Chapter 21
Detection of Complex Sounds in Quiet Conditions by Seals and Sea Lions

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Abstract To test how accurately baseline audiometric data predict detection of complex stimuli, absolute detection thresholds for frequency-modulated (FM), amplitude-modulated (AM), and harmonic stimuli were obtained for one *Phoca vitulina* (harbor seal) and one *Zalophus californianus* (California sea lion) at frequencies spanning the functional range of hearing. These thresholds were then compared with a priori predictions based on the tonal audiograms of these subjects. Predicted thresholds were accurate for most FM signals and for AM signals for the California sea lion. Predictions were unreliable for harmonic signals for both species and for AM signals for the harbor seal.

Keywords California sea lion • Harbor seal • Pinniped • Threshold • Hearing

1   Introduction

Basic audiometric data are often used to predict the effects of anthropogenic noise on marine mammals. Because these audiometric data are generated using pure-tone or narrowband stimuli, such predictions are based on the assumption that hearing thresholds for simple sounds are similar to hearing thresholds for natural sounds with complex spectral and temporal features. In unmasked conditions, a species-specific audiogram consisting of a series of absolute detection thresholds for pure-tone or very narrowband signals at frequencies spanning the functional range of hearing can be extrapolated to predict the detectability of a simple signal. However,

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biologically relevant sounds, including animal vocalizations, tend to exhibit certain complex features. How the presence of such complex features affect signal detectability and, therefore, the accuracy of predictions made based on audiogram data remains largely unknown.

Complex spectral and temporal features, particularly amplitude modulation (AM), frequency modulation (FM), and the presence of multiple harmonics, are found in many animal vocalizations across a variety of species. Not surprisingly, specific structures have been identified within the auditory system to detect and process these common features (Suga 1992). As an example, recordings obtained from the auditory cortex of the cat show that individual neurons are sensitive to different rates and directions of FM (Mendelson and Cynader 1985) and that neuronal firing rates modulate with the AM of a stimulus (Nelken et al. 1999). The presence of such structures suggests that, at least for certain species, the detection of complex signals may be fundamentally different from the detection of pure-tone or narrow-band signals, and there is some empirical evidence suggesting that this is indeed the case. Turnbull and Terhune (1994), for example, found that both human and harbor seal listeners had lower detection thresholds for ascending frequency sweeps compared with the same stimulus with a descending structure. Such findings underscore the need to further investigate how well audiograms and other baseline audiometric data predict detection of complex sounds.

Understanding such auditory phenomena in animals is more important now than ever because the levels of anthropogenic noise in the ocean have risen rapidly over the past century, with largely unknown effects on marine mammal species (Southall et al. 2008). To understand and anticipate these effects, knowledge of how marine mammals perceive complex stimuli is needed. This study focuses on the ability of two pinnipeds, one California sea lion and one harbor seal, to detect complex sounds in quiet conditions. Behavioral detection thresholds were obtained for AM and FM signals as well as for harmonic complexes at a set of frequencies spanning the functional range of hearing. These were then compared with a priori predictions made based on the tonal audiograms of these individuals. The results of these comparisons can help determine how baseline hearing data can best inform regulatory criteria for marine mammal noise exposure as well as provide valuable insight into how the phocid and otariid auditory systems process complex sounds.

2 Psychoacoustics

All thresholds were obtained behaviorally using a go/no-go testing procedure. In this procedure, the subject swam down to a listening station where a trial light turned on to indicate the beginning of a 4-s trial interval. On signal trials, a stimulus was presented at random within the trial interval; on a catch trial, no stimulus was presented. For a signal trial, a correct response consisted of the subject moving from the listening station to touch a nearby response target with its nose. For signal-absent (catch) trials, a correct response consisted of the animal remaining on the

listening station until the trial light was extinguished. Correct responses of either type were reinforced at an equal ratio with a fish reward. Incorrect responses, including touching the response target when no signal was presented (false alarm) and remaining at the station when a signal was played (miss), were never reinforced.

Sound pressure levels of the psychoacoustic stimuli were calibrated before each session. Within a session, the levels were adjusted using a staircase procedure with a 4-up/2-down step size until a minimum of 5 hit-to-miss transitions were completed. Cumulative false alarm rates were maintained at rates greater than 0% and less than or equal to 25% by manipulating the signal-to-catch ratio within a session. This ensured a stable response bias across all testing conditions. Sessions in which the subject was under poor stimulus control, as evidenced by excessively high false alarm rates or excessively variable miss levels, were discarded. Subjects were run until within-session estimated threshold levels were consistent across three sessions. All thresholds were calculated at the 50% correct response level using the average of the hit-to-miss transitions.

3   Results by Stimulus Type

The accuracy of a priori predictions based on audiogram data varied according to stimulus type as well as by species. In general, FM stimuli were best predicted by audiogram data, whereas predictions for harmonic stimuli were least successful. The accuracy of predictions for AM stimuli varied by subject.

3.1   FM Stimuli

FM signals comprised an octave-band linear upsweep and were generated at four center frequencies: 500, 2,000, 16,000, and 38,000 Hz. These frequencies were chosen to span the functional range of underwater hearing for these species. Octave-band sweeps were chosen to ensure that the FM bandwidth exceeded one critical band at all center frequencies (Southall et al. 2003). Sweep duration was 500 ms for all frequencies.

Absolute detection thresholds for these FM signals were well predicted by the audiogram. A priori predictions were made based on linear interpolation of the two nearest audiogram data points for each subject that bracketed the center frequency of the FM sweep (Reichmuth et al. 2013). All observed thresholds were within 5 dB of the predicted value for both subjects, with the exception of the sea lion threshold that was at a 38-kHz center frequency, which was 7 dB lower than predicted.

This discrepancy for the sea lion at 38 kHz is likely due to the fact that the sweep crosses the region of the sea lion audiogram where hearing sensitivity is decreasing rapidly with increasing frequency, i.e. the high-frequency roll-off. Because the bandwidth of the octave-band sweep is greater than a single critical band and

because the auditory integration time is likely less than the duration of the signal at this frequency (Kastelein et al. 2010), the earlier lower frequency portion of the sweep is probably determining the observed threshold, resulting in the lower than expected value. That is to say, this stimulus at threshold is likely perceived by the sea lion subject as a shorter duration sound with a lower center frequency.

3.2 AM Stimuli

To create AM stimuli, a pure-tone carrier was modulated sinusoidally with a modulation depth of 6 dB. Four carrier frequencies, identical to the center frequencies of the FM stimuli, were used: 500, 2,000, 16,000, and 38,000 Hz. To test the possibility of increased detectability of common natural signals, a 50-Hz modulator frequency was chosen to imitate modulation patterns common to pinniped vocalizations. An ad hoc analysis of pinniped underwater and aerial vocalizations, including barks, growls, and pup attraction calls of phocids and otariids, was conducted to determine this modulation frequency.

Absolute detection thresholds for AM signals were well predicted by the audiogram for the California sea lion but not for the harbor seal. A priori threshold predictions were made based on a linear interpolation of the audiogram at the carrier frequency. All observed thresholds were within 5 dB of the predicted value for the California sea lion. Thresholds observed for the harbor seal varied less than expected with changes in the carrier frequency. Although the predicted thresholds for this subject and this stimulus varied by 12 dB across carrier frequencies, the measured thresholds for all four carriers were within 5 dB of one another, possibly indicating that, for this animal, the characteristics of the envelope, which remain constant across stimuli, were more critical to detection than the frequency of the carrier signal. Further work is needed to determine if this is a trait that varies by species, by individual, or both.

3.3 Harmonic Stimuli

Harmonic stimuli were created by summing four narrowband linear FM upsweeps: the fundamental frequency and its first three linear multiples. The FM bandwidth for all harmonic components was set to one-fourth octave of the fundamental frequency. Fundamental frequencies of 500 and 2,000 Hz were used to generate two distinct signals. Target harmonic sound pressure levels decreased relative to the fundamental in the projected signal such that the first harmonic was −3 dB relative to the fundamental, the second −6 dB, and the third −12 dB. However, reverberant conditions within the test pool resulted in distorted relative levels at the receiver. Because of this, the levels of all harmonics were recorded immediately before all experimental sessions and predictions were made based on the relative levels for that session.

Absolute detection thresholds for harmonic stimuli were lower than those predicted for both species and both fundamental frequencies. A priori predictions were made based on the minimum threshold for any of the individual harmonics contained within the signal. Signal levels were calibrated based on the sound pressure level of the fundamental, and daily threshold predictions were adjusted based on the observed harmonic levels relative to the fundamental. Five sessions, each containing five hit-to-miss transitions, were obtained for each animal for fundamental frequencies of 500 and 2,000 Hz. For all five sessions, at both frequencies, for both animals, observed thresholds were lower than predicted, as shown in Fig. 21.1. The difference between threshold predictions and observations ranged from 1 to 12 dB. Larger differences were observed for the harbor seal at both fundamental frequencies, and the 2,000-Hz fundamental stimuli showed larger differences in both species.

These results are interesting relative not only to concerns about ocean noise but also to how the auditory system processes complex signal features, including multiple harmonics. The fact that threshold predictions based on what should be the perceptually loudest harmonic component are too high suggests that, in quiet conditions, detection of harmonic stimuli involves the comparison of information across multiple-frequency channels. That is, the fact that detection occurs at sound pressure levels where all of the individual harmonic components should be undetectable implies that information is being integrated across critical bands at levels below the narrowband thresholds for the individual frequency components to determine the detectability of a signal. Furthermore, this result implies that even at these
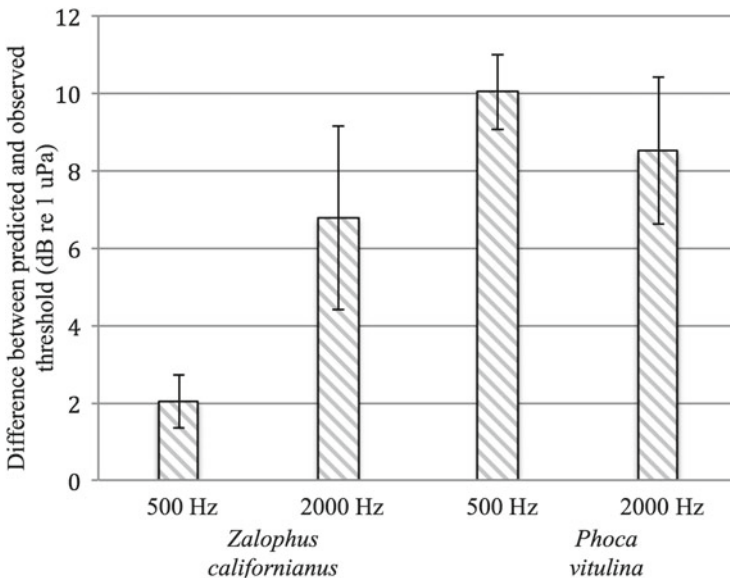

Fig. 21.1 Differences ±95% confidence intervals between average predicted and observed thresholds for harmonic stimuli with fundamental frequencies of 500 and 2,000 Hz for a California sea lion and a harbor seal

subthreshold levels, enough stimulation occurs at multiple regions along the basilar membrane to pass information along to higher order processing regions.

4 Future Directions

An expanded understanding of absolute detection thresholds is only one piece of the puzzle needed to set appropriate noise-exposure criteria for marine mammals. Future work should focus on establishing which parameters most influence masked detection thresholds for complex signals. Current masking models rely on critical ratios observed for pure tones in flat-spectrum noise (Dooling et al. 2009). However, it is known that the presence of certain spectral and temporal features, particularly AM that is coherent across multiple auditory filters (comodulation), can strongly influence a listener's ability to detect signals in noise (Hall et al. 1984; Branstetter and Finneran 2008). Furthermore, depending on how the information contained within a signal is being utilized, a signal level adequate for simple detection is not always sufficient for functional hearing. Understanding how signals are used by listeners and how thresholds vary for more difficult perceptual tasks, such as auditory discrimination and recognition, must be developed. Only by generating a more complete model of auditory processing of complex signals can we hope to set appropriate noise-exposure criteria that ensure that anthropogenic noise is not interfering with hearing processes critical to the long-term health of marine mammal species.

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