Auditory sensitivity of seals and sea lions in complex listening scenarios

Kane A. Cunningham[a)]
Department of Ocean Sciences, Long Marine Laboratory, University of California, Santa Cruz, 100 Shaffer Road, Santa Cruz, California 95060

Brandon L. Southall[b)]
Southall Environmental Associates (SEA), Inc., 9099 Soquel Drive, Suite 8, Aptos, California 95003

Colleen Reichmuth
Institute of Marine Sciences, Long Marine Laboratory, University of California, Santa Cruz, Santa Cruz, California 95060

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Standard audiometric data, such as audiograms and critical ratios, are often used to inform marine mammal noise-exposure criteria. However, these measurements are obtained using simple, artificial stimuli—i.e., pure tones and flat-spectrum noise—while natural sounds typically have more complex structure. In this study, detection thresholds for complex signals were measured in (I) quiet and (II) masked conditions for one California sea lion (*Zalophus californianus*) and one harbor seal (*Phoca vitulina*). In Experiment I, detection thresholds in quiet conditions were obtained for complex signals designed to isolate three common features of natural sounds: Frequency modulation, amplitude modulation, and harmonic structure. In Experiment II, detection thresholds were obtained for the same complex signals embedded in two types of masking noise: Synthetic flat-spectrum noise and recorded shipping noise. To evaluate how accurately standard hearing data predict detection of complex sounds, the results of Experiments I and II were compared to predictions based on subject audiograms and critical ratios combined with a basic hearing model. Both subjects exhibited greater-than-predicted sensitivity to harmonic signals in quiet and masked conditions, as well as to frequency-modulated signals in masked conditions. These differences indicate that the complex features of naturally occurring sounds enhance detectability relative to simple stimuli. © *2014 Acoustical Society of America*. [http://dx.doi.org/10.1121/1.4900568]

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I. INTRODUCTION

Increases in marine ambient noise levels coincident with increases in certain human activities—such as commercial shipping and seismic exploration—indicate that anthropogenic noise has altered the acoustic environment of the world's oceans over the past century (NRC, 2003; McDonald *et al*., 2006). This has raised concern over the negative effects that altered soundscapes may have on marine mammals, including behavioral disturbance, temporary or permanent hearing loss, and auditory masking of ecologically relevant sounds (e.g., Richardson *et al*., 1995; Southall *et al*., 2007; Clark *et al*., 2009). The ability to predict such effects for specific noise-generating activities is important for noise management that adequately protects marine mammal populations.

In order to accurately predict anthropogenic noise effects, an understanding of the basic auditory capabilities of marine mammals is needed. Scientists examining auditory abilities within and across species often begin by measuring audiograms and critical ratios. Audiograms are absolute sensitivity profiles constructed from detection thresholds measured in quiet conditions for narrowband signals across a range of frequencies. Audiograms are often used in comparative hearing assessments because they indicate to which frequencies an auditory system is most sensitive (e.g., Masterton *et al*., 1969). Critical ratios are measures of sensitivity to narrowband signals in the presence of flat-spectrum masking noise. Specifically, the critical ratio is the minimum ratio of the sound pressure level (SPL) of a narrowband signal to the spectral density level of a flat-spectrum masking noise required for auditory detection (Fletcher, 1940). Like audiograms, critical ratios are commonly used as comparative hearing metrics as they provide an indirect measure of preciseness of frequency tuning in the auditory system, which partially determines ability to detect sounds in noise as well as ability to discriminate sounds from one another (e.g., Saunders *et al*., 1979).

Recently, these traditionally comparative metrics have been applied as foundational components in quantitatively predicting how anthropogenic noise may affect different marine mammal species. For example, audiograms have been used to create auditory weighting functions, which are utilized in predicting the effects of noise at different frequencies for a particular species (e.g., Nedwell *et al*., 2007; Southall *et al*., 2007), and species-specific critical ratios have been used as the basis for predictive models of auditory

[a)]Author to whom correspondence should be addressed. Electronic mail: kaacunni@ucsc.edu
[b)]Also at: Institute of Marine Sciences, Long Marine Laboratory, University of California, Santa Cruz, Santa Cruz, California 95060.

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masking (Jensen *et al.*, 2009; Dooling *et al.*, 2013). While the use of audiograms and critical ratios as comparative metrics within and across species is well established, using these measures to predict noise effects is a relatively new phenomenon, and as such, must be empirically evaluated.

Of particular concern is the uncertainty regarding how well these two metrics predict auditory sensitivity in natural listening conditions. This uncertainty stems from the fact that both audiograms and critical ratios are measured using simple audiometric stimuli—i.e., narrowband signals and flat-spectrum masking noise—while natural sounds tend to have more complex spectral and temporal features. Using simple stimuli in the laboratory is practical as they are controllable and replicable, unlike most natural sounds. However, several studies indicate that mammalian auditory systems have evolved to process certain spectro-temporal features of natural sounds—such as frequency modulation (FM), amplitude modulation (AM), and the presence of multiple harmonics (Mendelson and Cynader, 1985; Rees and Møller, 1987; Frisina *et al.*, 1990; Suga, 1992; Nelken *et al.*, 1999)—suggesting that sensitivity to complex sounds may be fundamentally different from sensitivity to simple sounds. If audiograms and critical ratios are to play central roles in the management of noise-exposure levels for marine mammals, the question of how accurately these metrics predict sensitivity to complex sounds must be addressed experimentally. In this study, behavioral detection thresholds were measured in quiet and masked conditions and compared to predictions based on subject audiograms and critical ratios for one California sea lion (*Zalophus californianus*) and one harbor seal (*Phoca vitulina*).

II. EXPERIMENT I

A. Methods

1. Overview

In Experiment I, behavioral detection thresholds were measured for complex signals in quiet conditions. Experiments were conducted from January to October 2013 in an acoustically mapped underwater testing environment. Thresholds were measured for three types of complex signals: FM signals, AM signals, and multi-component harmonic signals. Four center frequencies for FM and AM signals were chosen to span the known functional range of hearing for each subject (Reichmuth *et al.*, 2013), and two fundamental frequencies were chosen to build harmonic signals with all components within the functional range of hearing. The detection thresholds measured for these ten complex signals were compared to threshold predictions based on audiogram data for the same two subjects.

2. Subjects and test environment

Two trained pinnipeds participated in this study: A 3-yr-old female California sea lion identified as *Ronan* (NOA0006602) and a 24-yr-old male harbor seal identified as *Sprouts* (NOA0001707). Both subjects had multiple years of experience participating in psychophysical hearing studies.

Experimental sessions were conducted at Long Marine Laboratory in Santa Cruz, CA in an outdoor, semi inground, circular, concrete test pool (7.6 m diameter, 1.8 m depth) filled with natural seawater ranging in temperature from 10 °C–16 °C. An experimental apparatus made of perforated polyvinyl chloride (PVC) pipe was suspended into the pool such that the pipes filled with water. A PVC chin station was located on the apparatus such that the subject's head was at 1 m depth during testing. An underwater light was placed 40 cm in front of the chin station and a flat, square, PVC response target was positioned 20 cm to the left of the station. A closed-circuit underwater camera was located slightly above the underwater light so that the chin station, light, and response target were all within the field of view.

Sessions were conducted by a trainer, who was in direct contact with the animal subject, and a remote experimenter, who was not. The trainer was blind to the specific trial condition and was responsible for directing the animal to the station at the appropriate time, as well as providing fish rewards. The experimenter was located in a control room that was hidden from the subject's view, but had visual access to the subject during trials via the underwater camera. The experimenter controlled the onset of test trials as well as the presentation of acoustic stimuli.

3. Psychophysics

A go/no-go procedure was applied as the signal detection task. On each trial, the trainer cued the subject to dive to the chin station. Once the subject was motionless in the station, the experimenter turned on an underwater light, indicating the beginning of a 4-s trial interval during which an acoustic signal might be presented. The subject had been previously trained to leave the station and press its nose to the response target upon hearing a signal. Correct responses occurred either when the subject touched the target after a signal presentation (termed a "hit"), or when the subject remained on the station for the full trial interval when no signal had been presented. Incorrect responses occurred either when the subject failed to touch the target after a signal presentation (a "miss"), or when the subject went to the target when no signal had been presented (a "false alarm"). All correct responses were reinforced with a single piece of fish; incorrect responses were never reinforced.

Experimental sessions consisted of 40–60 trials. Signal-present and signal-absent trials were presented in a mixed order, with a maximum run length of four for either trial type. During each session, the signal level was varied using an adaptive staircase procedure with a 4 dB ascending step size and a 2 dB descending step size (as in Reichmuth *et al.*, 2013; Sills *et al.*, 2014). The subject's response bias was maintained at a stable level by adjusting the ratio of signal-present to signal-absent trials between sessions (Schusterman and Johnson, 1975). The proportion of signal-present trials varied from 50% to 70%.

Complex signals were tested in a mixed order that differed for each subject. Subjects completed testing with each signal-type/frequency combination before progressing to the next treatment. In order for a subject to complete testing for a given treatment, three experimental sessions that met the following criteria had to be completed: Within each session, the last 5 consecutive hit-to-miss transitions were within 6 dB of one another; within-session averages of hit-to-miss transitions were within 3 dB of one another; and the false alarm rate—defined as the proportion of signal-absent trials that resulted in false alarms calculated over the trials encompassed by the last 5 hit-to-miss transitions—was greater than 0 and less than 0.3.

For each signal treatment, the most recent three experimental sessions that met these criteria were used in the final threshold calculation. From each of these sessions, the trials bracketed by the last five hit-to-miss transitions were extracted and probit analysis (Finney, 1947) was used to calculate the 50% detection threshold, 95% confidence intervals, and standard errors. Criteria for final threshold determination were confidence intervals no wider than 5 dB and $p \geq 0.1$ for a Chi-squared goodness of fit test applied to the probit model.

4. Audiogram data

In order to generate threshold predictions for complex sounds, recent and reliable underwater audiogram data were needed for both subjects. An underwater audiogram for the California sea lion had been recently measured (2011–2012) at the same facility, under similar test conditions, using similar psychophysical procedures (Reichmuth *et al.*, 2013). Because of this, additional audiogram measurements were deemed unnecessary for this subject. For the harbor seal, only a composite audiogram, measured under similar test conditions, consisting of recently measured mid- to high-frequency data (2008–2010) combined with older low-frequency data (1998) was available (Kastak and Schusterman, 1998; Reichmuth *et al.*, 2013), and it was deemed necessary to re-measure low- to mid-frequency hearing thresholds for this subject.

Two major factors made retesting necessary: The harbor seal subject's thresholds at low-frequencies were elevated relative to other harbor seal data (Kastelein *et al.*, 2009), suggesting that the previous measurements for this subject may have been constrained by background noise; and in 2007 this subject suffered a permanent threshold shift of 7–10 dB at 5.8 kHz (Kastak *et al.*, 2008). The frequency regions tested in this experiment were intentionally distant from the frequency region of permanent threshold shift.

The narrowband signals used to collect audiogram data in this study were similar to those used in several recent pinniped hearing studies (e.g., Mulsow *et al.*, 2012; Reichmuth *et al.*, 2013; Sills *et al.*, 2014), and consisted of 10% bandwidth, linear FM sweeps. Narrowband FM sweeps were chosen over pure-tones because it has been shown that, while both signal types result in similar detection thresholds, narrowband FM sweeps exhibit less spatial variability in reverberant testing environments (Kastelein *et al.*, 2002; Finneran and Schlundt, 2007). Center frequencies of 0.5, 2, and 3.2 kHz were chosen to target uncertainties in the harbor seal subject's audiogram as needed for threshold predictions. Narrowband signals were generated using HTP software (Finneran, 2003).

5. Signal types

Three types of complex signals were synthesized for this experiment using MATLAB (MathWorks, Natick, MA). While each signal type had different features, all were of 500 ms duration with 25 ms linear on and off ramps.

Each FM signal comprised an octave-band linear upsweep at a given center frequency. Mathematically, the amplitude of these signals as a function of time is given by

$$A(t) = \sin\left(2\pi \int_0^T \left\{ f_{\text{start}} + \frac{f_{\text{stop}} - f_{\text{start}}}{T} t \right\} dt \right), \quad (1)$$

where T is the duration of the signal, f_{start} is the start frequency of the upsweep, and f_{stop} is the end frequency of the upsweep. FM signals were synthesized at center frequencies 0.5, 2, 16, and 38 kHz, chosen to span the subjects' functional hearing ranges and to encompass the frequencies of many biologically relevant sounds.

AM signals were created through sinusoidal modulation of a pure-tone carrier with a modulation rate of 50 Hz and a modulation depth of 0.5. A 50 Hz modulation rate was selected based on an *ad hoc* analysis of a variety of pinniped vocalizations, which revealed common modulation rates between 1 and 80 Hz. A modulation depth of 0.5 was chosen to ensure that the modulation was detectable. Mathematically, the amplitude of these signals as a function of time is given by

$$A(t) = \sin(2\pi f_c t)(1 + A_m \sin(2\pi f_m t)), \quad (2)$$

where f_c is the frequency of the carrier signal, f_m is the modulation frequency, and A_m is the modulation depth. AM signals were synthesized at carrier frequencies 0.5, 2, 16, and 38 kHz, mirroring the center frequencies of the FM signals.

Harmonic signals contained components at the fundamental frequency and its first three linear multiples. All components had the same bandwidth, which was set to 1/4-octave of the fundamental frequency. Harmonic signals were synthesized with fundamental frequencies of 0.5 and 2 kHz. Higher fundamental frequencies (16 and 38 kHz) were not used because the higher-frequency components would have been beyond the subjects' high-frequency hearing limits. When the harmonic signals were designed and calibrated, each component was filtered such that the difference in SPL at the location of the subject's head between the first harmonic and the fundamental was −3 dB, between the second harmonic and the fundamental was −6 dB, and between the third harmonic and the fundamental was −9 dB. To account for day-to-day variability in the relative SPL between harmonic components due to environmental factors (e.g., changes in water temperature), levels for each component were recorded immediately prior to the start of each session and the appropriate adjustments were made in the threshold analysis.

6. Signal generation and calibration

Outgoing signals were sent from a PC to a NI USB-6259 (National Instruments Corp., Austin, TX) data acquisition system for digital-to-analog conversion, bandpass filtered using a Krohn-Hite 3364 (Krohn-Hite, Brockton, MA) analog filter, attenuated using a TDT PA5 (Tucker-Davis Technologies, Alachua, FL) programmable attenuator, and amplified using a Hafler P1000 (Hafler Professional, Tempe, AZ) amplifier when necessary. Depending on frequency, signals were projected from either an ITC 1042 (International Transducer Corp., Santa Barbara, CA) hydrophone mounted on PVC pipe and suspended into the test pool, or from an NUWC J11 (Naval Undersea Warfare Center, Newport, RI) projector suspended from a metal cable. The projected signal was received by a Reson TC4032 (Teledyne-RESON A/S, Slangerup, Denmark) hydrophone located at the position of the center of the subject's head during testing. Analog-to-digital conversion of the received signal was performed using the same NI USB-6259 at a sampling rate of 500 kHz.

Before testing began with a specific signal type, the signal SPL was measured at 24 positions within a 14 cm × 14 cm × 14 cm cubic grid—centered around the daily calibration position—to ensure that received SPLs were within ±3 dB of one another (as in Sills *et al.*, 2014). Prior to each experimental session, projected signals were calibrated using HTP software and the ambient noise in the test environment was measured using a B&K 2250 (Brüel & Kjær A/S, Nærum, Denmark) sound-level meter connected to the Reson TC4032.

In the calibration process, received signal SPLs were calculated within specific frequency bands, the limits of which changed depending on the signal. For narrowband, FM, and AM signals, received levels were measured within the full signal band limits, i.e., across a band encompassing all spectral energy of the particular signal. For harmonic signals, received levels were measured relative to the band limits of the fundamental component. The frequency range of calibration was taken into account when calculating threshold predictions (as described below).

7. Predictions based on audiograms

Threshold predictions for FM, AM, and harmonic signals were made based on linear interpolation of subject-specific audiogram data: The two closest available audiogram data points that bracketed a given complex signal center frequency were selected, and a straight line was fit between these two points. This line was then used to make an inverse prediction of detection threshold at the desired center frequency.

The hearing model used for this experiment assumed that the auditory periphery acts as a series of non-overlapping 1/3-octave, bandpass filters, and that signal detectability is determined entirely by the filter with the highest probability of detection (i.e., information from multiple filters cannot be combined to enhance detection). The choice of a 1/3-octave bandwidth is consistent with human hearing models and is appropriate for pinnipeds based on direct critical bandwidth measurements (Southall *et al.*, 2003). Within this model, signals with bandwidths exceeding 1/3-octave relative to the center frequency (FM and harmonic signals) are processed piecewise by different auditory filters. To simulate this, wideband signals were decomposed into multiple narrowband components for which predictions were generated. Octave-band FM sweeps were decomposed into three, 1/3-octave-band FM sweeps with center frequencies

$$f_{1/3} = f_c * 2^{k/3}, \quad \text{for } k = -1, 0, 1, \tag{3}$$

where f_c is the center frequency of the octave-band signal. The durations of the 1/3-octave-band FM sweeps were determined by the length of time for which the instantaneous frequency of the signal fell within the given 1/3-octave band limits (131, 163, and 206 ms for the lower, middle, and upper 1/3-octave bands). Three predictions were calculated for FM signals based on interpolation of audiogram data, one at the center frequency of each 1/3-octave band component. Harmonic signals were decomposed into their four individual harmonic components. Four predictions were then calculated based on interpolation of audiogram data, one at the center frequency of each component.

Because the durations of the 1/3-octave band components of the decomposed octave-band FM sweep were likely less than the auditory integration time at three of the four center frequencies tested, threshold predictions at these frequencies were adjusted based on studies of temporal integration of narrowband signals in harbor seals (Kastelein, *et al.*, 2010) and a California sea lion (Holt *et al.*, 2012). Predictions for FM signals at 0.5, 2, and 16 kHz were increased by 4, 2, and 1 dB, respectively. The 0.2 kHz integration data from Kastelein *et al.* (2010) that were inconsistent with data from Reichmuth *et al.* (2012) were not applied.

Further adjustments to predicted thresholds were made depending on how the received levels of FM and harmonic signals were calibrated. For example, because harmonic signals were calibrated relative to the SPL at the fundamental frequency, threshold predictions were adjusted according to the SPL of each harmonic component relative to the fundamental component. That is, if the received SPL of the second harmonic component was 3 dB less than the fundamental, 3 dB would be added to the threshold prediction for that component. Similar adjustments were made for the three 1/3-octave band signals that composed the octave-band FM sweep. In this case, predictions were adjusted relative to the SPL of the full octave band (the level used for calibration).

Once thresholds were estimated for all components of a given signal, the minimum of these thresholds was taken as the final prediction. The selection of the minimum predicted threshold is consistent with a hearing model in which the listener attends to auditory filters independently, and the individual filter with the greatest sensation level at threshold determines detection. As a practical metric of comparison, the difference between this final prediction and the measured detection threshold was calculated, where a positive difference indicated that sensitivity was greater than predicted, and a negative difference indicated that sensitivity was less than predicted. This metric is subsequently referred to as the *sensitivity difference from predicted*.

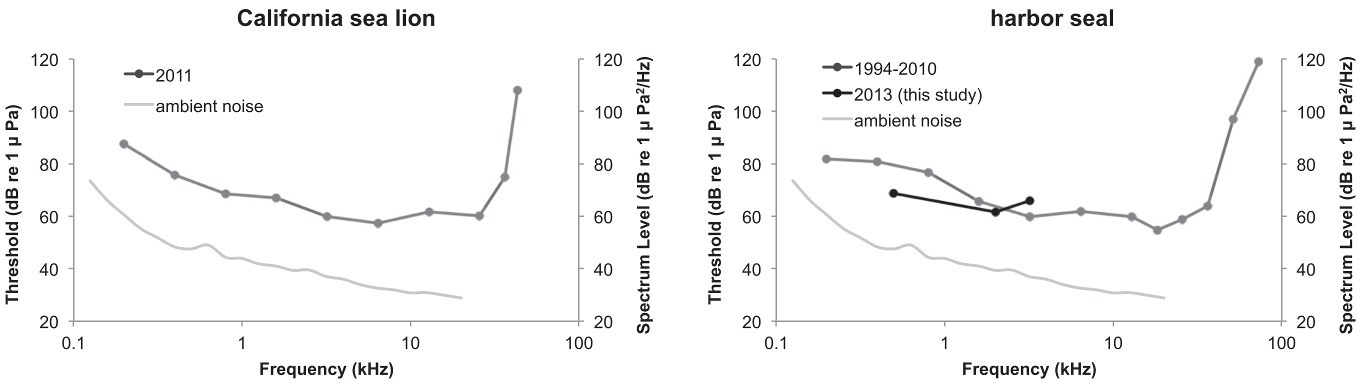

FIG. 1. Audiograms for the California sea lion and harbor seal subjects. Audiogram data are plotted as 50% correct detection thresholds (left axis) and ambient noise data for the test enclosure are plotted as spectrum levels estimated from 1/3-octave band levels (right axis). All data were collected at the same facility using similar methods. Dates indicate the years over which data were collected. Note that threshold predictions for the harbor seal at frequencies below 6.4 kHz were based on the more recent (2013) data. Data not from this study are summarized in Reichmuth *et al*. (2013). Ambient noise measurements were made in 2011–2012 and validated during testing.

B. Results

1. Narrowband signals and audiograms

The harbor seal's detection thresholds measured for narrowband signals were 69, 62, and 66 dB re 1 μPa at 0.5, 2, and 3.2 kHz, respectively. The thresholds at 0.5 and 3.2 kHz exceeded the spectrum level of the background noise by at least one critical ratio (as measured in Experiment II), indicating that these measurements were not limited by ambient noise in the enclosure. However, higher than expected critical ratio measurements made it impossible to rule out noise limitation of the harbor seal subject's threshold at 2 kHz. The threshold measured at 0.5 kHz in this study was more than 10 dB lower than the thresholds at 0.4 and 0.8 kHz measured by Kastak and Schusterman (1998), suggesting that the older threshold data may have been noise limited; therefore, only the new measurements were used to generate audiogram predictions for this study. The harbor seal's present and prior audiogram data, along with prior audiogram data for the sea lion, are provided in Fig. 1.

2. Frequency modulated, amplitude modulated, and harmonic signals

Detection thresholds measured for the octave-band FM signals were well predicted by the audiogram for both the sea lion and the harbor seal (Table I). For the sea lion, the mean sensitivity difference from predicted across all center

TABLE I. Predicted and observed unmasked detection thresholds from Experiment I for one harbor seal and one California sea lion and three types of complex signals: Octave-band FM, 50 Hz AM, and multi-component harmonic signals. Frequency values represent center frequency for FM signals, carrier frequency for AM signals, and fundamental frequency for harmonic signals. Thresholds for FM and AM signals are given in terms of the overall signal SPL, and for the harmonic signal are given in terms of the SPL of the fundamental component. A positive sensitivity difference indicates that the animal was more sensitive to the signal than predicted, i.e., the observed threshold was lower than predicted. False alarm rates and standard errors are also included.

Signal type	Subject	Frequency [kHz]	Predicted threshold [dB re 1 μPa]	Observed threshold (Std. Err.) [dB re 1 μPa]	Sensitivity difference from predicted [dB]	FA rate
Octave FM	Sea lion	0.5	76	73 (0.4)	2.9	0.10
Octave FM	Sea lion	2	65	67 (0.5)	−1.2	0.15
Octave FM	Sea lion	16	61	66 (0.5)	−5.2	0.21
Octave FM	Sea lion	38	73	77 (0.5)	−4.0	0.15
Octave FM	Harbor seal	0.5	71	70 (0.5)	1.0	0.15
Octave FM	Harbor seal	2	62	62 (0.5)	0.0	0.15
Octave FM	Harbor seal	16	56	58 (0.5)	−2.5	0.22
Octave FM	Harbor seal	38	67	70 (0.5)	−3.1	0.21
50 Hz AM	Sea lion	0.5	74	70 (1.0)	4.5	0.16
50 Hz AM	Sea lion	2	65	65 (1.0)	0.7	0.09
50 Hz AM	Sea lion	16	61	62 (0.5)	−0.7	0.03
50 Hz AM	Sea lion	38	84	87 (0.7)	−3.6	0.10
50 Hz AM	Harbor seal	0.5	69	65 (1.2)	3.8	0.16
50 Hz AM	Harbor seal	2	62	63 (0.5)	−1.4	0.04
50 Hz AM	Harbor seal	16	57	65 (0.4)	−8.0	0.17
50 Hz AM	Harbor seal	38	68	67 (0.3)	1.0	0.12
Harmonic	Sea lion	0.5	69	67 (0.5)	2.1	0.15
Harmonic	Sea lion	2	60	53 (0.4)	6.9	0.20
Harmonic	Harbor seal	0.5	67	59 (0.5)	7.7	0.10
Harmonic	Harbor seal	2	62	56 (0.3)	6.2	0.14

frequencies was −2 dB. At center frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the sea lion were 3, −1, −5, and −4 dB, respectively. For the harbor seal, the mean sensitivity difference from predicted was −1 dB. At center frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the harbor seal were 1, 0, −2, and −3 dB, respectively.

Detection thresholds measured for the 50 Hz AM signals were well predicted by the audiogram for both the sea lion and harbor seal (Table I). For the sea lion, the mean sensitivity difference from predicted across all carrier frequencies was 0 dB. At carrier frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the sea lion were 4, 1, −1, and −4 dB, respectively. For the harbor seal, the mean sensitivity difference from predicted was −1 dB. At carrier frequencies 0.5, 2, 16, and 38 kHz, the sensitivity differences from predicted for the harbor seal were 4, −1, −8, and 1 dB, respectively.

The measured detection thresholds for harmonic signals were lower than predicted for both subjects (Table I). For the sea lion, the mean sensitivity difference from predicted across both fundamental frequencies was 4 dB. At fundamental frequencies 0.5 and 2 kHz, sensitivity differences from predicted for the sea lion were 2 and 7 dB, respectively. For the harbor seal, the mean sensitivity difference from predicted was 7 dB. At fundamental frequencies 0.5 and 2 kHz, sensitivity differences from predicted for the harbor seal were 8 and 6 dB, respectively. Sensitivity differences from predicted for FM, AM, and harmonic signals are summarized in Fig. 2.

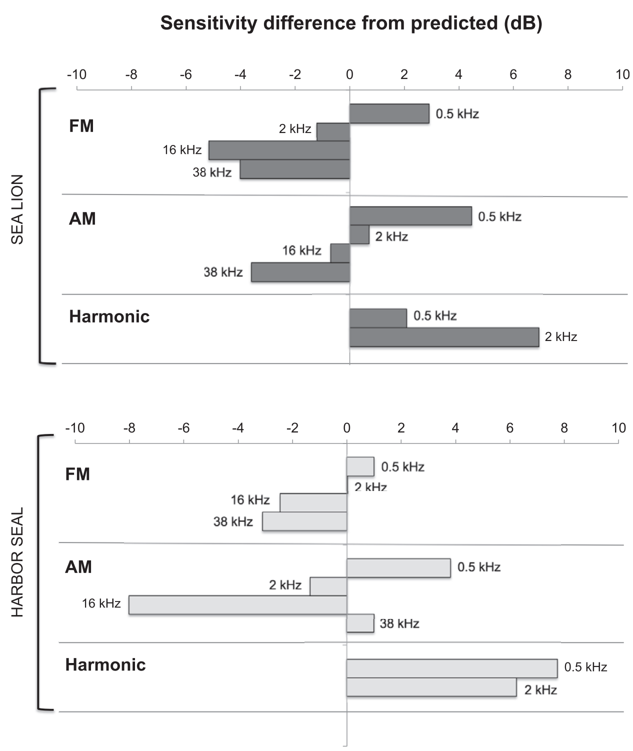

FIG. 2. Sensitivity differences relative to predicted values for two pinniped subjects performing a detection task with complex signals in quiet conditions (Experiment I). Positive values indicate greater than predicted sensitivity. Three types of signals were tested: Octave-band FM, 50 Hz AM, and multi-component harmonic complexes. Frequencies indicate center frequency (FM), carrier frequency (AM), or fundamental frequency (harmonic). Predictions were based on subject audiograms combined with a basic hearing model.

C. Discussion

Absolute detection thresholds were well predicted by the audiogram for octave-band FM and 50 Hz AM signals, but harmonic signal thresholds were consistently lower than predicted, indicating greater than predicted sensitivity to harmonic signals in quiet conditions. These trends were consistent across both subjects, despite the fact that they represent two distinct pinniped lineages. The enhanced sensitivity measured for harmonic signals is consistent with data for human subjects. Buus *et al.* (1998) demonstrated that human detection thresholds for multi-tone harmonic complexes were lower than detection thresholds for any isolated tone within the complex by as much as 9 dB. These combined results suggest that information from multiple auditory filters is integrated in order to enhance detection of harmonic signals in both pinniped and human listeners.

Thresholds for octave-band FM signals were well predicted by the audiogram despite the fact that the bandwidth of these signals was greater than the bandwidth of an auditory filter at the signal center frequency (i.e., greater than one critical band; Southall *et al.*, 2003). This indicates that there was no gain in sensitivity as the result of integration of energy across multiple auditory filters for these signals. However, the nature of these FM signals is such that while the spectrum taken over the 500 ms signal duration is broadband, the signal is narrowband at any moment in time. The absence of simultaneous energy in multiple auditory filters may prevent across-channel comparisons.

For the harbor seal subject, the mean sensitivity difference from predicted for AM signals was low, but detection thresholds varied less than predicted as a function of carrier frequency. Predicted thresholds ranged from 57–69 dB re 1 μPa, but observed values ranged only from 63–67 dB re 1 μPa, indicating that sensitivity was near constant across frequencies. Because the modulation rate is constant for the AM signals, the amplitude envelope of the signal is the same at all carrier frequencies. The observed constant sensitivity combined with the constant modulation rate suggests that the amplitude envelope of the signal—not just the carrier frequency—may have played an important role in determining detection thresholds for this subject. Further experimentation is necessary to test this hypothesis.

III. EXPERIMENT II

A. Methods

1. Overview

In Experiment II, detection thresholds for complex signals were measured for the same pinniped subjects in noisy (masked) conditions. Octave-band FM, 50 Hz AM, and multi-component harmonic signals were masked by either a white noise with no regular amplitude fluctuations, or by recorded shipping noise that exhibited regular amplitude fluctuations. The objective of Experiment II was to compare masked thresholds for complex stimuli to predictions based on traditional critical ratios. To generate these predictions, critical ratios were measured for both subjects using simple stimuli and combined with a basic hearing model.

Psychophysical procedures were similar to those used in Experiment I, with the addition of masking noise on each trial. Masking noise was projected from the same underwater transducer as the signal to prevent spatial release from masking (Turnbull, 1994). The onset of the masking noise coincided with the onset of the light indicating the start of a trial; the noise offset occurred after the end of the 4-s trial interval. The masking noise level was identical for all trials within a session, while the signal level was varied between trials. Threshold analysis (probit analysis: Finney, 1947) and completion criteria were the same as in Experiment I. Testing for Experiment II was conducted from July 2013 through January 2014.

2. Signals

Narrowband, FM, AM, and harmonic signals were used as in Experiment I. Experiment II tested low signal frequencies (2.4 kHz and lower), where much anthropogenic noise energy is concentrated.

Narrowband signals were the same 10% bandwidth FM sweeps that were used in Experiment I, but with center frequencies 0.3, 6, 1.2, and 2.4 kHz. Octave-band FM and 50 Hz AM signals were also the same as in Experiment I, but with a center or carrier frequency of 0.6 kHz. A single harmonic signal with a fundamental frequency of 0.3 kHz was created for Experiment II. In order to create a harmonic signal that was comparable to the signals used in Experiment I in terms of both bandwidth and number of components, a five-component signal was used with components at 0.3, 0.6, 0.9, 1.2, and 1.5 kHz, each with bandwidths 1/4-octave of the fundamental frequency. The harmonic signal was selectively filtered such that the individual SPLs of all five harmonic components of the received signal were equal.

3. Masking noise

Two types of masking noise were used in this experiment: Flat-spectrum, white noise bands and recorded shipping noise. The creation of flat-spectrum masking noise took place in three steps. First, 6 s of white noise with 50 ms linear on and off ramps was generated, bandpass filtered, and saved as a WAV file using MATLAB. This noise was then projected into the test pool and the received spectrum was measured at the location of the subject's head during testing. The received spectrum was examined visually and the noise selectively filtered using custom MATLAB functions to obtain a flat spectrum for the received sound. This process of projection and filtering was repeated until fluctuations in the spectrum level were minimal, and the 1/3-octave band levels were within ±3 dB of the center 1/3-octave band level.

Two flat-spectrum masking noises were created for testing with complex signals. The first had a noise band ranging from 0.3–1.2 kHz (1 octave below and 1 octave above 0.6 kHz). This masking noise was combined with the FM and AM signals. The second masking noise was combined with the harmonic signal and had a noise band ranging from 0.15–3 kHz (note that a wider noise band was needed to encompass all components of the harmonic signal). Three additional flat-spectrum masking noises were used in measuring predictive critical ratios. These were created using the same procedure as above and had noise bands of 0.15–0.6, 0.6–2.4, and 1.2–4.8 kHz.

In addition to flat-spectrum noise, a 6-s sample of recorded shipping noise was used to mask signals (Fig. 3). This sample was taken from a longer recording of the Bulk Carrier *Hanjin Istanbul* made at a distance of 3 km. Linear on and off ramps of 50 ms duration were applied to the 6-s sample. This noise had energy concentrated below 1 kHz and exhibited regular temporal fluctuations in amplitude. In addition, this noise exhibited co-modulation across multiple 1/3-octave frequency bands below 1 kHz. The shipping noise was combined with narrowband, FM, and AM signals, but not with the harmonic signal due to incompatible bandwidths.

4. Signal and noise calibration

The procedure used to generate and calibrate signals in Experiment II was the same as that used in Experiment I. Masking noise was sent from Windows Media Player software on a PC, through a Hafler P1000 amplifier, to the same NUWC J11 that was used to project signals. During calibration, masking noise was received using a Reson TC4032 hydrophone connected to a battery-powered laptop PC through a Roland Quad-Capture (Roland Corp., Los Angeles, CA) external sound card set to a sampling rate 192 kHz. SpectraPlus software (Pioneer Hill Software LLC, Poulsbo, WA) was used to measure the 1/3-octave band SPLs. Prior to each session, the amplifier level was adjusted until the masking noise SPL within the 1/3-octave band (ANSI, 1985) encompassing the center frequency of the signal being tested—or the fundamental frequency for harmonic signals—was within 1 dB of 110 dB re 1 μPa (note that by maintaining a constant 1/3-octave band SPL, masking noises at lower center frequencies had lower spectrum levels than noise at high center frequencies). This SPL was chosen to ensure that masking noise levels were at least 20 dB above the noise floor of the test environment, and 10–20 dB above the absolute hearing threshold at the frequency of the signal. In order to generate critical-ratio-based threshold predictions for all auditory filters that contained signal energy, the SPL of the noise was also measured for all

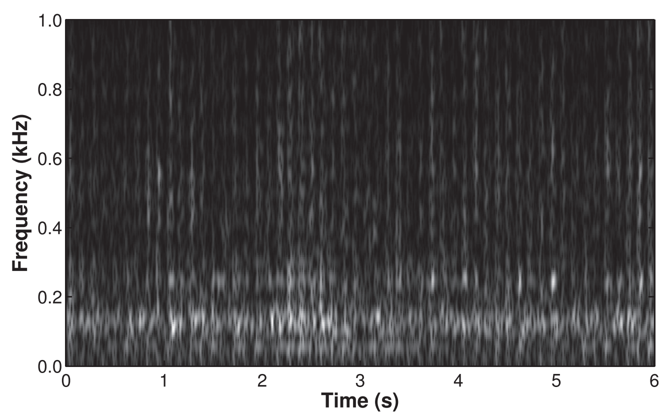

FIG. 3. Spectrogram of the shipping noise used to mask simple and complex signals in Experiment II. Lighter shades represent high-energy regions. The presence of repeated vertical bands of energy indicate that this noise is co-modulated.

1/3-octave bands that overlapped with the spectrum of the signal prior to each session.

Prior to testing with any specific signal/noise combination, SPL measurements of both signal and noise were taken within the same 24-point cubic grid used in Experiment I to ensure that: (1) All signal SPLs were within ±3 dB of one another, and (2) noise SPLs within all 1/3-octave bands that overlapped with the signal spectra were within ±3 dB of one another.

5. Predictions based on critical ratios

In order to generate masked-threshold predictions for complex stimuli, critical ratios were measured at frequencies 0.3, 0.6, 1.2, and 2.4 kHz. To determine a critical ratio, the subject's 50% detection threshold for a narrowband signal masked by constant-volume white noise was measured, and the spectrum level of the masking noise at the signal center frequency was estimated. To estimate the spectrum level, the average SPL of the flat-spectrum masking noise within the 1/3-octave band encompassing the signal was calculated for the three experimental sessions used in threshold analysis; 10log(B) was subtracted from this value, where B is the 1/3-octave bandwidth of the noise band. The critical ratio was then calculated as the difference between the detection threshold and the estimated noise spectrum level.

In order to predict detection thresholds for complex signal and noise combinations, a 1/3-octave band plus critical ratio model of masking was applied. This type of model has been used to predict masked thresholds for a variety of species (e.g., Jensen *et al.*, 2009; Dooling *et al.*, 2013), and is derived from the power spectrum model of masking. The power spectrum model is based on a number of assumptions, including that (1) the auditory periphery can be modeled as a series of linear bandpass filters, (2) the listener attends to the output of a single filter, and (3) the long-term energy spectra of the signal and noise determine detectability, rather than variations in temporal fine structure or phase (Moore, 1993). The model used in this study is similarly built on these assumptions with the added assumption that auditory filter bandwidths are well approximated by 1/3-octave bandwidths, which is consistent with direct critical bandwidth measurements in pinnipeds (Southall *et al.*, 2003).

These model assumptions were combined with masking noise levels and critical ratio measurements in order to predict detection thresholds. Critical ratios were estimated for each animal at the center frequency of the signal being tested using a linear interpolation of the measured critical ratios at 0.3, 0.6, 1.2, and 2.4 kHz. These estimates were then added to noise spectrum levels—calculated from 1/3-octave bands—giving an estimate of the minimum received signal SPL necessary for 50% correct detection.

In this hearing model, signals with bandwidths greater than 1/3-octave of their center frequency are processed by multiple filters, and because of this, critical ratios and noise spectrum levels were calculated at multiple center frequencies when wideband signals—harmonic or FM—were being tested. For harmonic signals, these calculations were made at the center frequencies of all five harmonic components. For FM signals, the octave-band signal was processed as 3 discrete, 1/3-octave band signals with center frequencies of 0.476, 0.600, and 0.756 kHz and durations of 131, 163, and 206 ms, respectively. Because the durations of the individual 1/3-octave components of the octave-band FM signal are likely less than the integration time for both species at 0.6 kHz, 4 dB was added to the predicted thresholds for these signals. This value was estimated based on studies of the effect of duration on detection thresholds for harbor seals (Kastelein *et al.*, 2010) and a California sea lion (Holt *et al.*, 2012).

Because threshold predictions were based on 1/3-octave bands, but the calibrated level of the signal was not, predictions were adjusted relative to the calibrated level. For signals with bandwidths less than 1/3-octave of the center frequency—narrowband and AM signals—no adjustment was necessary because the 1/3-octave band signal level was the same as the calibrated level. For signals with bandwidths wider than 1/3-octave—harmonic and FM signals—the signal SPL within each 1/3-octave band containing signal energy was measured relative to the calibration level in HTP. For the harmonic signal, received SPLs were calibrated relative to the fundamental component. So, for example, if the average SPL measured prior to experimental sessions for the first harmonic component was 1 dB less than the SPL of the fundamental, 1 dB would have been added to the predicted threshold for the first harmonic component, giving a prediction relative to the calibration level for that component. For the FM signal, SPL was calculated for each of the 1/3-octave bands encompassed by the octave-band signal. These levels were compared to the calibration level taken over the entire octave-band sweep and the appropriate adjustments were made to threshold predictions for each 1/3-octave component of the broadband signal.

In the power spectrum model of masking, detectability is determined entirely by the output of the single auditory filter that gives the highest probability of detection. In line with this model, once predicted levels were determined for the individual 1/3-octave bands of interest (relative to the calibration level), the minimum of these values was used as the final masked-threshold prediction. As in Experiment I, the sensitivity difference from predicted was calculated as the difference between this final prediction and the measured detection threshold, where a positive difference indicates greater sensitivity than predicted, and a negative difference indicates poorer sensitivity than predicted.

B. Results

1. Critical ratio measurements

Critical ratios for the sea lion were measured as 16, 21, 23, and 24 dB at frequencies 0.3, 0.6, 1.2, and 2.4 kHz, respectively (Table II). These values are similar to existing data in this frequency range for California sea lions (Southall *et al.*, 2000), and show a slope of 2.8 dB/octave (Fig. 4), similar to the expected mammalian pattern of 3 dB/octave (Fay, 1988).

Critical ratios for the harbor seal were 17, 19, 27, and 24 dB at frequencies 0.3, 0.6, 1.2, and 2.4 kHz, respectively (Table II). These data also showed a slope of 2.8 dB/octave.

TABLE II. Critical ratio data for one harbor seal and one California sea lion in the low- to mid-frequency range, including false alarm rates. The critical ratio is calculated as the difference between the observed narrowband signal threshold in terms of SPL and the spectrum level of a white masking noise.

Subject	Center frequency [kHz]	Noise spectrum level [dB re 1 μPa^2/Hz]	Observed threshold (Std. Err.) [dB re 1 μPa]	Critical ratio [dB]	FA rate
Sea lion	0.3	91	107 (0.5)	16	0.11
Sea lion	0.6	88	109 (0.4)	21	0.25
Sea lion	1.2	85	109 (0.6)	23	0.20
Sea lion	2.4	82	106 (0.3)	24	0.08
Harbor seal	0.3	91	109 (0.4)	17	0.24
Harbor seal	0.6	88	107 (0.6)	19	0.13
harbor seal	1.2	85	113 (0.4)	27	0.17
Harbor seal	2.4	82	106 (0.5)	24	0.05

Measured critical ratios were greater than existing values for this species, with the only other available data in this frequency range coming from the same harbor seal subject, but 16 years younger (Southall *et al.*, 2000; measurements taken in 1997). Comparison of the two datasets suggest that the subject's critical ratios increased by 4–7 dB across the entire 0.3–2.4 kHz range, but that the pattern as a function of frequency remained the same (Fig. 4).

2. Complex signals in flat-spectrum and shipping masking noise

Sensitivity was greater than predicted for complex signals embedded in flat-spectrum masking noise for both subjects across all three signal types, indicating an enhanced ability to detect complex signals relative to simple signals in noisy conditions (Table III). Observed thresholds for AM signals were the most accurately predicted, with a sensitivity difference from predicted of 1 dB for both the sea lion and harbor seal. For the FM signals, sensitivity differences from predicted were 4 and 2 dB for the sea lion and harbor seal, respectively. Observed thresholds for the harmonic signals were the least accurately predicted, with sensitivity differences from predicted of 7 and 4 dB for the sea lion and harbor seal, respectively.

Observed detection thresholds for the narrowband signal masked by recorded shipping noise were lower than predicted for both the sea lion and harbor seal; sensitivity differences from predicted were 6 and 3 dB, respectively (Table III). Observed detection thresholds for both subjects were also lower than predicted for the octave-band FM signal embedded in the shipping masking noise, with sensitivity differences from predicted of 8 and 7 dB for the sea lion and harbor seal, respectively. For the AM signal, the sensitivity difference from predicted was 4 dB for the sea lion subject, and −3 dB for the harbor seal subject. A summary of sensitivity differences from predicted for complex signals in masked conditions is given in Fig. 5.

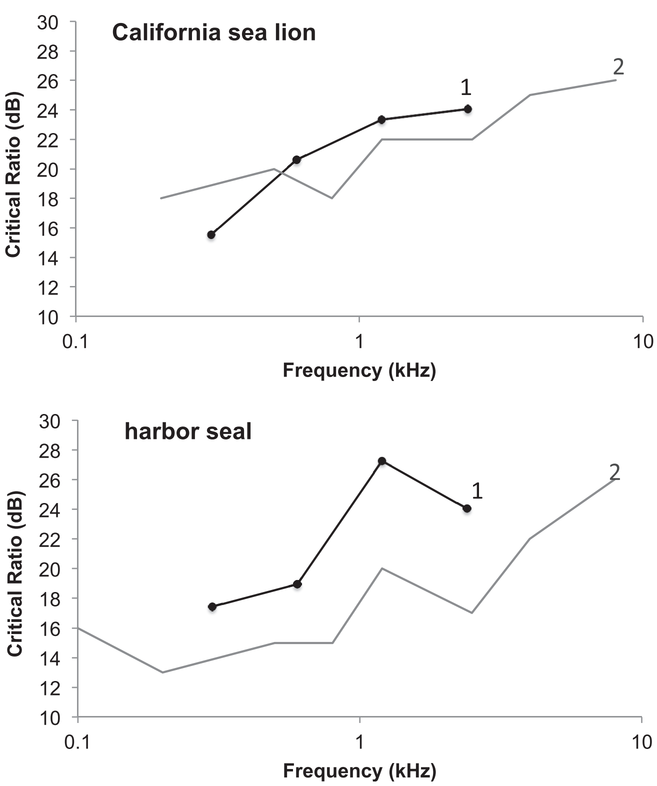

FIG. 4. Critical ratios for one California sea lion and one harbor seal plotted with existing data for these species. Data are from either: (1) This study, or (2) Southall *et al.* (2000). Sea lion data represent two different female subjects; harbor seal data were collected from the same male subject at 9 and 25 yrs old. While the harbor seal sensitivity patterns are similar at both ages, the more recent data from this study are elevated relative to the older data, likely as a result of age-related loss of frequency selectivity.

C. Discussion

Auditory detection thresholds were measured for a total of six masking scenarios involving complex signals and noise for two pinniped subjects. Greater-than-predicted sensitivity was observed in 11 of the 12 treatments. This indicates an enhanced ability to differentiate signal and noise when complex spectral and temporal features were present. Masking release was most prominent for FM and harmonic signals, and the thresholds were lower for signals embedded in shipping noise versus white noise. The results likely reflect the capacity of the subjects' auditory systems to exploit the complex acoustic features found in natural sounds to enhance detection.

The phenomenon of greater-than-expected sensitivity to harmonic signals in noise is consistent with observations in human listeners of enhanced sensitivity to noise-masked multi-tone complexes relative to their individual components (Green, 1958; Buus *et al.*, 1986). Further, this phenomenon is consistent with the results of Experiment I, and with the proposed explanation: Detection is enhanced by the ability

TABLE III. Predicted and observed masked detection thresholds from Experiment II for narrowband and complex signals masked by either flat-spectrum noise or shipping noise. The narrowband and FM center frequencies, as well as the AM carrier frequency, were all 0.6 kHz. The harmonic signal fundamental frequency was 0.3 kHz. A positive sensitivity difference indicates that the animal was more sensitive than predicted, i.e., the observed threshold was lower than predicted. Narrowband signals in white noise (critical ratios) are treated as controls because they served as the basis for predictions. False alarm rates and standard errors are also included.

Noise type	Signal type	Subject	Predicted threshold [dB re 1 μPa]	Observed threshold (Std. Err.) [dB re 1 μPa]	Sensitivity difference from predicted [dB]	FA rate
Flat	Narrowband	Sea lion	—	109 (0.4)	—	0.25
Flat	Narrowband	Harbor seal	—	107 (0.6)	—	0.13
Flat	Octave FM	Sea lion	111	107 (0.6)	4	0.19
Flat	Octave FM	Harbor seal	109	107 (0.5)	2	0.26
Flat	50 Hz AM	Sea lion	109	109 (0.5)	1	0.17
Flat	50 Hz AM	Harbor seal	107	106 (0.8)	1	0.13
Flat	Harmonic	Sea lion	107	100 (0.9)	7	0.12
Flat	Harmonic	Harbor seal	108	104 (0.5)	4	0.17
Shipping	Narrowband	Sea lion	109	103 (0.6)	6	0.13
Shipping	Narrowband	Harbor seal	107	104 (0.6)	3	0.13
Shipping	Octave FM	Sea lion	111	103 (0.4)	8	0.10
Shipping	Octave FM	Harbor seal	110	103 (0.4)	7	0.13
Shipping	50 Hz AM	Sea lion	109	105 (0.6)	4	0.19
Shipping	50 Hz AM	Harbor seal	107	111 (0.3)	−3	0.17

of the auditory system to integrate information across multiple auditory filters.

The observation of enhanced detectability of FM signals in noise is consistent with observations that natural noise can often be expressed as the product of a function of frequency alone and a function of time alone (i.e., a carrier and an envelope), while many natural signals—such as animal vocalizations containing FM—cannot, and the corresponding hypothesis that signals that are not separable in such a way may be more easily extracted from separable noise by the auditory system (Nelken *et al.*, 1999).

It was possible to test the narrowband, FM, and AM signals using both the shipping noise and the flat-spectrum noise, resulting in 6 conditions (3 signals × 2 subjects) that were tested with both masking noises. Detection thresholds were lower when signals were masked by shipping noise versus white noise in 5 out of 6 of these conditions, indicating that a release from masking occurred in the shipping noise condition. This masking release was likely due to co-modulation within the shipping noise, that is, it exhibited consistent temporal amplitude fluctuations across multiple frequency bands. Co-modulation masking release has been observed in multiple mammalian species (e.g., Hall *et al.*, 1984; Branstetter and Finneran, 2008; Klink *et al.*, 2010), and is hypothesized to result from the comparison of amplitude envelope patterns across multiple auditory filters.

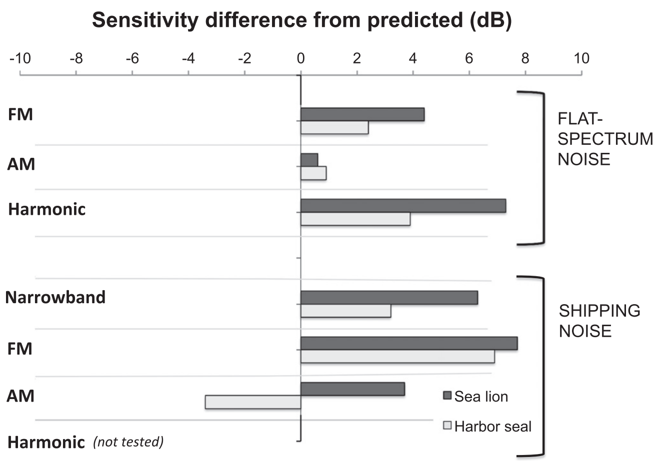

FIG. 5. Sensitivity differences relative to predicted values for two pinniped subjects performing a detection task with complex signals masked by either flat-spectrum noise or recorded shipping noise (Experiment II). Positive values indicate greater than predicted sensitivity. Four types of signals were tested: Narrowband, 50 Hz AM, octave-band FM, and a multi-component harmonic complex. Predictions were based on subject critical ratios combined with a power spectrum model of auditory masking.

The AM signal in shipping noise for the harbor seal was the only instance in Experiment II where the observed threshold exceeded the predicted threshold. The reasons for this are unclear, but as both the signal and noise exhibit regular amplitude fluctuations in time, it is possible that detection of the AM signal was limited by perceptual similarities between signal and noise, rather than merely by overlapping spectral energy. A similar effect has been observed in a bottlenose dolphin (*Tursiops truncatus*) subject listening for a tonal signal embedded in perceptually similar ice-squeak noise (Branstetter *et al.*, 2013). However, why perceptual similarities between signal and noise would affect the harbor seal, but not the sea lion, is uncertain.

It is worth noting that, because only a single 6-s sample of shipping noise was used here, these results are not necessarily generalizable to all types of shipping noise, which tends to vary with vessel type, speed, distance, and operational conditions. Further, it is possible that the unpredictability of actual shipping noise could make signal detection more difficult compared to a laboratory task involving a familiar masking noise. It is also important to mention that the elevated critical ratios measured for the harbor seal indicate that this subject may not have species-typical hearing. These elevated critical ratios are likely the result of deterioration of frequency selectivity with age. Patterson *et al.* (1982) demonstrated a similar pattern of reduced frequency selectivity for human listeners aged 60 yrs relative to listeners aged 20 yrs, but such patterns have yet to be demonstrated in pinnipeds. Whether or not decreased frequency selectivity would impact the relative effects of complex acoustic features on the subject's signal detection abilities is unknown.

IV. CONCLUSIONS

The results of this study indicate an enhanced ability to process sounds with certain complex features—similar to those found in natural sounds—for two pinniped subjects. Both subjects consistently detected signals at lower than predicted SPLs in certain complex listening scenarios, with maximum differences between observed and predicted thresholds of 8 dB in both quiet and masked conditions. This suggests that the audiogram and critical ratio based hearing models used in this study will not accurately predict the effects of anthropogenic noise in certain natural listening scenarios. Consequently, regulators charged with determining safe levels of anthropogenic noise should exercise caution when employing such models.

The data from this study suggest two underlying auditory abilities that allow for enhanced detectability of complex sounds: The ability to integrate information across multiple auditory filters, and the ability to separate a sound into a carrier signal and its amplitude envelope to enhance detection in noise. The ability to integrate information across multiple auditory filters likely leads to the enhanced detectability of harmonic signals in both quiet and masked conditions (Buus *et al.*, 1986). The ability to separate a sound into a carrier and an envelope may account for the enhanced detectability of FM signals in masked conditions by the fact that only the noise is separable, and not the signal (Nelken *et al.*, 1999). Both of these abilities are combined in the case of the comodulation release from masking seen for the shipping noise: The auditory system is able to extract and compare amplitude envelopes from multiple auditory filters in order to enhance detectability (Hall *et al.*, 1984). Given the similar trends for two pinniped subjects from distinct families, as well as similar patterns found in humans and other mammals (e.g., Green, 1958; Hall *et al.*, 1984; Buus *et al.*, 1986; Buus *et al.*, 1998; Branstetter and Finneran, 2008; Klink *et al.*, 2010), it is likely that such abilities are shared across many species. Because of this, it is advisable that hearing models used to predict the effects of anthropogenic noise on marine mammals and other animals take these two factors into account.

As this study included only two subjects and a small set of complex signals, further investigation is needed to understand how the auditory systems of pinnipeds and other mammals exploit the complex features of natural sounds. Particularly, future studies should examine how subjects detect inseparable signals in separable noise relative to scenarios where both signal and noise are separable, neither signal nor noise are separable, and the signal is separable, but the noise is not. Such studies will further test the hypothesis of Nelken *et al.* (1999) that is supported by the findings reported here, and provide insight into the extent to which baseline audiometric data can be used to predict noise effects.

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