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## Psychophysical audiogram of a California sea lion listening for airborne tonal sounds in an acoustic chamber

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Many species-typical audiograms for marine mammals are based on data from only one or a few individuals that are not always tested under ideal conditions. Here, we report auditory thresholds across the frequency range of hearing for a healthy, five-year-old female California sea lion identified as Ronan. Ronan was trained to enter a hemi-anechoic acoustic chamber to perform a go/no-go audiometric experiment. Auditory sensitivity was measured first by an adaptive staircase procedure and then by the method of constant stimuli. Minimum audible field measurements were obtained for 500 ms frequency-modulated tonal upsweeps with 10% bandwidth and 5% rise and fall times. Thresholds were measured at 13 frequencies: in one-octave frequency steps from 0.1 to 25.6 kHz, and additionally at 18.0, 22.0, 36.2, and 40.0 kHz. Sensitivity was greatest between 1 and 23 kHz, with best hearing of 0 dB re 20  $\mu$ Pa at 12.8 kHz. Hearing range, determined at the 60 dB re 20  $\mu$ Pa level, extended from approximately 0.2 kHz to 38 kHz. Sensitivity was comparable to that of three other sea lions tested in similarly controlled conditions, and much better than that of two other sea lions tested in less controlled conditions.



## 1. BACKGROUND

Measures of hearing are important to understanding many aspects of behavior, sensory ecology, evolutionary biology, and conservation. This is especially true for amphibious mammals, who have markedly different auditory sensitivity—and in some cases, frequency ranges of hearing—depending on whether they are submerged in water or hauled out on land or ice (Nummela, 2008; Reichmuth et al., 2013). Sea lions and fur seals (Family Otariidae, Order Carnivora) are marine mammals whose ancestors transitioned to semi-aquatic living approximately 25 million years ago (Berta et al., 2006). Behavioral observations of individuals in social (whelping, breeding) and solitary (predator avoidance, orientation) contexts indicate that the detection of sounds in both media is important to these amphibious animals (Schusterman et al., 2000).

Hearing data are presently available for three of 14 extant otariid species, including the California sea lion (*Zalophus californianus*). Frequency-specific sensitivity measures, or audiograms, have been reported for California sea lions tested using behavioral methods both under water (Cunningham and Reichmuth, 2016; Kastak and Schusterman, 1998; Mulsow et al., 2012; Reichmuth et al., 2013; Reichmuth and Southall, 2012; Schusterman et al., 1972) and in air (Kastak and Schusterman, 1998; Moore and Schusterman, 1987; Mulsow et al., 2011; Reichmuth et al., 2013; Schusterman, 1974) since 1972, making them one of the earliest and best studied marine mammal species with respect to hearing. At present, most species-typical audiograms available for marine mammals (Erbe et al., 2016; Finneran, 2016) are based on data from only one or a few individuals that are not always tested under ideal conditions (see Reichmuth et al., 2013). Therefore, the opportunity to evaluate hearing in several individuals of a given marine mammal species is significant, and can inform methodological considerations and demographic evaluations.

Here, we report auditory thresholds across the frequency range of hearing in air for a California sea lion identified as *Ronan*. *Ronan* was trained to enter a hemi-anechoic acoustic chamber to perform a go/no-go audiometric task using two successive psychophysical procedures. Minimum audible fields measured for airborne tones between 0.1 and 40 kHz were compared to previously reported aerial audiograms for other California sea lions tested in similar enclosures and in less controlled settings. Performance of this individual in air was also compared to her previously published audiogram for underwater tonal sounds in order to evaluate hearing sensitivity in both media.

## 2. METHODS

The subject was a female, 5-year-old California sea lion (*Ronan*, NOA0006602) in good health. She had no known otological problems and no previous exposure to ototoxic medications. She had participated in several prior behavioral studies using auditory cues both in air (Cook et al., 2013) and under water (Cunningham et al., 2014a, 2014b; Reichmuth et al., 2013), and was experienced in performing cooperative auditory detection tasks under water. For the present study, she was trained to move from her living enclosure to a nearby hemi-anechoic testing chamber. This chamber (described in detail by Sills et al., 2014) included a 3.3 x 2.3 x 2.2 m testing room for the sea lion with an adjacent control room that housed the equipment and experimenter. The ambient noise floor of the testing enclosure is provided in Section 3 (Results).

Stimuli were projected from one of several mounted speakers in the testing chamber, depending on test frequency: a JBL 2245H (0.1 kHz), JBL 2123H (0.2 – 3.2 kHz), Fostex FT96H (6.4 – 36.2 kHz), or an Avisoft Viva (40 kHz). The speakers were individually mounted 0.6 – 1.2 m directly in front of the subject, at a distance exceeding the near-field boundary for the relevant test frequency. Sound field calibration was conducted daily by measuring the received level of a reference signal at the exact position of the subject's right or left ear during testing (whichever had a higher received level) using a Josephson C550H microphone

(0.1 – 3.2 kHz), a Microtech MK301 microphone capsule with an ACO Pacific 4016 preamplifier and PS9200 power supply (12.8 – 36.2 kHz), or a Brüel and Kjær 4136 microphone (40 kHz). Sound field mapping was completed for each frequency prior to testing, and occurred in a similar fashion over a larger area: received levels were measured at seven points surrounding (and including) the position of each ear, with 2 cm spacing (forward/back, left/right, and up/down) between each point and the ear position, for a total of 14 points. The speaker position for each frequency was selected to ensure that variability in received levels between the left and right ears was  $\leq 2$  dB, and that all other mapped points had received levels within 3 dB of one another. Calibration and mapping activities took place in the acoustic chamber in the absence of the test subject. The noise floor of the testing environment was measured and recorded with a calibrated Brüel and Kjær 2250 sound level meter (0.01 – 20 kHz) prior to testing at each frequency in test-ready conditions.

Hearing sensitivity was measured at 13 test frequencies in one-octave steps from 0.1 to 25.6 kHz, and additionally at 18.0, 22.0, 36.2, and 40.0 kHz. Stimuli were 500 ms, frequency-modulated tonal upsweeps, with 10% bandwidth and 5% rise and fall times. Test tones were generated using HTP software (Finneran, 2003) run from a LabVIEW platform (LabVIEW v 12.0f3, with NI-DAQ USB-6259) on a desktop computer. Signals were passed from the NI-DAQ USB-6259 to the speakers in the testing room through an equipment chain that included a Krohn-Hite 3364 filter, a TDT PA5 digital attenuator, and in some cases, a Halfer P1000 amplifier. Calibration signals were returned from the microphone through the same filter, NI hardware, and HTP software used for signal generation.

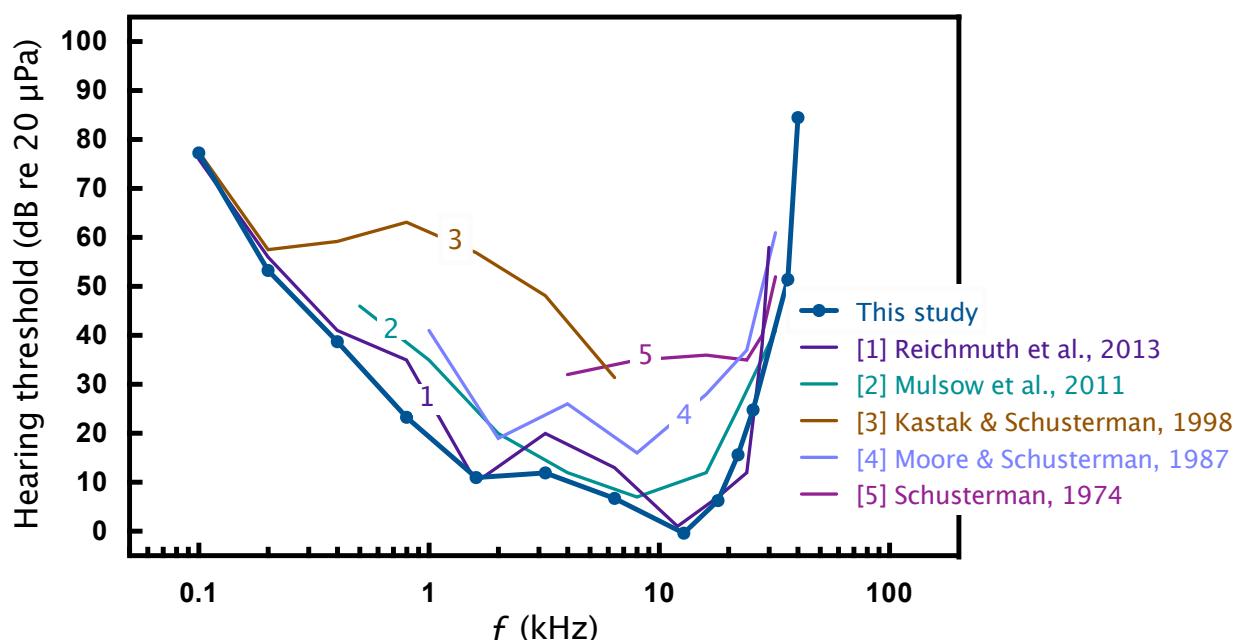
The task was a go/no-go detection procedure in which the sea lion moved her head from a precise position in the calibrated sound field—marked by a rounded chin cup with an electronic switch that served as a stationing device—to touch a response target to her left upon detection of a test tone. A trial light mounted directly in front of the chin cup served to delineate each 4-s trial interval, which began once the sea lion was appropriately positioned at the station. A closed-circuit video camera allowed the experimenter in the adjacent room to observe the sea lion, control the trial light and test stimuli, and record the sea lion's response on each trial. The experimenter could indicate correct responses (correct detections of the signal and correct rejections when no signal was present) to the subject with a conditioned reinforcer (a soft but audible bell) played in the testing enclosure through a nearby speaker. The bell sound was followed by a primary reinforcer (piece of fish delivered to the sea lion through a portal in the chamber wall). Incorrect responses (false alarms and misses) were not marked or reinforced. A video description of the testing enclosure and the sea lion's behavior is available at <https://pinnipedlab.ucsc.edu/multimedia/index.htm>.

Hearing thresholds were determined one frequency at a time in a mixed order. To allow for best performance to be measured following acclimation to each signal frequency, the sea lion was tested with two psychoacoustic procedures. First, an adaptive up-down staircase procedure (Cornsweet, 1962) was applied with a 4 dB increase in signal level following each miss and a 2 dB decrease in signal level following each correct detection. These up-down sessions were continued until the sea lion's performance was stable (3 to 7 sessions, comprising 30 to 70 reversals). Next, the sea lion was tested with the method of constant stimuli (Stebbins, 1970). Five signal levels were selected in 2 dB increments surrounding the threshold estimated with the staircase procedure. Each signal level was presented five times per session in a shuffled order, for a minimum of two sessions, so that the final threshold could be determined using probit analysis (Finney, 1971). This involved fitting the psychometric function to the proportion of correct responses at each signal level and determining threshold at the 50% correct detection level. Throughout testing, the proportion of trials that contained a signal—relative to the proportion of trials that did not—was varied (across but not within sessions) between 55 and 70% to maintain a stable response bias. Only trials that contained signals were used to determine the hearing threshold. The remaining 30 to 45% of trials were used to determine the sea lion's false alarm rate, or the proportion of signal-absent trials for which she incorrectly reported detection of a signal.

### 3. RESULTS

Minimum audible fields measured for this sea lion at each frequency are depicted graphically in Figure 1. Threshold values and corresponding 95% confidence intervals and false alarm rates for each of the 13 test frequencies are provided in Table 1. Auditory sensitivity for airborne tones was greatest between 1 and 23 kHz, with best sensitivity of 0 dB re 20  $\mu$ Pa near 12 kHz. Hearing range—reported as the interval within which thresholds were below 60 dB re 20  $\mu$ Pa—extended from approximately 0.2 to 38 kHz; this bandwidth also corresponded (in this case) to the frequency range of hearing determined 60 dB above the lowest threshold. The sea lion's response bias was stable throughout testing (false alarm rates between 7% and 23%), indicating that the hearing thresholds determined at each frequency could be directly compared. Noise floor measurements (calculated as the noise spectral density level within the one-third octave band surrounding each test frequency) show that the quiet environment of the acoustic chamber was likely sufficient for absolute (unmasked) sensitivity to be measured (see Southall et al., 2003).

In comparison to previously published aerial audiograms available for this species (Figure 1), this sea lion (*Ronan*, 5 years) had hearing that most closely resembled that of another female (*Rio*, 16 years) tested in the same acoustic chamber (Reichmuth et al., 2013). These sea lions had lower thresholds than two other sea lions (*JFN*, male, 1.5 years and *Rocky*, female, 3 years) tested in noise-attenuating enclosures (Moore and Schusterman, 1987; Mulsow et al., 2011). However, similar frequency-dependent patterns of sensitivity were evident for all four individuals. In contrast, two sea lions (*Rocky*, female, 18 years and *Sam*, male, 6 years) tested in outdoor environments either with headphones (Kastak and Schusterman, 1998) or in a direct field (Schusterman, 1974) had significantly higher thresholds than the four sea lions tested in acoustically-controlled indoor enclosures.



**Figure 1.** California sea lion audiograms in air: **bold**, this study (*Ronan*), 1 (Reichmuth et al., 2013) (*Rio*), 2 (Mulsow et al. 2011) (*JFN*), 3 (Kastak & Schusterman 1998) (*Rocky*), 4 (Moore & Schusterman 1987) (*Rocky*), 5 (Schusterman 1974) (*Sam*). Note that the individual tested in [3] and [4] is the same animal; note that [3] was obtained with headphones while all other measurements were obtained in calibrated sound fields with loudspeaker projectors. Note that this study and [1] were obtained in the same acoustic chamber, [2] and [4] were obtained in similar *ad hoc* noise-attenuating testing rooms, while [3] and [5] were obtained outdoors. Note that thresholds in [1-4] were measured at the 50% hit rate while [5] was measured at the 75% hit rate.

**Table 1.** 50% detection thresholds are reported for sea lion *Ronan* for each of 13 frequencies, along with 95% confidence intervals, false alarm (FA) rates (pooled across method of constant stimuli sessions), and corresponding noise in the acoustic test chamber. False alarm rates were determined from responses on signal-absent trials during testing, excluding any trials during supra-threshold warm-up or cool-down periods. Ambient noise levels are provided in units of power spectral density (PSD), and were calculated from the median of unweighted, 1/3-octave band 50th percentile measurements that included each test frequency. Equipment limitations prevented absolute noise measurements lower than 0 dB re 20  $\mu$ Pa at frequencies above 20 kHz.

Frequency (kHz)	Hearing Threshold (dB re 20 $\mu$ Pa)	95% Confidence Interval	FA rate	Ambient noise PSD [dB re (20 $\mu$ Pa) <sup>2</sup> /Hz]
0.1	77	76 – 78	0.23	14
0.2	53	52 – 54	0.19	-2
0.4	39	38 – 40	0.07	-14
0.8	23	22 – 24	0.21	-19
1.6	11	10 – 12	0.14	-20
3.2	12	11 – 13	0.19	-23
6.4	7	5 – 8	0.22	-22
12.8	0	-2 – 2	0.16	-28
18.0	6	5 – 7	0.13	-28
22.0	16	15 – 17	0.16	< 0
25.6	25	24 – 26	0.12	< 0
36.2	51	50 – 52	0.11	< 0
40.0	85	83 – 86	0.23	< 0

## 4. CONCLUSION

These data bolster our understanding of species-typical hearing in sea lions. This is true not only within the genus *Zalophus* but also for the Otariid family, which has been classified as a functional hearing group including 14 species (Mulsow et al., 2012). In addition to the data now available for the California sea lion, aerial hearing sensitivity has been examined in two other otariid species: the Steller sea lion, *Eumetopias jubatus* (Mulsow and Reichmuth, 2010) and the northern fur seal, *Callorhinus ursinus* (Babushina et al., 1991; Moore and Schusterman, 1987). Collectively, these data indicate that—when testing occurs in optimal acoustic conditions—auditory sensitivity in otariids can rival that of humans and some terrestrial carnivores (Fay, 1988).

Despite having reduced pinnae and auditory meatus, anatomical evidence generally supports the notion that sea lions and other otariids have retained the bony structure of a terrestrial carnivore ear (Nummela, 2008). The findings of the present study—combined with earlier descriptions of underwater hearing sensitivity in this individual (Reichmuth et al., 2013)—confirm that while sea lions are sensitive to acoustic cues received in water, they have not lost the ability to detect quiet sounds in air. Sea lions have generally similar ranges of hearing in both media, with the frequency range of best sensitivity in water (0.4 to 37 kHz) somewhat wider than that expressed in air (1 to 23 kHz). In nearshore terrestrial environments, including breeding rookeries, the ability of sea lions to detect sounds at most frequencies is constrained by ambient conditions rather than their inherent auditory capabilities.

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## SUPPORT

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