LETTERS TO THE EDITOR

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Temporal processing of low-frequency sounds by seals (L)[a]

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In a recent study, Kastelein *et al.* [(2010) J. Acoust. Soc. Am. **127**, 1135–1145] reported auditory integration times for harbor seals (*Phoca vitulina*) exceeding 3000 ms for 200 Hz tonal signals. This finding is unexpected and potentially significant given that time constants measured in mammals for tones above 1 kHz are typically less than 500 ms. To further explore this result, the hearing of another harbor seal was measured in air and water for 200 Hz tones with durations of 500 and 2500 ms. Threshold comparisons, as well as reaction time measures, revealed no gain in audibility as signal duration increased above 500 ms.
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I. INTRODUCTION

Concerns about the potential effects of noise on marine mammals underscore the need for psychoacoustic studies of signal processing. Such studies provide direct information about how sounds are received in time and frequency domains and ultimately perceived by individuals. In diving mammals, the relationship between a signal's duration and its detection threshold has been described for a few species and for different types of stimuli including tonal and transient sounds (see, e.g., Johnson, 1967; Au *et al.*, 1988; Terhune, 1988). As in other mammals (for review, see 1988a), hearing thresholds decrease with increasing signal duration to a certain time constant, beyond which thresholds do not continue to improve with additional available processing time. The dependence of time constants on signal frequency is less well understood, as many studies tend to focus measurements within the range of best hearing sensitivity.

Studies of temporal processing in marine mammals have rarely emphasized low-frequency signals (but see Johnson, 1967). However, Kastelein *et al.* (2010) recently described threshold-duration relationships for two Atlantic harbor seals (*Phoca vitulina vitulina*) tested over a wide range of frequencies. Their study determined an inverse correlation between time constants and signal frequency, with calculated integration times exceeding 3000 ms for 200 Hz tonal signals, the lowest frequency tested. This latter finding is unexpected and potentially significant given that time constants measured in mammals for tones above 1 kHz are typically less than 500 ms (see Brown and Maloney, 1985; Fay, 1988b). Furthermore, conventional explanations of the neural and cognitive mechanisms that underlie auditory temporal processing cannot account for integration times on the order of several seconds (Mauk and Buonomano, 2004).

Accurate measures of temporal processing are relevant to studies of auditory perception, communication, and anthropogenic noise effects; they are also critical to the appropriate design and interpretation of auditory experiments. In order to better understand these results and the nature of low-frequency hearing in seals, we sought to probe the 200 Hz thresholds reported by Kastelein *et al.* (2010) by assessing whether hearing sensitivity in another trained harbor seal would also improve with increasing signal duration from 500 to 2500 ms. We predicted a 9 to 11 dB reduction in hearing threshold across the two duration conditions on the basis of the earlier study and used high-resolution measures of sensitivity and reaction times to evaluate auditory performance.

II. METHODS

A. Subject

The low-frequency hearing ability of a trained 23-year-old male Pacific harbor seal (*P. v. richardii*) was evaluated in the task. This individual (identified as Sprouts, NOA0001707) was highly practiced in behavioral audiometric tasks. This seal showed no evidence of presbycusis and had presumed normal hearing below 1 kHz.

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B. Testing environments

The measurements were conducted at Long Marine Laboratory in Santa Cruz, California. Aerial hearing measurements were obtained in April and May 2011 in a 3.3 m × 2.3 m × 2.2 m custom-designed, hemi-anechoic testing chamber (Eckel Industries) that was located near the seal's living enclosure (for details, see Southall *et al.*, 2003). Underwater hearing measurements were obtained in November 2011 in a seawater-filled, partially in-ground 7.6 m diameter, 1.8 m deep concrete circular pool.

Ambient noise in the testing environment was measured prior to every session at the position of the seal's head during the experiment. Aerial noise measurements were recorded with a self-powered Brüel and Kjær 2250 hand-held analyzer and calibrated Brüel and Kjær 4189 free-field microphone. Underwater noise measurements were obtained with the same instrument using a calibrated Reson TC4032 low-noise hydrophone. Noise spectral density levels were calculated from 1/3-octave band levels sampled over 1 min. Additionally, the noise floor was measured from 20 Hz to 20 kHz using 1 Hz bandwidth FFT analysis. Due to higher levels of background noise in water, quieting measures were applied throughout the facility prior to testing to reduce sound in the 1/3-octave band surrounding 200 Hz.

C. Signal generation and calibration

The signals were always 200 Hz pure tones. The duration was either 500 or 2500 ms including a 25 ms rise/fall time. The tones were generated in a custom National Instruments (NI) LABVIEW virtual instrument (vi) and passed through an NI USB-6259 BNC M-series DAQ module, a Krohn-Hite 3364 anti-aliasing filter, and a Tucker Davis Technologies PA5 digital attenuator to a transducer. The tones were projected into the acoustic chamber from a JBL 2123 H mid-range speaker or into the pool from a J11 transducer provided by the US Naval Undersea Warfare Center.

Calibration signals were measured immediately before every session at several supra-threshold levels using either a Josephson C550H microphone or a Reson TC4032 low-noise hydrophone placed at the position of the seal's head during the experiment. These signals were returned through the digital filter to the same NI hardware and custom software used to produce the stimuli. The incoming signal was sampled at a rate of 30 kHz or higher using a flat-top analysis window. The linearity of the stimulus attenuation system was verified during daily calibration.

Prior to threshold testing in air and under water, the received level of a 200 Hz calibration signal was mapped at 25 positions in a 14 cm × 14 cm × 14 cm grid encompassing the position of the seal's head during testing. This was done to ensure that the maximum spatial variability in the sound field did not vary from the daily calibration position by more than 3 dB.

D. Psychoacoustic testing

Testing was conducted first in air as the acoustic chamber afforded optimum control over the background noise and the capability to accurately measure reaction times during threshold testing. Further, we believed that any threshold shift that might occur as a function of stimulus duration would be preserved regardless of the testing medium.

A remote experimenter that viewed the session on closed-circuit video conducted the sessions. The seal was trained to enter the acoustic chamber and rest his chin in a U-shaped station. The front of the station included a plexiglass switch cover that the seal depressed with his nose to initiate a trial. Each trial had a fixed interval of 6 s. A small light that was positioned 85 cm in front of the station, directly below the speaker, marked the trial interval for the seal. On 50% of the trials, a tone was presented during the trial interval. The seal reported detection by releasing the switch to touch a response target 30 cm to his left. When no tone was detected, he remained stationed until the light was extinguished. Appropriate responses to signal-present and signal-absent trials were marked by a conditioned reinforcer followed by one fish, delivered to the seal through a PVC tube. False alarms (reporting a signal when none was given) and misses (remaining stationed on a signal-present trial) were not reinforced. Reaction times were measured automatically for correct signal detection trials by the LABVIEW vi as the time (in ms) between the onset of the tone and the release of the switch.

The seal completed two sessions of 40 to 60 trials per day. One of the sessions included only 500 ms tones, while the other included only 2500 ms tones. The sequence of trials was randomized for every session but constrained to include no more than four signal-present or signal-absent trials in succession. The use of this schedule was intended to further reduce the likelihood of the subject predicting the trial type over a typical Gellermann (1933) trial series. Audiometry was accomplished using two methods. First, a preliminary threshold for each duration condition was estimated by an adaptive staircase method using 2 dB steps in sessions that contained at least 9 reversals. Sessions were repeated until the mean of the reversal points for three sessions fell within 3 dB to ensure absence of any practice effects. The preliminary threshold was then used to select five to seven stimulus levels for additional testing with the method of constant stimuli (MCS). These levels surrounded the threshold estimate in 2 dB increments (e.g., −4 dB, −2 dB, 0 dB, +2 dB, +4 dB re preliminary threshold). Each stimulus level was presented five times in every MCS session in a shuffled order. These sessions were continued until the difference between the upper and lower 95% confidence limits surrounding the calculated threshold was less than 3 dB.

The same psychophysical procedures were later used to measure thresholds for the 500 and 2500 ms tones in water. The seal performed the task in the pool at a depth of 1 m at a water-filled PVC apparatus that included a video camera, trial light, response target, and chin station. The station was located 5.7 m from the J11 transducer, which was at a depth of 1.5 m. During underwater testing, 60% of trials contained a signal in order to maintain false alarm rates that were similar to those observed in air. Prior to each trial, a trainer that was blind to the stimulus condition directed the seal to the submerged station and either provided fish reinforcement

TABLE I. Absolute hearing thresholds measured for 200 Hz tones in a trained harbor seal. Aerial thresholds are reported in dB re 20 μPa and underwater thresholds are reported in dB re 1 μPa, and both are shown with 95% confidence intervals. False alarm rates are reported as the percentage of trials on which the seal reported a detection when no signal was present.

	200 Hz			
	Duration	Threshold	95% Confidence Limits	FA Rate
Aerial	500 ms	30 dB	28.2–31.2 dB	19%
	2500 ms	30 dB	28.2–31.0 dB	20%
Underwater	500 ms	75 dB	74.0–76.1 dB	29%
	2500 ms	74 dB	73.6–75.0 dB	22%

after the conditioned reinforcer was given by the remote experimenter, or recalled and redirected the seal back to the station after an incorrect trial. Reaction times were not measured during underwater testing.

E. Data analysis

The seal's final hearing thresholds in air and water for the 500 and 2500 ms conditions were determined from the MCS data. This was accomplished by using probit analysis (Finney, 1971) to fit the psychometric function to the observed proportion of correct detections at each stimulus level. An inverse prediction was then used to determine the stimulus level, or threshold, corresponding to the 50% correct detection probability on signal-present trials. Thresholds were not adjusted to account for differences in false alarm rates because a similar response bias was maintained across all testing conditions. The difference in the hearing thresholds calculated for the 500 and 2500 ms tones in each medium were evaluated against the initial prediction of 9 to 11 dB improvement for the longer duration signals. The reaction times measured in air were also compared between the two duration conditions to determine whether the longer duration signals had correspondingly longer reaction times.

III. RESULTS

This seal's 200 Hz hearing thresholds, with corresponding 95% confidence intervals and false alarm rates, are provided in Table I. His aerial threshold for the 500 ms tone was the same as for the 2500 ms tone: 30 dB re 20 μPa. The ambient noise in the acoustic chamber was sufficiently low to rule out possible masking effects,[1] as the spectrum level was -4 dB re 20 $\mu\text{Pa}/\sqrt{\text{Hz}}$ in the 1/3 octave band surrounding the test frequency. The MCS method yielded confidence intervals less than 3 dB, ensuring that the predicted differences in thresholds could have been detected, if present. The reaction time data showed that the seal never used all of the available signal duration in order to detect the signal; while the maximum signal duration was 2500 ms, the longest reaction time observed in this experiment was 1270 ms. Typical reaction times to near-threshold level tones were $<$700 ms for signals of both durations. The minimum reaction time to supra-threshold level tones was 257 ms.

Hearing thresholds for this seal were also similar for both duration conditions in water: the threshold for the 500 ms tone was 75 dB 1 μPa and the threshold for the 2500 ms tone was 74 dB re 1 μPa. During testing, noise spectrum levels were below 58 dB re 1 $\mu\text{Pa}/\sqrt{\text{Hz}}$ in the 1/3 octave band at 200 Hz, indicating that the threshold values, while closer to the ambient noise floor, were not limited by background noise.[2]

IV. CONCLUSIONS

The substantive data and issues presented by Kastelein *et al.* (2010) in the context of temporal processing are relevant to studies of seals and also to models of auditory perception. These authors support a revised model of the relationship between mammalian hearing thresholds and signal duration that is based on a minimum number of cycles for which hearing thresholds are independent of tone duration (see also Terhune, 1988). This view is strongly influenced by the low-frequency data reported for the two harbor seals in their study.

Our findings with another harbor seal tested with a subset of the 200 Hz tone durations used in the prior study clarify the nature of low-frequency hearing in seals as a function of signal duration. In particular, the thresholds obtained in quiet conditions in air using high-resolution psychophysical methods show no difference in sensitivity as tone duration increased from 500 to 2500 ms, demonstrating that the integration time constant for these signals must be less than 500 ms. Reaction times measured during testing further support this finding. If integration time exceeds signal duration, then reaction times should also exceed signal duration at near-threshold levels. This was not the case in the present study, as the seal never used the entire available duration prior to reporting the presence of the longer signal; rather, his reaction time was about the same for the 500 and the 2500 ms tones.

Whether seals are listening for sounds in air or water should not alter their ability to integrate temporal information, as this processing is generally understood to take place at relatively high levels of the auditory nervous system (e.g., Viemeister and Plack, 1993; Frisina, 2001). However, review of the available underwater hearing data for harbor seals also provides relevant information. The two seals in the Kastelein *et al.* (2010) study had hearing thresholds of 73 and 74 dB re 1 μPa for 200 Hz tones that were 500 ms in duration, similar to the value of 75 dB reported in the present study. In a separate earlier study, the same two harbor seals showed similar thresholds ($\leq$1 dB) for 200 Hz tones with a duration of 900 ms (Kastelein *et al.*, 2009). A *post hoc* analysis of the reaction time data from that study indicated that although the seals were provided a signal duration of 900 ms, they did not use all of the available duration to detect a signal (Kastelein *et al.*, 2011). Even when close to the threshold, the seals responded during the signal rather than after its termination.

While the underwater thresholds for the harbor seal in our study did not improve as signal duration increased from 500 to 2500 ms, the two seals tested by Kastelein *et al.* (2010) showed a consistent pattern of threshold decline over this range extending 9 to 11 dB. When signal duration was increased further to a maximum of 5000 ms, their hearing thresholds continued to decline by another few dB. This consistent pattern of threshold decline with increasing tone duration led the authors to determine a time constant of 3624 ms for these seals, with some mention of possible anomalous results. Due to the significant implications of the reported integration time, it is important for us to note that their finding at 200 Hz is not supported by our sensitivity or reaction time measurements.

Our results suggest that the improved detection of long-duration, low-frequency signals described in the earlier study does not arise from auditory integration times exceeding 500 ms, but rather is more likely a consequence of other controlling factors. Given the time-varying nature of both environmental and internal noise, particularly at low frequencies, it is possible that longer signal duration may simply increase the probability of detection at near-threshold levels. This would provide a more parsimonious explanation of the Kastelein *et al*. (2010) results than a revision of established models of mammalian temporal integration. At any rate, the claim that "most published harbor seal hearing thresholds for sounds $\leq$1 kHz are not absolute hearing thresholds, as they were derived with signals shorter than the integration time constant of the species for those frequencies" (Kastelein *et al*., 2010, p. 1143) is not tenable given the information presently available. The question of how seals and other marine mammals process low-frequency auditory information, including intermittent and transient signals common to both communicative and anthropogenic sounds, would benefit from additional research.

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[1]The aerial critical ratio reported by Southall *et al*. (2003) for this harbor seal for 200 Hz tones is 12 dB; therefore, the lowest threshold that could have been measured for this seal at 200 Hz in this testing environment was 12 dB over the -4 dB noise spectral density level in the environment, or 8 dB re 20 μPa. Note that this background noise level was sufficient to detect a threshold decline of up to 22 dB relative to the 500 ms condition.

[2]The underwater critical ratio reported by Southall *et al*. (2000) for this harbor seal for 200 Hz tones is 13 dB; therefore, the lowest threshold that could have been measured for this seal at 200 Hz in this testing environment was 13 dB above the 58 dB noise spectral density level in the environment, or 71 dB re 1 μPa. Note that this background noise level was only sufficient to detect a threshold decline of up to 4 dB relative to the 500 ms condition.

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