mammals*, edited by R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall (De Spil, Woerden, The Netherlands), pp. 197–211.

Dolphin, W. F., Au, W. W. L., and Nachtigall, P. (**1995b**). ‘‘Modulation transfer function to low-frequency carriers in three species of cetaceans,’’ J. Comp. Physiol. A **177**, 235–295.

Dubrovsky, N. A., Krasnov, P. S., and Titov, A. A. (**1971**). ‘‘On the emission of echolocation signals by the Azov harbor porpoise,’’ Sov. Phys. Acoust. **16**, 444–447.

Elberling, C., and Don, M. (**1987**). ‘‘Threshold characteristics of the human auditory brain stem response,’’ J. Acoust. Soc. Am. **81**, 115–121.

Ford, J. K. B. (**1989**). ‘‘Acoustic behavior of resident killer whales (*orcinus orca*) off Vancouver Island, British Columbia,’’ Can. J. Zoo. **67**, 727–745.

Gorga, M. P., Kaminski, J. R., Beauchaine, K. A., and Jesteadt, W. (**1988**). ‘‘Auditory brainstem responses to tone bursts in normally hearing subjects,’’ J. Speech Hear. Res. **31**, 87–97.

Hall, J. D., and Johnson, C. S. (**1972**). ‘‘Auditory thresholds of a killer whale *Orcinus orca Linneaus*,’’ J. Acoust. Soc. Am. **51**, 515–517.

Heffner, R. S., and Heffner, H. E. (**1982**). ‘‘Hearing in the elephant (*Elphas Maximus*): Absolute sensitivity, frequency discrimination, and sound localization,’’ J. Comp. Physiol. Psychol. **96**, 926–944.

Jacobs, D. W., and Hall, J. D. (**1972**). ‘‘Auditory thresholds of a fresh water dolphin, *Inia geoffrensis* Blainville,’’ J. Acoust. Soc. Am. **51**, 530–533.

Johnson, C. S. (**1968**). ‘‘Relation between absolute threshold and duration-of-tone pulses in the bottlenosed porpoise,’’ J. Acoust. Soc. Am. **43**, 757–763.

Johnson, C. S. (**1967**). ‘‘Sound detection thresholds in marine mammals,’’ in *Marine Bio-Acoustics*, edited by W. N. Tavolga (Pergamon, New York), Vol. 2, pp. 247–260.

Kamminga, C. A., and Beitsma, G. R. (**1990**). ‘‘Investigations on cetacean sonar IX: Remarks on dominant sonar frequencies from *Tursiops truncatus*,’’ Aquat. Mam. **16**, 14–20.

Ketten, D., Lien, J., and Todd, S. (**1993**). ‘‘Blast injury in humpback whale ears: Evidence and implications,’’ Invited paper, J. Acoust. Soc. Am. **94**, 1849–1850.

Ketten, D., Moore, P. W. B., Dankiewicz, L. A., Brill, R. A., and Van Bonn, W. (**1998**). ‘‘The slippery slope of a Johnsonian ear: Natural variability versus natural loss,’’ J. Acoust. Soc. Am. **102**, 3101.

Ladygina, T. F., and Supin A. Ya. (**1970**). ‘‘The acoustic projection in the dolphin cerebral cortex,’’ Fiz. Zh. SSSR **56**, 1554–1560.

Moore, P. W. B., Hall, R. W., Friedl, W. A., and Nachtigall, P. E. (**1984**). ‘‘The critical interval in dolphin echolocation: What is it?’’ J. Acoust. Soc. Am. **76**, 314–417.

Popov, V. V., and Supin, A. Ya. (**1985**). ‘‘Determination of characteristics of dolphin hearing using brain stem evoked potentials,’’ Dokl. Akad. Nauk SSSR **283**, 496–499.

Popov, V. V., and Supin, A. Ya. (**1990a**). ‘‘Auditory brain stem responses in characterization of dolphin hearing,’’ J. Comp. Physiol. A **166**, 385–393.

Popov, V. V., and Supin, A. Ya. (**1990b**). ‘‘Electrophysiological studies of hearing in some cetaceans and manatee,’’ in *Sensory Abilities of Cetaceans*, edited by J. A. Thomas and R. A. Kastelein (Plenum, New York), pp. 405–415.

Richardson, W. J., Greene, C. R., Jr., Malme, C. I., and Thomson, D. H. (**1991**). ‘‘Effects of noise on marine mammals,’’ USDI/MMA/OCS study 90-0093, LGL Ecological Research Assoc., Bryan, Texas.

Richardson, W. J., Greene, C. R., Jr., Malme, C. I., and Thomson, D. H. (**1995**). *Effects of Noise on Marine Mammals* (Academic, San Diego), pp. 576.

Ridgway, S. H., and Brownson, R. H. (**1984**). ‘‘Relative brain sizes and cortical surface areas in odontocetes,’’ J. Comparative Bio. **172**, 149–152.

Ridgway, S. H., Bullock, T. H., Carder, D. A., Seeley, R. L., Woods, D., and Galambos, R. (**1981**). ‘‘Auditory brainstem response in dolphins,’’ Proc. Natl. Acad. Sci. USA **78**, 1943–1947.

Ridgway, S. H., and Carder, D. A. (**1993**). ‘‘High-frequency hearing loss in old (25+ years old) male dolphins,’’ J. Acoust. Soc. Am. **94**, 1830.

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

Sauerland, M., and Dehnhardt, G. (**1998**). ‘‘Underwater audiogram of a tucuxi (*Sotalia fluviatilis guianensis*),’’ J. Acoust. Soc. Am. **103**, 1199–1204.

Szymanski, M. D., Bain, D. E., and Henry, K. R. (**1995a**). ‘‘Auditory evoked potentials of a killer whale (*Orcinus orca*),’’ in *Sensory Systems of Aquatic Mammals*, edited by R. A. Kastelein, J. A. Thomas, and P. E. Nachtigall (De Spil, Woerden, The Netherlands), pp. 1–10.

Szymanski, M. D., Supin, A. Ya, Henry, K. R., and Bain, D. E. (**1995b**). ‘‘The killer whale (*Orcinus orca*) auditory system assessed with evoked potentials: Click rates and audiograms,’’ The 11th Biennial Conference on the Biology of Marine Mammals, Soc. Mar. Mam. Abstracts.

Szymanski, M. D., Supin, A. Ya., Bain, D. E., and Henry, K. R. (**1998**). ‘‘Killer whale auditory evoked potentials to rhythmic clicks,’’ Mar. Mam. Sci. **14**(4), 676–691.

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

Tremmel, D. P., Thomas, J. A., Ramirez, K. T., Dye, G. S., Bachman, W. A., Orban, A. N., and Grim, K. K. (**1998**). ''Underwater hearing sensitivity of a Pacific white-sided dolphin *Lagenorhynchus obliquidens*,'' Aquat. Mam. **24**, 63–69.

White, M. J., Jr, Norris, J., Ljungblad, D., Baron, K., and di Sciara, G. (**1978**). ''Auditory thresholds of two beluga whales (*Delphinapterus leucas*),'' in HSWRI Tech. Rep. No. 78-109, Hubbs Marine Research Institute, San Diego, CA.