

Psychophysical and electrophysiological aerial audiograms of a Steller sea lion (*Eumetopias jubatus*)^{a)}

Jason Mulsow^{b)}

Department of Ocean Sciences, Long Marine Laboratory, University of California, Santa Cruz, 100 Shaffer Road, Santa Cruz, California 95060

Colleen Reichmuth

Institute of Marine Sciences, Long Marine Laboratory, University of California, Santa Cruz, 100 Shaffer Road, Santa Cruz, California 95060

(Received 23 August 2009; revised 21 January 2010; accepted 25 January 2010)

A within-subject comparison of auditory steady-state response (ASSR) and psychophysical measurements of aerial hearing sensitivity was conducted with an individual of the largest otariid species, the Steller sea lion. Psychophysical methods were used to obtain an unmasked aerial audiogram at 13 frequencies, spanning a range of 0.125–34 kHz. The subject had a hearing range (frequencies audible at 60 dB_{rms} re 20 μ Pa) of about 0.250–30 kHz, and a region of best hearing sensitivity from 5–14.1 kHz. The psychophysical aerial audiogram of this Steller sea lion was remarkably similar to aerial audiograms previously obtained for California sea lions and northern fur seals, suggesting that the otariid pinnipeds form a functional hearing group. ASSR thresholds, measured at frequencies of 1, 2, 5, 10, 20, and 32 kHz, were elevated relative to corresponding psychophysical thresholds, ranging from +1 dB at 20 kHz, to +31 dB at 1 kHz. The ASSR audiogram accurately predicted the subject's high-frequency cutoff, and provided a reasonable estimate of hearing sensitivity at frequencies above 2 kHz. In testing situations where psychophysical methods are not possible, ASSR methods may provide an objective and efficient estimate of behavioral hearing sensitivity in otariid pinnipeds.

© 2010 Acoustical Society of America. [DOI: 10.1121/1.3327662]

PACS number(s): 43.80.Lb, 43.64.Ri [WWA]

Pages: 2692–2701

I. INTRODUCTION

The otariid pinnipeds (family *Otariidae*, the sea lions and fur seals) lead an amphibious existence, foraging at sea, and carrying out reproductive functions in coastal haul-out areas. Aerial vocalizations are critical for communication among individuals in these crowded rookeries (see [Schusterman and Van Parijs, 2003](#) for a review). For example, the vocalizations emitted by mature males are used to maintain breeding territories ([Peterson and Bartholomew, 1969](#); [Fernandez-Juricic et al., 2001](#); [Gwilliam et al., 2008](#)), and vocal interactions aid in the reunion of mothers and pups in crowded breeding colonies ([Insley et al., 2003](#)).

Despite the importance of aerial acoustic cues to otariid reproductive behavior, aerial hearing sensitivity curves (audiograms) have been reported for only two of the 14 otariid species: the California sea lion (*Zalophus californianus*) and the northern fur seal (*Callorhinus ursinus*). Following the first otariid aerial audiogram obtained with a California sea lion ([Schusterman, 1974](#)), [Moore and Schusterman \(1987\)](#) conducted refined aerial hearing sensitivity measurements

with one California sea lion and two northern fur seal subjects using psychophysical methods in a sound-attenuating booth. The audiograms of all three individuals displayed generally similar characteristics: a gradual increase in sensitivity from the low frequencies up to 2 kHz, best sensitivity near 8 to 16 kHz, and a sharp loss in sensitivity indicating an upper-frequency limit between 16 and 32 kHz. [Babushina et al. \(1991\)](#) reported a similar aerial audiogram for a northern fur seal with a range of best hearing sensitivity from 2–16 kHz.

In addition to providing comparative data on marine mammal auditory function, the few published investigations on aerial hearing in otariids have been important in designing criteria to mitigate the negative effects of anthropogenic noise in coastal marine environments (e.g., [Southall et al., 2007](#)). However, the available data are limited to small sample sizes of captive individuals, making it difficult to form conclusions regarding the variability of hearing sensitivity among individuals within a population, as well as between otariid species. This lack of basic information has led to recommendations that the number of otariid individuals and species for which hearing data exists should be increased ([National Research Council 2000, 2005](#)).

A method which has shown promise for objectively estimating hearing sensitivity in an increased number of marine mammals is the recording of the auditory brainstem response (ABR), which comprises electrophysiological responses generated by the auditory system following acous-

^{a)} Portions of this research were presented at the Second International Conference on Acoustic Communication by Animals in Corvallis, Oregon, August 12–15, 2008, and the 157th meeting of the Acoustical Society of America in Portland, Oregon, May 18–22, 2009.

^{b)} Author to whom correspondence should be addressed. Current address: U.S. Navy Marine Mammal Program, Space and Naval Warfare Systems Center, San Diego, Code 71510, 53560 Hull Street, San Diego, California 92152. Electronic mail: jason.mulsow@gmail.com

tic stimulation. Hearing screening using ABR methods is a rapid and non-invasive procedure that does not require the training of subjects, and is now a standard procedure with newborn infants in the United States (see Hall, 2007). In order to extend ABR-based methods to pinnipeds, Wolski *et al.* (2003) measured aerial hearing sensitivity using both behavioral and ABR methods in an individual harbor seal (*Phoca vitulina*). The electrophysiological thresholds, defined as the lowest stimulus level for which an ABR elicited by tone bursts was visually detectable, were reasonable predictors of behavioral thresholds. Electrophysiological methods therefore appear to provide a means of efficiently estimating behavioral hearing sensitivity in pinnipeds.

The traditional methods of visually detecting ABRs in electrophysiological recordings are subjective, and may be prone to high variability as a result of inter-observer detection biases and extraneous electrical noise in recordings (e.g., Arnold, 1985; Vidler and Parker 2004). As a means of reducing such confounding effects in the detection of an ABR, objective statistical detection of an auditory evoked potential can be facilitated in the frequency domain through the measurement of the auditory steady-state response (ASSR). ASSRs can be recorded as rhythmic potentials generated by the auditory brainstem that are phase-locked to a modulation pattern (i.e., amplitude modulation) imposed on an acoustic stimulus (Kuwada *et al.*, 1986; Lins *et al.*, 1995, Kuwada *et al.*, 2002). Thus, an ASSR can be detected in the frequency-domain representation of the electrophysiological record as a spectral peak present at the stimulus modulation rate. The application of ASSR methods has recently proven to be useful for measuring the hearing sensitivity of odontocete cetaceans (dolphins and porpoises) in a number of settings where behavioral methods were not readily available (Nachtigall *et al.*, 2005, 2008a; Cook *et al.*, 2006; Houser *et al.*, 2008; Supin *et al.*, 2001).

In order to determine if ASSR methods can provide a useful prediction of behaviorally measured hearing sensitivity in otariids, we measured unmasked aerial hearing sensitivity in a 1-year-old male Steller sea lion (*Eumetopias jubatus*) using both psychophysical and ASSR methods. The Steller sea lion, the largest of otariid species, inhabits a range in the North Pacific from Japan to the central coast of California (Loughlin *et al.*, 1984; National Research Council, 2003). This species has garnered recent attention due to an 80% population decline over the last 3 decades, and its listing in 1997 as an Endangered Species under the United States Endangered Species Act (National Research Council, 2003). This study was completed while the Steller sea lion subject was temporarily housed at Long Marine Laboratory in Santa Cruz, California, prior to his transfer to a permanent captive facility. This opportunity allowed for the first measurements of aerial hearing sensitivity to be made for this endangered species, and enabled a direct comparison of hearing thresholds obtained using psychophysical and ASSR methods.

II. MATERIALS AND METHODS

A. Psychophysical audiogram

1. Subject

The subject of the study was a 1-year-old male Steller sea lion identified as “Astro” (NMFS Identification Number: NOA0006398). For the duration of the psychophysical study, the sea lion was housed in a saltwater pool with adjacent haul-out areas at Long Marine Laboratory, at the University of California, Santa Cruz. His diet consisted of a mix of fish (herring and capelin, 6.8 kg total per day), approximately one-third to one-half of which was provided during experimental sessions. The subject was previously naive to psychophysical research, but had participated in training for husbandry purposes. Training for audiometric sessions was initiated on January 1, 2008. Data collection took place during the period of January 14, 2008 to February 25, 2008, with one to two audiometric sessions conducted per day.

2. Experimental apparatus and testing environment

All sessions were conducted in a $4.0 \times 2.8 \times 2.4$ m³ hemi-anechoic, sound-attenuating chamber (Eckel Industries), previously described by Holt *et al.* (2004a). The experimental apparatus consisted of a 52 cm tall PVC chin cup that served as a station, placed 1 m in front of the speakers used for test signal production (see Sec. II A 3 below), and a 9×9 cm² PVC response target placed 50 cm to the left of the chin cup. In order to indicate the time interval that delineated individual trials, a small “trial light” was placed immediately next to the speaker. A second speaker (Audiovox Advent AD570), used to produce a bell tone marking a correct response, was placed on the floor to the right of the subject, near the front wall of the chamber.

One of two trainers was present in the test chamber for all experimental sessions. During a session, the trainers wore headphones with sound-attenuating earmuffs that rendered them unable to hear test stimuli. The subject was therefore unable to gain information regarding the presence or absence of an acoustic signal, based on inadvertent cues from the trainer. The experimenter was located in an adjacent $1.3 \times 2.8 \times 2.4$ m³ control room, and monitored the sessions using surveillance cameras and a monitor. Thus, both the subject and the trainer were out of visual and auditory contact with the experimenter during data collection.

3. Acoustic stimuli and calibration

Test stimuli were pure tones of 500 ms duration with a linear rise-fall time of 40 ms. This duration was chosen as it exceeds the temporal integration time constant for otariids, below which threshold is dependent on stimulus duration (Holt *et al.*, 2004b; Ghoul *et al.*, 2009). Stimuli were generated by a custom National Instruments LABVIEW virtual instrument, and sent through a National Instruments PXI-6229 data acquisition (DAQ) card with an attached National Instruments BNC-2120 breakout box. Signals were then attenuated with a Tucker-Davis Systems PA5 programmable attenuator, followed by band-pass filtering using a Krohn-Hite 3550 filter. In some cases (0.125, 0.25, 4, 28.2, and 34

kHz), outgoing stimuli were amplified using a Hafler Trans Ana P1000 power amplifier. The stimuli were projected using one of four speakers, depending on frequency: a JBL 2245H low frequency loudspeaker (0.125 kHz), JBL 2123H/J midrange transducer (0.250, 0.500, 1, 2, 4, and 5 kHz), JBL 2404H ultra-high frequency transducer (5, 10, and 14.1 kHz), or a Fostex FT96H Horn Super Tweeter (20, 28.2, 30, and 34 kHz).

Signals were calibrated before and after each audiometric session in the absence of the subject using either a Josephson engineering C550H microphone (0.02–20 kHz \pm 2 dB) or an Aco-Pacific 7016 microphone (0.005–120 kHz \pm 2 dB), placed at the position corresponding to the center of the subject's head during testing. The incoming calibration signal was band-pass filtered to prevent aliasing, amplified by 20 dB using a Krohn-Hite 3364 filter, and then sent through the BNC-2120 breakout box to the PXI-6229 DAQ card. Signal SPLs (dB_{rms} re 20 μ Pa) were calibrated in the LABVIEW virtual instrument using an averaged FFT with a flat top window. In addition to this standard calibration procedure, the sound field was measured at every frequency at three points in a 20 cm transect (10 cm increments approximating a line through the ears) to ensure that the calibration point was indicative of the subject's received levels. For all frequencies, except for 10 and 20 kHz, the levels measured at each location were within \pm 3 dB of the calibration location at the center of the chin station. Sound levels at 10 and 20 kHz differed from those at the center of the chin station by \pm 4 dB and \pm 6 dB, respectively.

Noise levels were measured in the testing chamber with a Brüel & Kjær 2250 sound level meter (1-min unweighted recording, 1/3-octave band analysis), placed at a position corresponding to the center of the subject's head. Noise measurements at frequencies higher than 20 kHz were not available due to limitations of the B&K 2250, however, some explorative measurements were made using the Aco-Pacific 7016 microphone and a spectrum analyzer.

4. Test procedure

The experimental task was a go/no-go procedure, in which the subject was trained to touch the response target, placed immediately to the left of the chin station when he perceived a signal as being present, and to remain motionless at the chin station when a signal was not detected. When the subject oriented toward the speaker with his head placed firmly within the chin station, the experimenter signaled the beginning of a trial by turning on the trial light located in front of the subject. Both signal-absent and signal-present trials were 4 s in duration, during which time the trial light remained on. In the case of a signal-present trial, the test tone was presented in an unpredictable fashion by varying the delay at which it was triggered within the 4 s window. If the subject touched the response target after the test tone was presented (a *hit*), the bell tone marking a correct response was played through the AD570 speaker, and the trainer rewarded the sea lion with one capelin. The subject was similarly rewarded for remaining motionless in the chin station for the entire 4 s duration of a signal-absent trial (a *correct rejection*). When the subject responded by touching the re-

sponse target on a signal-absent trial (a *false alarm*), or failed to respond during the 4 s trial interval on a signal-present trial (a *miss*), the trial light was turned off, no reward was provided, and the following trial was initiated, following a short delay. In the case that the subject pressed the response target before the presentation of signal, the response was scored as a false alarm. The experiment was double-blind in nature, in that both the subject and the trainer did not have any *a priori* knowledge of the trial type.

An adaptive up-down descending methods of limits, or staircase, procedure was used to determine hearing thresholds at each frequency (Cornsweet, 1962). At the start of each session, initial signal levels were set to a "warm-up" level, approximately 25 dB above the subject's predicted threshold. The signal level was attenuated by 4 dB after each hit until the first miss. After this point, all signal level adjustments were made in 2 dB increments, with the signal level elevated by 2 dB following each miss and attenuated by 2 dB following each hit. Trials were conducted in this fashion until nine reversals (transitions from miss to hit, and vice versa) had occurred. After the ninth reversal, the signal was re-elevated to the starting level, and a "cool-down" phase consisting of six trials was conducted. Sessions typically comprised 45 to 50 trials and lasted approximately 10 min. Signal-present and signal-absent trials were generated in a pseudo-random order. The probability of a signal-present trial occurring was 50%, 60%, or 65% (adjusted between sessions over the course of the experiment in order to maintain a response bias corresponding to a false alarm rate between 0% and 30%).

5. Data analysis

Thresholds for individual sessions were calculated in the fashion of Dixon and Mood (1948) using signal-present trial data from the first through the ninth reversal. Data collection for a threshold was complete when the subject had reached a stable threshold (i.e., a standard deviation of less than or equal to 3 dB for three consecutive sessions at a given frequency), and the average false alarm rate of the three sessions was greater than 0% and less than 30%. Final thresholds were calculated as the mean of these three consecutive sessions. The threshold at 20 kHz was the only exception to these criteria; data collection at this frequency was completed with a false alarm rate of 0% due to time constraints.

The thresholds obtained in this experiment were compared to the results of a previous study of underwater hearing in one male and one female Steller sea lion reported by Kastelein *et al.* (2005). Comparisons were made, both using sound pressure and sound intensity (assuming plane-wave propagation) as the relevant metric of sound detection [see Kastak and Schusterman (1998), regarding aerial and underwater hearing comparisons in pinnipeds]. Pressure comparisons were made by converting underwater thresholds (reported originally in dB_{rms} re 1 μ Pa by Kastelein *et al.*) to dB_{rms} re 20 μ Pa. Sound intensity thresholds were estimated in W/m² using the following relationship for plane-wave propagation conditions:

$$I = p^2 / \rho c, \quad (1)$$

where I is sound intensity in W/m^2 , p is rms sound pressure in Pa, ρ is the density of the medium (estimated at values of $\rho=1.2 \text{ kg}/\text{m}^3$ for air, $\rho=1030 \text{ kg}/\text{m}^3$ for seawater), and c is the speed of sound in the medium (estimated at values of $c=340 \text{ m}/\text{s}$ for air, $c=1500 \text{ m}/\text{s}$ for seawater) (Kinsler *et al.*, 1982). It should be noted that the values for density and sound speed are estimates, and that plane-wave sound propagation conditions likely did not exist in the pool where the underwater pressure thresholds were obtained; thus, sound intensity thresholds can only be approximated.

B. ASSR audiogram

1. Testing environment and subject state

Collection of electrophysiological data took place three months after the completion of the psychophysical study, following the subject's transport to Mystic Aquarium and Institute for Exploration for permanent housing. ASSR recordings were obtained in a veterinary surgery room, following the completion of an unrelated surgical procedure. Prior to the surgical procedure, the subject was administered with an intra-muscular injection of 30 mg of diazepam, 19.5 mg midazolam, and 2.6 mg medetomidine. Following intubation, 1%–2% isoflurane was used to keep the subject unconscious for the surgery and subsequent ASSR data collection. He was positioned in ventral recumbence and monitored continuously by the attending veterinarian and veterinary technicians during the ASSR recording procedure.

2. Acoustic stimuli and calibration

Thresholds were determined for sinusoidally amplitude-modulated (SAM) pure tone stimuli with carrier frequencies matched to five of the data points from the psychophysical audiogram: 1, 2, 5, 10, and 20 kHz. During the ASSR experiment, 32 kHz was tested instead of 34 kHz, due to the limitations of the headphones and the calibration microphone used in the experiment (see below). The SAM tones were continuous on a given trial to avoid “stimulus-on” or “stimulus-off” neural potentials in the ASSR recordings, and the polarities of the waveforms alternated between positive and negative on successive presentations to reduce electrical artifacts in the ASSR records. The rate of amplitude modulation for the SAM tones was 153.9 Hz. Following generation using the Evoked Response Study Tool (EVREST) (Finneran, 2009) and digital-to-analog conversion by a USB-6251 DAQ card, the SAM signals were first passed through a Krohn-Hite 3C series low-pass filter module (–3 dB at 150 kHz), and then passed through a custom attenuator controlled by EVREST. The conditioned signals were sent binaurally to a pair of Telephonics TDH-39 headphones, which had been custom fit with sound-attenuating supra-aural “earmuffs” (3 to 17 dB of noise attenuation at test frequencies) designed to fit over the subject's ears without altering the natural orientation of the pinnae.

Signal calibration levels for the each of the tested frequencies were based on mean SPLs measured during electrophysiological testing of sea lion subjects conducted prior to this procedure using a similar experimental set-up. For these calibrations, an Etymotic ER-7C probe microphone

(0.25–10 kHz \pm 2.5 dB) was placed underneath a subject's headphone near the meeting of the pinna and the scalp. Incoming electrical signals from the microphone were low-pass filtered using a second Krohn-Hite 3C series filter module to prevent aliasing (–3 dB at 200 kHz), followed by analog-to-digital conversion with the USB-6251 card and subsequent recording and coherent averaging by EVREST. The frequency responses of the two headphones were similar there was less than 3 dB difference at all test frequencies. For frequencies above the nominal range of the ER-7C microphone, calibration values were corrected, based on the microphone's frequency response.

Ambient noise levels were measured immediately following data collection using a custom LABVIEW virtual instrument and the Etymotic ER-7C probe microphone placed underneath the subject's Telephonics TDH-39 headphones.

3. ASSR collection

ASSRs were recorded using a three-electrode montage comprising Grass F-E3M-72 12 mm \times 30 gauge stainless steel subdermal needle electrodes. An active (non-inverting) electrode was placed on the dorsal midline of the subject's head, midway between the ears, a reference (inverting) electrode was placed on the subject's dorsal midline, just posterior to the nape of the neck and near the scapula, and a ground electrode was placed just posterior to the ribcage. Incoming electrophysiological signals were amplified 100,000 times and bandpass filtered (0.1 to 1 kHz, –6 dB at cutoffs) using a Grass IP511 differential bio-potential amplifier. Following amplification and filtering, electrophysiological signals underwent analog-to-digital conversion with the USB-6251 card. The EVREST software sampled ($F_s = 5.618 \text{ kHz}$), recorded, and averaged the ASSR waveforms over a 64.97 ms recording window. An FFT (rectangular window) of the averaged 64.97 ms window was used to transform the electrophysiological record into the frequency domain. The 64.97 ms duration of the window allowed for a frequency bin in the spectra that was centered at the 153.9 Hz modulation rate. Any recording window containing a voltage of absolute peak magnitude greater than 25 μV was considered to contain spurious electrical artifacts, and was therefore rejected without being included in the waveform average. The first four epochs at a given level were also automatically rejected from each record to avoid the inclusion of onset responses to the SAM signal.

Up to 2000 individual 64.97 ms epochs were coherently averaged in real time in order to eliminate extraneous electrical noise. At intervals of 250 epochs, a magnitude-squared-coherence (MSC) test was used to determine if an ASSR at the 153.9 Hz modulation rate was present in the record. The MSC test created 20 sub-averages from the grand average record, and provided a ratio of the power at the SAM modulation rate in the grand average to the average power at the modulation rate in the sub-averages (Dobie and Wilson, 1989, 1995). An ASSR was considered to be present if the MSC statistic was larger than a critical value at the level of $\alpha=0.01$ (critical values obtained from Amos and

TABLE I. Aerial hearing thresholds for a juvenile male Steller sea lion obtained using psychophysical methods. The mean thresholds are the average of the three consecutive session thresholds reported. Also shown are the average false alarm rates for each frequency and the order in which testing occurred for each frequency.

Frequency (kHz)	Mean threshold (dB re 20 μ Pa)	Session thresholds (dB re 20 μ Pa)	False alarm (%)	Testing order
0.125	66	68, 65, 67	25	10
0.25	55	54, 54, 57	17	8
0.5	43	45, 43, 40	13	7
1	21	22, 21, 20	25	5
2	29	29, 29, 29	24	3
4	20	22, 19, 18	26	9
5	8	7, 10, 8	12	1
10	7	7, 7, 7	6	2
14.1	14	16, 12, 15	17	11
20	29	29, 30, 29	0	4
28.2	39	38, 39, 39	25	12
30	54	52, 54, 56	12	6
34	81	79, 82, 82	15	13

Koopmans, 1963 and Brillinger, 1978). If an ASSR was not detected using the MSC test after 2000 averaged epochs, it was considered that no ASSR was present.

For threshold determination, SAM stimuli at each frequency were set to an initial level assumed to be above the subject's threshold. In the case of a hit at this level (an ASSR was detected using the MSC test), the signal for the subsequent trial was then attenuated 10 dB relative to the previous level. A miss was scored when a statistically significant ASSR was not detected after 2000 epochs. Following the first miss, a signal level 5 dB above the miss was tested. Thresholds at each frequency were defined as the signal level corresponding to the lowest detectable response. Before thresholds were accepted at a frequency, two misses at 5 and 10 dB below the lowest hit were collected to confirm that threshold had been reached. The total time for collection of the ASSR audiogram was approximately 70 min.

III. RESULTS

A. Psychophysical audiogram

The subject's aerial thresholds and false alarm rates at each frequency tested are provided in Table I, and the psychophysical audiogram is shown in Fig. 1. The audiogram had a U-shape with a shallow low frequency roll-off below 1 kHz, and a steep high-frequency roll-off above 28.2 kHz. The subject's hearing range (defined as the range of frequencies audible at 60 dB SPL) was about 0.250 kHz to 30 kHz. Maximum sensitivity of 7 dB SPL was found at 10 kHz, with a range of best hearing (defined as the range of frequencies audible at 10 dB above maximum sensitivity) of 5 to 14.1 kHz. The shape of the audiogram was remarkably similar to aerial audiograms previously obtained for two other otariid species (Fig. 2). A prominent feature of this Steller sea lion's audiogram was an increase in sensitivity at 1 kHz, relative to 0.500 kHz, followed by a decrease in sensitivity at 2 kHz.

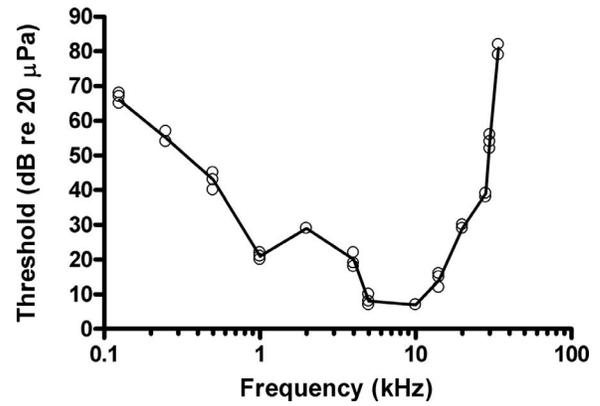


FIG. 1. Aerial audiogram for a juvenile male Steller sea lion obtained using psychophysical methods. Thresholds for three individual sessions per frequency (from Table I) are shown with open circles. The contour of the mean of the three session thresholds is shown by a solid black line.

Thresholds and false alarm rates among sessions for each frequency were fairly consistent and allowed for false alarm rate and threshold standard deviation criteria (see Sec. II above) to be met over the course of a few days of testing. A single exception to this occurred during testing at 20 kHz, where the subject's false alarm rate was consistently 0%. Due to the unusually conservative response bias at this frequency, the threshold value of 29 dB SPL at 20 kHz may be an underestimation of sensitivity relative to other frequencies.

Noise spectral density levels in the test chamber (Fig. 3(a)) decreased with increasing frequency; levels fell below 0 dB re (20 μ Pa)²/Hz above 0.200 kHz, and were generally limited by the self-noise of the B&K 2250 (-20 dB re (20 μ Pa)²/Hz) from 1.25–20 kHz. Exploratory measurements with the Aco-Pacific 7016 microphone indicated that noise levels appeared to be sufficiently low to prevent masking of thresholds above 20 kHz.

The underwater thresholds obtained by Kastelein *et al.* (2005) are shown with the aerial audiogram from our Steller sea lion subject in Fig. 4. When comparisons are made in terms of sound pressure [Fig. 4(a)], all thresholds were lower in air with the exception of the highest frequencies tested by Kastelein *et al.* The underwater thresholds were lower than aerial thresholds at the low and high ends of the audiogram when sound intensity was used as the relevant metric of de-

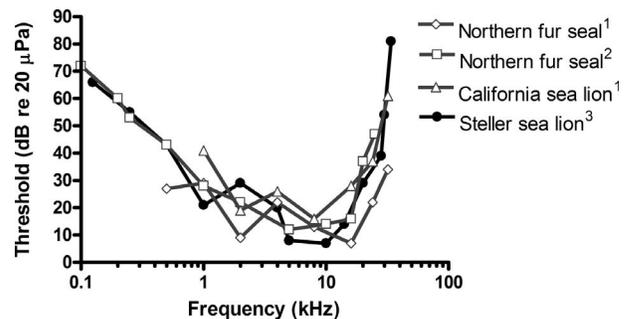


FIG. 2. Aerial audiograms for three species of otariid obtained using psychophysical methods: ¹Moore and Schusterman, 1987, California sea lion ($n=1$), northern fur seals ($n=2$); ²Babushina *et al.*, 1991, northern fur seal ($n=1$); ³this study.

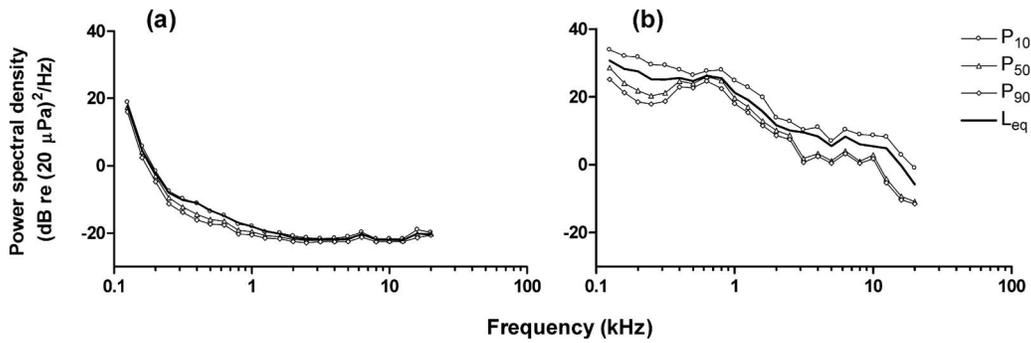


FIG. 3. Ambient noise in (a) the sound-attenuating chamber used for the behavioral audiogram and (b) the surgery room in which the ASSR audiogram was conducted. Noise levels for the ASSR audiogram were further attenuated by headphones placed over the subject's ears. Power spectral density levels are derived from 1-min unweighted recordings using 1/3-octave band analysis. The 10th, 50th, and 90th percentiles of the noise level distribution are shown in addition to the L_{eq} . Note the positive skew of the noise level distribution in the surgery room due to the intermittent activity of the anesthesia ventilator.

tection [Fig. 4(b)]. However, estimated aerial intensity thresholds were lower than estimated underwater intensity thresholds in the range of best hearing sensitivity (5–14.1 kHz) for the subject of the present study.

B. ASSR audiogram

The last detectable ASSR responses at each tested frequency, determined using the MSC test described in Sec. II (above), are provided in Table II. A comparison with the psychophysical audiogram obtained for this subject shows that there is a good agreement between thresholds obtained using the two methods (Fig. 5). All ASSR thresholds were elevated above psychophysical thresholds obtained at corre-

sponding frequencies, although, to varying degrees: differences of greater than 10 dB were found at the lowest tested frequencies, 1 and 2 kHz, as well as at 10 kHz.

Noise spectral density levels measured under the subject's headphones decreased with increasing frequency up to 1 kHz, where levels were below 0 dB re $(20 \mu\text{Pa})^2/\text{Hz}$ (61 Hz bin resolution). Above 1 kHz, noise levels were limited by the self-noise of the probe microphone, but it is a fair assumption that noise spectrum levels above 1 kHz were lower in amplitude than those measured at 1 kHz as the room was kept quiet during testing, with all doors closed and equipment use kept to a minimum. In order to further characterize the acoustic noise levels in the surgery room, noise measurements were made at a later date using a Brüel & Kjær 2250 sound level meter (1-min unweighted recording, 1/3-octave band analysis), in a testing configuration that approximated that of the ASSR experiment. Noise levels [Fig. 3(b)] decreased approximately linearly with increased log-frequency, with levels of 21 dB re $(20 \mu\text{Pa})^2/\text{Hz}$ at 1 kHz, falling below 0 dB re $(20 \mu\text{Pa})^2/\text{Hz}$ at 16 kHz. Intermittent sound generated by compression of the anesthesia ventilator (about 1 compression per 7 s) caused the noise distribution at most frequencies to be positively skewed (i.e., actual noise levels were generally less than the 1-min L_{eq} level during testing).

IV. DISCUSSION

A. Comparison of ASSR and psychophysical methods

The psychophysical thresholds obtained in the sound-attenuating chamber reliably depict the aerial hearing capa-

TABLE II. Aerial hearing thresholds for a juvenile male Steller sea lion, obtained using the ASSR method. Thresholds are defined as the last statistically detectable ASSR response.

Frequency (kHz)	ASSR threshold (dB re $20 \mu\text{Pa}$)	Testing order
1	52	2
2	44	4
5	15	5
10	22	1
20	30	3
32	82	6

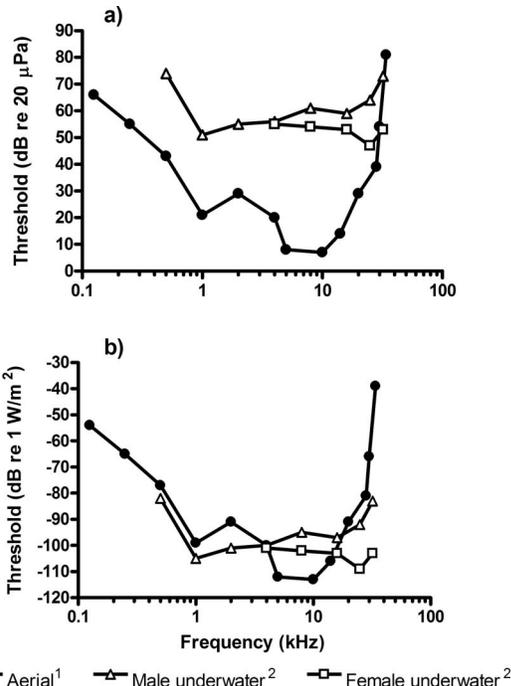


FIG. 4. A comparison of the aerial audiogram from a juvenile male Steller sea lion with underwater audiograms from one male and one female Steller sea lion (this study; Kastelein *et al.*, 2005). All audiograms were obtained using psychophysical methods. (a) Audiograms are compared in terms of sound pressure by converting the underwater thresholds to dB re $20 \mu\text{Pa}$. (b) Audiograms are compared in terms of estimated sound intensity by converting all sound pressure thresholds to dB re 1 W/m^2 (assuming plane-wave propagation conditions).

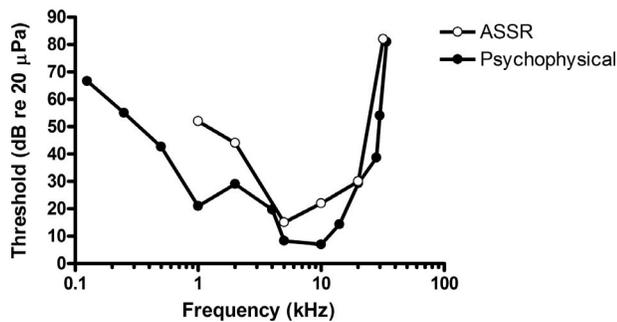


FIG. 5. A comparison of aerial hearing sensitivity measured using psychophysical and ASSR methods with the same juvenile male Steller sea lion.

bilities of this Steller sea lion. The audiogram is unmasked, based on the noise levels measured in the testing chamber and otariid critical ratios obtained for California sea lions (Southall *et al.*, 2003). The only data point for which the potential for masking exists is 14.1 kHz, as a result of ambient tonal noise at 15.7 kHz with amplitude below 20 dB SPL. This noise could potentially fall within the critical bandwidth for 14.1 kHz, assuming an otariid critical band of 25% of the center frequency (Southall *et al.*, 2003). However, any elevation of this data point due to masking is most likely minimal, as the 14.1 kHz threshold is similar in magnitude to thresholds at 10 and 20 kHz.

The correspondence between this psychophysical audiogram and the ASSR audiogram is qualitatively similar to the findings of similar studies with delphinid species (Yuen *et al.*, 2005; Finneran and Houser 2006; Schlundt *et al.*, 2007) and human subjects (see Picton *et al.*, 2003 for a review) in that thresholds obtained using the ASSR method are similar, although elevated, relative to psychophysical thresholds. Based on noise levels in the surgery room, which served as the testing environment, the potential for auditory masking by ambient noise must be considered in the interpretation of elevated ASSR thresholds. The surgery room was not designed for sound attenuation, and the ventilator that was used to administer gas anesthesia created intermittent broadband noise. Although it is difficult to quantitatively determine the influence of background noise on the ASSR thresholds, the greatest potential for masking exists at the lowest tested frequencies of 1 and 2 kHz, where noise levels were highest. This may have contributed to the marked elevation above behavioral thresholds at these frequencies (see, e.g., Lins *et al.*, 1996). The ASSR thresholds at frequencies higher than 2 kHz are relatively similar to the unmasked behavioral thresholds, and masking effects are most likely minimal. The ASSR threshold at 10 kHz is an exception to this trend and difficult to explain, based on the limited electrophysiological data from this study. It is possible that the discrepancy at this frequency is due to random error in the ASSR measurement, an issue which may be resolved by repeated within-subject threshold measurements in future studies.

An increased discrepancy between behavioral and ASSR measurements of underwater hearing sensitivity in a bottlenose dolphin (*Tursiops truncatus*) was also found at the lowest tested frequencies in a study by Schlundt *et al.* (2007).

The authors attribute this to the fact that low frequency SAM stimuli are not especially effective at evoking ASSRs due to mechanical properties of the inner ear. Some effort should be put into resolving the problem of estimating hearing at low frequencies in future electrophysiological assessments of hearing in pinnipeds. The use of frequency-specific stimuli, such as trains of repeated tone bursts, which elicit higher-amplitude ASSRs than those elicited by SAM tone stimuli (Supin and Popov, 2007) and improved methods of extracting electrophysiological signals from noise, such as weighted averaging of epochs (Elberling and Wahlgreen, 1985), may allow for higher ASSR signal-to-noise ratios at low frequencies. Specially constructed, sound-attenuating testing environments for electrophysiological hearing procedures can additionally help by reducing the potential for auditory masking.

The use of different transducers (i.e., speakers in a direct field vs. headphones in the psychophysical and the ASSR experiments, respectively) presents a potential problem when comparing psychophysical and electrophysiological thresholds. A comparison of free-field aerial hearing thresholds and circumaural headphone thresholds in a pinniped species, the harbor seal (*Phoca vitulina*) (Holt *et al.*, 2001), failed to show any marked differences (although differences in head and ear structure between the harbor seal and the Steller sea lion should be noted). Large transducer-dependent threshold differences in our comparison thus seem unlikely, and in any case, the demonstration that the ASSR method provided a reasonable estimate of behavioral hearing sensitivity is of main importance.

The two-month time period required to obtain a reliable psychophysical audiogram demonstrates the utility of conducting psychological testing with stranded marine mammals who are housed in captive research facilities (see Nachtigall *et al.*, 2008b). In situations where the training of subjects is not feasible, ASSR methods may efficiently predict features of the audiogram such as range of best sensitivity and upper-frequency cutoff. One relevant application of ASSR methods is the detection of age-related hearing loss at the high-frequency end of the audiogram, which has been previously demonstrated in a California sea lion subject (Schusterman *et al.*, 2002). Additionally, the underwater and aerial upper-frequency limits of hearing in otariids appear to occur at similar frequencies (Schusterman *et al.*, 1975; Moore and Schusterman, 1987; Babushina *et al.*, 1991; Hemilä *et al.*, 2006), therefore, ASSR measurements of aerial hearing sensitivity may be of use in estimating otariid underwater audiograms.

B. Comparative otariid hearing

Although somewhat elevated above the absolute sensitivities of terrestrial carnivores (see Fay, 1988), the psychophysical hearing thresholds in the region of best hearing indicate acute aerial sensitivity in the Steller sea lion. The absolute sensitivities and frequency range of hearing of the Steller sea lion are especially similar to those of the California sea lion and northern fur seal. The close correspondence of these three species is remarkable, as the northern fur seal

is the most evolutionarily distinct of the living otariid species, belonging to the monophyletic group that diverged from all other extant otariid species more than 5 million years ago (see Heyning and Lento, 2002). It is therefore a reasonable assumption that the common ancestor of all extant otariids possessed hearing characteristics similar to the California and Steller sea lions and the northern fur seal, and that all extant otariids form a functional hearing group with similar aerial hearing characteristics. Further testing of a fur seal representing the *Arctocephalus* genus (for which no hearing data are currently available) would help to confirm the uniformity of otariid aerial hearing.

A feature similar to the decrease in sensitivity at 2 kHz relative to 1 kHz in the Steller sea lion audiogram is also present in audiograms for the two previously tested otariid species, the northern fur seal, and the California sea lion (Moore and Schusterman, 1987), as well as a phocid species, the harbor seal (Møhl, 1968). Noting the relationship between resonance frequency and the length of the human external auditory meatus found by Wiener and Ross (1946), Møhl suggested that an increase in sensitivity at 2 kHz in the harbor seal audiogram is a result of quarter length resonance in an external auditory meatus with an estimated length of 50–60 mm. It is conceivable that resonant properties of outer and/or middle ear structures could result in the “notches” of increased or decreased sensitivity in the mid-frequency region of otariid audiograms. The underwater audiograms of the otariids do not display such notches (Schusterman *et al.*, 1975; Moore and Schusterman, 1987; Babushina *et al.*, 1991; Kastelein *et al.*, 2005). This is congruent with the suggestion that these features are not cochlear in origin, but rather related to differences in the conformation of the outer and/or middle ear in aerial and underwater environments. Further description of the outer and middle ear structures of pinnipeds and their conformations, both in air and under water, would be of use in confirming this hypothesis.

The similarity of the aerial hearing capabilities in otariids is applicable in validating criteria designed to mitigate the impacts of anthropogenic noise in marine environments. For example, Southall *et al.* (2007) have generated *M*-weighting curves that are qualitatively similar to the *A* and *C* weighting functions used in human noise exposure regulation (see Kryter, 1994). *M*-weighting functions for a number of marine mammal functional hearing categories (e.g., high-frequency cetaceans, pinnipeds in air) are based on the audiograms of marine mammal species, and are designed to estimate the effects of anthropogenic noise as a function of noise amplitude and spectral characteristics. For example, a “pinniped in air” *M*-weighting function effectively eliminates frequency components below 50 Hz and above 50 kHz, as sound beyond these limits falls outside of the aerial hearing range of every tested pinniped species. Our findings suggest that the “pinniped in air” *M*-weighting function can be appropriately extrapolated to all otariids in conservatively estimating the effects of aerial anthropogenic noise.

Comparison of the aerial and underwater hearing capabilities determined for the Steller sea lion lend weight to the notion that otariid hearing is well adapted for aerial function

(Kastak and Schusterman, 1998; Schusterman *et al.*, 2000). When comparisons are made based on acoustic pressure (which Kastak and Schusterman concluded to be the relevant metric of comparison for pinnipeds), the Steller sea lion’s hearing is 30–50 dB better in air throughout the range of best sensitivity. Threshold comparisons, based on estimated sound intensity, would suggest that auditory sensitivity is essentially similar in air and under water at all, except for the highest frequencies in the hearing range of the Steller sea lion. When either sound pressure or estimated intensity is used as the metric of comparison, it appears that adaptations of the otariid ear for underwater function, such as modifications of osseous structures in the skull, cavernous tissue in the middle ear, and diminished tympanic membrane size relative to the oval window (Odend’hal and Poulter, 1966; Repenning, 1972) have resulted in only a relatively small loss of aerial sensitivity relative to terrestrial carnivores.

A few caveats must be noted in the comparison of the aerial thresholds from the Steller sea lion in this study with the underwater thresholds reported by Kastelein *et al.* (2005). The comparisons were not made using the same subject or testing configuration, and the possibility exists that some of the differences between thresholds are based on inter-individual or methodological differences. Second, we have calculated intensity based on sound propagation in a free field, an assumption that is probably not valid for testing environments such as the small pool used by Kastelein *et al.* (2005).

The acute aerial hearing capabilities of the Steller sea lion should be considered in the context of the perception of vocal signals. The majority of Steller sea lion vocalizations have energy mainly below 3 kHz (Schusterman *et al.*, 1970; Campbell *et al.*, 2002; Park *et al.*, 2006). Although Steller sea lions appear to have good aerial hearing sensitivity within a wide range of frequencies between 1 kHz and 20 kHz, they are relatively insensitive below 1 kHz, where the dominant energy in many of their vocalizations occurs. Thus, the region of best hearing sensitivity in this species is not correlated with the dominant frequencies of vocalization. Harmonic components in the calls of Steller sea lions can extend to the mid-frequencies (Park *et al.*, 2006) where this species is especially sensitive, and these spectral components may be especially important in a Steller sea lion’s perception of vocalizations by conspecifics. Future work including playback studies, field measurement of vocalization parameters, and psychophysical studies with captive subjects will provide insight on the relationship between the physical characteristics of vocal signals and detection and recognition by otariid species.

ACKNOWLEDGMENTS

This study would not have been possible without the involvement of Traci Kendall and Beau Richter, who conducted all animal training associated with psychophysical data collection. The authors also thank Frances Gulland, Terrie Williams, Tracy Romano, Lisa Mazzaro, and Mike Osborn for providing access to the subject, and Martin Haulena and the veterinary staff of Mystic Aquarium for providing

veterinary care. James J. Finneran developed the EVREST software used to collect the ASSR audiogram, and provided helpful technical support. Brian Lynn provided assistance during the evoked potential portion of the study. The authors gratefully acknowledge Ronald Schusterman and two anonymous reviewers for their critical comments on this manuscript. The electrophysiological portion of this study was supported in part by the NOAA Ocean Acoustics program in the National Marine Fisheries Service Office of Science and Technology. All research was conducted under NMFS Marine Mammal Permit No. 932-1489-09, and the authors thank Teri Rowles and the NMFS Office of Protected Resources for their participation in this effort. This study was approved by the Institutional Animal Care and Use Committees at the University of California, Santa Cruz and the Mystic Aquarium and Institute for Exploration.

Amos, D. E., and Koopmans, L. H. (1963). *Tables of the Distribution of the Coefficient of Coherence for Stationary Bivariate Gaussian Processes* (Sandia Corporation, Livermore, CA).

Arnold, S. A. (1985). "Objective versus visual detection of the auditory brain stem response," *Ear Hear.* **6**, 144–150.

Babushina, Y. S., Zaslavskii, G. L., and Yurkevich, L. I. (1991). "Air and underwater hearing characteristics of the northern fur seal: Audiograms, frequency and differential thresholds," *Biophysics (Engl. Transl.)* **36**, 909–913.

Brillinger, D. R. (1978). "A note on the estimation of evoked response," *Biol. Cybern.* **31**, 141–144.

Campbell, G. S., Gisiner, R. C., Helweg, D. A., and Millette, L. L. (2002). "Acoustic identification of female Steller sea lions (*Eumetopias jubatus*)," *J. Acoust. Soc. Am.* **111**, 2920–2928.

Cook, M. L. H., Varela, R. A., Goldstein, J. D., McCulloch, S. D., Bossart, G. D., Finneran, J. J., Houser, D., and Mann, D. A. (2006). "Beaked whale auditory evoked potential hearing measurements," *J. Comp. Physiol. [A]* **192**, 489–495.

Cornsweet, T. N. (1962). "The staircase method in psychophysics," *Am. J. Psychol.* **75**, 485–491.

Dixon, W. J., and Mood, A. M. (1948). "A method for obtaining and analyzing sensitivity data," *J. Am. Stat. Assoc.* **43**, 109–126.

Dobie, R. A., and Wilson, A. J. (1989). "Analysis of auditory evoked potentials by magnitude-squared coherence," *Ear Hear.* **10**, 2–13.

Dobie, R. A., and Wilson, A. J. (1995). "A comparison of *t* test, *F* test, and coherence methods of detecting steady-state auditory-evoked potentials, distortion-product otoacoustic emissions, or other sinusoids," *J. Acoust. Soc. Am.* **97**, 3042–3050.

Elberling, C., and Wahlgreen, O. (1985). "Estimation of auditory brainstem response, ABR, by means of Bayesian inference," *Scand. Audiol.* **14**, 89–96.

Fay, R. R. (1988). *Hearing in Vertebrates: A Psychophysics Databook* (Hill-Fay Associates, Winnetka, IL).

Fernandez-Juricic, E., Campagna, C., Enriquez, V., and Ortiz, C. L. (2001). "Vocal rates and social context in male South American sea lions," *Marine Mammal Sci.* **17**, 387–396.

Finneran, J. J. (2009). "Evoked response study tool: A portable, rugged system for single and multiple auditory evoked potential measurements," *J. Acoust. Soc. Am.* **126**, 491–500.

Finneran, J. J., and Houser, D. S. (2006). "Comparison of in-air evoked potential and underwater behavioral hearing thresholds in four bottlenose dolphins (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **119**, 3181–3192.

Ghoul, A., Holt, M. M., Reichmuth, C., and Kastak, D. (2009). "Auditory temporal summation in pinnipeds (A)," *J. Acoust. Soc. Am.* **125**, 2676.

Gwilliam, J., Charrier, I., and Harcourt, R. G. (2008). "Vocal identity and species recognition in male Australian sea lions (*Neophoca cinerea*)," *J. Exp. Biol.* **211**, 2288–2295.

Hall, J. W. (2007). *New Handbook of Auditory Evoked Responses* (Pearson Education, Boston, MA).

Hemilä, S., Nummela, S., Berta, A., and Reuter, T. (2006). "High-frequency hearing in phocid and otariid pinnipeds: Inertial and cochlear constraints," *J. Acoust. Soc. Am.* **120**, 3463–3466.

Heyning, J. E., and Lento, G. M. (2002). "The evolution of marine mam-

mals," *Marine Mammal Biology: An Evolutionary Approach*, edited by A. Rus Hoelzel, (Blackwell, Oxford), pp. 38–72.

Holt, M. M., Schusterman, R. J., Southall, B. L., and Kastak, D. (2004a). "Localization of aerial broadband noise by pinnipeds," *J. Acoust. Soc. Am.* **115**, 2339–2345.

Holt, M. M., Southall, B. L., Kastak, D., Reichmuth Kastak, C., and Schusterman, R. J. (2001). "Aerial hearing sensitivity in pinnipeds: A comparison of free-field and headphone thresholds," in *Proceedings of the 14th Biennial Conference on the Biology of Marine Mammals*, Vancouver, BC, November 28–December 5.

Holt, M. M., Southall, B. L., Kastak, D., Schusterman, R. J., and Reichmuth Kastak, C. (2004b). "Temporal integration in a California sea lion and a harbor seal: Estimates of aerial auditory sensitivity as a function of signal duration (A)," *J. Acoust. Soc. Am.* **116**, 2531.

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

Insley, S. J., Phillips, A. V., and Charrier, I. (2003). "A review of social recognition in pinnipeds," *Aquat. Mamm.* **29**, 181–201.

Kastak, D., and Schusterman, R. J. (1998). "Low frequency amphibious hearing in pinnipeds: methods, measurements, noise, and ecology," *J. Acoust. Soc. Am.* **103**, 2216–2228.

Kastelein, R. A., Van Schie, R., Verboom, W. C., and de Haan, D. (2005). "Underwater hearing sensitivity of a male and a female Steller sea lion (*Eumetopias jubatus*)," *J. Acoust. Soc. Am.* **118**, 1820–1829.

Kinsler, L. E., Frey, A. R., Coppens, A. B., and Sanders, J. V. (1982). *Fundamentals of Acoustic*, 3rd ed. (Wiley, New York).

Kryter, K. D. (1994). *The Handbook of Hearing and the Effects of Noise: Physiology, Psychology, and Public Health* (Academic, San Diego, CA).

Kuwada, S., Anderson, J. S., Batra, R., Fitzpatrick, D. C., Teissier, N., and D'Angelo, W. R. (2002). "Sources of the scalp-recorded amplitude-modulation following response," *J. Am. Acad. Audiol.* **13**, 188–204.

Kuwada, S., Batra, R., and Maher, V. L. (1986). "Scalp potentials of normal and hearing-impaired subjects in response to sinusoidally amplitude-modulated tones," *Hear. Res.* **21**, 179–192.

Lins, O. G., Picton, P. E., Picton, T. W., Champagne, S. C., and Durieux-Smith, A. (1995). "Auditory steady-state responses to tones amplitude-modulated at 80–110 Hz," *J. Acoust. Soc. Am.* **97**, 3051–3063.

Lins, O. G., Picton, T. W., Boucher, B. L., Durieux-Smith, A., Champagne, S. C., Moran, L. M., Perez-Abalo, M. C., Martin, V., and Savio, G. (1996). "Frequency-specific audiometry using steady-state responses," *Ear Hear.* **17**, 81–96.

Loughlin, T. R., Rugh, D. J., and Fiscus, C. H. (1984). "Northern sea lion distribution and abundance: 1956–80," *J. Wildl. Manage.* **48**, 729–740.

Møhl, B. (1968). "Auditory sensitivity of the common seal in air and water," *J. Aud. Res.* **8**, 27–38.

Moore, P. W. B., and Schusterman, R. J. (1987). "Audiometric assessment of northern fur seals (*Callorhinus ursinus*)," *Marine Mammal Sci.* **3**, 31–53.

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

Nachtigall, P. E., Reichmuth, C., and Schusterman, R. J. (2008b). "Healthy stranded animals and laboratory research," *Marine Mammal Sci.* **24**, 746.

Nachtigall, P. E., Yuen, M. M. L., 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.

National Research Council (2000). *Marine Mammals and Low-Frequency Sound: Progress Since 1994* (National Academy Press, Washington, DC).

National Research Council (2003). *Decline of the Steller Sea Lion in Alaskan Waters* (National Academy Press, Washington, DC).

National Research Council (2005). *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects* (National Academy Press, Washington, DC).

Odend'hal, S., and Poulter, T. C. (1966). "Pressure regulation in the middle ear cavity of sea lions: A possible mechanism," *Science* **153**, 768–769.

Park, T., Iida, K., and Mukai, T. (2006). "Characteristics of vocalizations in Steller sea lions," in *Proceedings of the 22nd Wakefield Fisheries Symposium, Sea Lions of the World: Conservation and Research in the 21st Century*, edited by A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea, and K. M. Wynne (Alaska Sea Grant Program, Anchorage, AK).

Peterson, R. S., and Bartholomew, G. A. (1969). "Airborne vocal communication in the California sea lion," *Anim. Behav.* **17**, 17–24.

- Picton, T. W., John, M. S., Dimitrijevic, A., and Purcell, D. (2003). "Human auditory steady state responses," *Int. J. Audiol.* **42**, 177–219.
- Repenning, C. A. (1972). "Underwater hearing in seals: Functional morphology," *Functional Anatomy of Marine Mammals*, edited by R. J. Harrison, (Academic, London), Vol. **1**, pp. 307–331.
- Schlundt, C. E., Dear, R. L., Green, L., and Houser, D. S. (2007). "Simultaneously measured behavioral and electrophysiological hearing thresholds in a bottlenose dolphin (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **122**, 615–622.
- Schusterman, R. J. (1974). "Auditory sensitivity of a California sea lion to airborne sound," *J. Acoust. Soc. Am.* **56**, 1248–1251.
- Schusterman, R. J., Balliet, R. F., and St. John, S. (1970). "Vocal displays underwater by the gray seal, the harbor seal, and the Steller sea lion," *Psychon. Sci.* **18**, 303–305.
- Schusterman, R. J., Barrett, B., and Moore, P. W. (1975). "Detection of underwater signals by a California sea lion and a bottlenose porpoise: Variation in the payoff matrix," *J. Acoust. Soc. Am.* **57**, 1526–1532.
- Schusterman, R. J., Kastak, D., Levenson, D. H., Reichmuth, C. J., and Southall, B. L. (2000). "Why pinnipeds don't echolocate," *J. Acoust. Soc. Am.* **107**, 2256–2264.
- Schusterman, R. J., Southall, B. L., Kastak, D., and Reichmuth, C. J. (2002). "Age-related hearing loss in sea lions and their scientists (A)," *J. Acoust. Soc. Am.* **111**, 2342–2343.
- Schusterman, R. J., and Van Parijs, S. (2003). "Pinniped vocal communication: An introduction," *Aquat. Mamm.* **29**, 177–180.
- Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R., Jr., Kastak, D., Ketten, D. K., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., and Tyack, P. L. (2007). "Marine mammal noise exposure criteria: Initial scientific recommendations," *Aquat. Mamm.* **33**, 412–521.
- Southall, B. L., Schusterman, R. J., and Kastak, D. (2003). "Auditory masking in three pinnipeds: Aerial critical ratios and direct critical bandwidth measurements," *J. Acoust. Soc. Am.* **114**, 1660–1666.
- Supin, A. Ya., and Popov, V. V. (2007). "Improved techniques of evoked-potential audiometry in odontocetes," *Aquat. Mamm.* **33**, 14–23.
- Supin, A. Ya., Popov, V. V., and Mass, A. M. (2001). *The Sensory Physiology of Aquatic Mammals* (Kluwer, Boston, MA).
- Vidler, M., and Parker, D. (2004). "Auditory brainstem response threshold estimation: Subjective threshold estimation by experienced clinicians in a computer simulation of the clinical test," *Int. J. Audiol.* **43**, 417–429.
- Wiener, F. M., and Ross, D. A. (1946). "The pressure distribution in the auditory canal in a progressive sound field," *J. Acoust. Soc. Am.* **18**, 401–408.
- Wolski, L. F., Anderson, R. C., Bowles, A. E., and Yochem, P. K. (2003). "Measuring hearing in the harbor seal (*Phoca vitulina*): Comparison of behavioral and auditory brainstem response techniques," *J. Acoust. Soc. Am.* **113**, 629–637.
- Yuen, M. M. L., Nachtigall, P. E., Breese, M., and Supin, A. Y. (2005). "Behavioral and auditory evoked potential audiograms of a false killer whale (*Pseudorca crassidens*)," *J. Acoust. Soc. Am.* **118**, 2688–2695.