

Temporal summation of airborne tones in a California sea lion (*Zalophus californianus*)

Marla M. Holt^{a)}

Marine Mammal & Seabird Ecology Team, Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), 2725 Montlake Blvd., East, Seattle, Washington 98112

Asila Ghoul and Colleen Reichmuth

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

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The trade-off between sound level and duration on hearing sensitivity (temporal summation) was investigated in a California sea lion (*Zalophus californianus*) using airborne pure-tone stimuli. Thresholds were behaviorally measured using the method of constant stimuli at 2.5, 5, and 10 kHz for nine signal durations ranging from 25 to 500 ms. In general, thresholds decreased as duration increased up to 300 ms, beyond which thresholds did not significantly improve. When these data were fitted separately to two versions of an exponential model, the estimated time constants (92–167 ms) were generally consistent between the two fits. However, the model with more free parameters generated fits with consistently higher R^2 values, while avoiding potential arbitrary decisions about which data to include. The time constants derived for the California sea lion were generally consistent with those reported for other mammals, including other pinnipeds. The current study did not show a clear correlation between time constant and test frequency. The results should be considered when conducting audiometric work, assessing communications ranges, and evaluating potential noise impacts of airborne tonal signals on California sea lions. [http://dx.doi.org/10.1121/1.4757733]

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I. INTRODUCTION

Acoustics play a major role in the perceptual world of pinnipeds (true seals, sea lions, fur seals, and walrus), who forage in the water but carry out reproductive activities while ashore. Sounds produced by pinnipeds, as well as by their prey and predators, are critical for reproduction, foraging, and predator avoidance in air and water. There has been a considerable amount of research on pinniped hearing capabilities in both media. Previous investigations have shown that representatives from a number of pinniped species are capable of detecting and localizing sounds in both air and water (see, for review, Schusterman, 1981; Wartzok and Ketten, 1999; Denhardt, 2002). Additionally, these species are susceptible to the auditory effects of noise exposure in both media (Richardson *et al.*, 1995; Kastak *et al.*, 1999; Kastak *et al.*, 2005; Kastak *et al.*, 2007; Finneran *et al.*, 2003; Southall *et al.*, 2000, 2003). However, there remains a paucity of information on some of the basic features of pinniped auditory systems, such as those related to temporal processing (National Research Council, 2000).

One aspect of auditory temporal processing is related to audibility. Sounds with durations shorter than some critical value or time constant are less audible to a listener. That is, below this time constant, the amplitude required for detection

increases with decreasing duration (Yost, 2000). The sensitivity trade-off between a sound's amplitude, or related parameter, and its duration implies that the auditory system integrates sound over a finite duration (termed temporal summation or temporal integration). Temporal summation is one of the most basic features of hearing. The processes that underlie this auditory phenomenon fundamentally determine how animals detect acoustic information in their environment.

The trading relationship between stimulus duration and level on hearing thresholds has been described by investigators in a few different ways. In the most basic form, it is assumed that the auditory system operates as an energy detector and the relationship may be described by perfect intensity integration. That is, for every halving of duration, the sound intensity required for detection must double in order to provide the same amount of energy. However, this assumption does not take into account that duration-dependent hearing sensitivity increases only up to a critical duration, beyond which hearing sensitivity does not change. Further, when mammalian data are subjected to identical analyses, results do not support perfect intensity integration in all cases, even for signals shorter than the time constant (Gerken *et al.*, 1990).

Temporal summation has also been described as an exponential function that relates the process of signal detection to that of a capacitor charging through some resistance (Plomp and Bouman, 1959; Zwislocki, 1960). The most commonly defined exponential function is

^{a)}Author to whom correspondence should be addressed. Electronic mail: Marla.Holt@noaa.gov

$$I_t/I_\infty = 1/[1 - \exp(-t/\tau)], \quad (1)$$

where I_t is the intensity of the sound at threshold for a given duration, t , I_∞ is the intensity of the sound at threshold for a long duration, and τ is the time constant. In practice, I_∞ is often defined as the intensity at threshold of the longest duration tested and the only parameter estimate provided by the model is τ (e.g., Kastelein *et al.* 2010).

A modified exponential function can be defined as

$$I_t = I_k \exp(-t/\tau) + I_\infty, \quad (2)$$

where I_k is a scaling parameter and the other variables are the same as in Eq. (1) (O'Connor *et al.*, 1999). O'Connor *et al.* (1999) allowed three parameters, I_k , I_∞ , and τ to be free, which avoids experimental decisions about when I_∞ is met. It is important to note that Eqs. (1) and (2) are purely descriptive functions, as are the vast majority of functions used in other temporal summation investigations, given that the neurophysiological mechanism(s), which underlie the auditory process are not fully understood. Nonetheless, both equations provide useful information about the limiting duration of temporal summation through the time constant (τ), which is a parameter of interest for comparative purposes.

The species-specific characteristics of auditory temporal summation seem to depend on the type of sound used. Time constants for tonal stimuli in a number of mammalian taxa typically vary between 30 and 800 ms, and some investigators have reported frequency-dependent effects (i.e., that time constants decrease with increasing frequency), whereas others have not (Fay, 1988; O'Connor *et al.*, 1999). In contrast, time constants reported for the detection of more broadband signals, such as clicks, are relatively much shorter in humans and other mammals, and are orders of magnitude shorter for echolocating dolphins and bats (Plomp and Bouman, 1959; Johnson, 1968; Au *et al.*, 1988; Viemeister and Wakefield, 1991; Weißenbacher *et al.*, 2002). However, in most cases, time constants for tonal signals were determined by different methods than for broadband sounds. That is, time constants for tones were determined by measuring detection thresholds of steady-state sounds as a function of their duration. On the other hand, time constants for clicks were determined by measuring detection thresholds as a function of the temporal separation between two clicks. Thus, the time constant differences reported between stimulus types might depend on both methodological and auditory processing differences between studies (see, for discussion, Krumbholz and Wiegrebe, 1998; Weißenbacher *et al.*, 2002). For example, time constants estimated in human subjects for tone bursts have been found to be as short or shorter than those for clicks when the same experimental procedure was used (Viemeister and Wakefield, 1991; Krumbholz and Wiegrebe, 1998).

Characterizing species-specific, temporal summation capabilities is important from several perspectives. First, in conducting audiometric investigations, accurate information about temporal summation is necessary to avoid underestimating hearing sensitivity to relatively long acoustic signals. This information is especially important for comparing hear-

ing thresholds obtained from procedures using different sound durations. Second, knowledge of the temporal summation properties of a given auditory system is also relevant when considering other auditory phenomena involved in temporal processing, such as forward and backward masking. Third, temporal summation must be considered when predicting communication ranges of acoustic signals, particularly in those species that produce relatively short sounds. Finally, the properties of temporal summation are important to consider when assessing the impacts of anthropogenic sounds. For example, species with longer time constants are expected to be less sensitive to shorter sounds. Consequently, the study of the temporal summation (or integration) properties of pinniped auditory systems, as well as those of other marine mammal groups, has been identified as a significant research priority (National Research Council, 2000).

The effects of signal duration on the hearing sensitivity of the harbor seal (*Phoca vitulina*) have been studied by a few investigators. Terhune (1988) reported that the underwater hearing thresholds of a harbor seal listening to a series of tone pulses decreased when the total duration fell below ~400 cycles. More recently, Kastelein *et al.* (2010) reported that the underwater hearing thresholds of two harbor seals listening to single pure tones across a range of frequencies decreased when the tone duration fell below ~780 cycles. These results show frequency-dependent effects of the temporal summation properties of the auditory system (i.e., the time constant monotonically decreased with increasing frequency).

The objective of this study was to measure the relationship between signal duration and level on hearing sensitivity in the California sea lion (*Zalophus californianus*). To accomplish this objective, time constants were estimated from threshold data obtained at three test frequencies from within the range of best aerial hearing sensitivity. Testing was conducted in air because this approach provided a more uniform sound field compared to testing in an underwater tank, where sound can become more easily distorted in its spectral and temporal characteristic. Although hearing sensitivity differs in air and water, we expected that time constants derived from thresholds measured in one medium should not vary from those measured in the other. The reasoning behind this assumption is that tau (τ) is derived from relative differences in hearing thresholds as a function of signal duration. Thus, it is reasonable to compare temporal integration data collected in air with corresponding data collected under water in amphibious mammals. The time constants reported in this study were derived from aerial hearing thresholds measured at nine signal durations between 25 and 500 ms, using steady-state, pure tone frequencies at 2.5, 5, and 10 kHz. Two versions of the exponential function [Eqs. (1) and (2)] were used to describe the data and estimate the time constant, tau (τ), for each frequency tested.

II. METHODS

A. Subject

The subject, a 22-year-old female California sea lion (Rio, NOA0004827), was a research animal at Long Marine

Laboratory in Santa Cruz, CA, and had extensive experience performing behavioral, auditory-detection tasks in air (e.g., [Kastak and Schusterman, 1998](#); [Southall et al., 2003](#); [Reichmuth and Southall, 2012](#)). Full aerial audiograms based on thresholds of 500 ms tones were available for this subject at 16, 20, 24, and 25 years of age. No age-related hearing loss was noted until she was 24 years old, particularly at frequencies above 6400 Hz ([Reichmuth et al.](#), unpublished data). For the current study, the sea lion subject received up to 50% of her daily food total (4.8–6.5 kg of mixed herring and capelin) during experimental sessions. This study was conducted under U.S. Marine Mammal Permit No. 1072-1771-00 of the U.S. National Marine Fisheries Service Office of Protected Resources. The research protocol was approved by the Chancellor's Animal Research Committee (CARC) at the University of California Santa Cruz.

B. Experimental apparatus and test stimuli

Testing occurred in a custom-built, double-walled, hemi-anechoic chamber (Eckel Industries), as described in [Southall et al. \(2003\)](#). A cup made of PVC was mounted 70 cm above the floor and the sea lion was trained to place her chin precisely in the cup at the beginning of each trial. One rectangular PVC, response target (11 × 9 cm) was also mounted to the floor and to the left of the chin cup at the same height. A small light, which was positioned in front of the subject, was illuminated at the beginning of each 4 s listening interval and extinguished at the end.

The experimenter operated testing equipment from a control room that was adjacent to the chamber. Pure tones were generated by a custom National Instruments (NI) LABVIEW virtual instrument and sent through an NI PXI 6229 data acquisition card and NI BNC-2010 connector block, and then a Krohn-Hite 3550 band-pass filter. For each test frequency, auditory thresholds were measured for each of the following signal durations: 25, 50, 100, 150, 200, 250, 300, 400, and 500 ms. The signals were shaped with linear rise and fall times that were both set at 4% of the total stimulus duration (e.g., a tone with a total duration of 500 ms had 20-ms rise and fall times). Tones at 2.5 kHz were presented through a JBL 2123H mid-range transducer and those at 5 and 10 kHz were presented through a JBL 2404H high-frequency transducer. Both transducers were fixed to the chamber wall and placed 0.8 m in front of the chin cup. The spectra of the signals for all durations tested were inspected in the frequency domain (using fast Fourier transform analysis) to ensure that spectral splatter was reduced to within the critical bandwidth ([Southall et al. 2003](#)), particularly for the shorter durations tested.

The average sound pressure level of the signal (given as dB re: 20 μ Pa based on root-mean-square pressure and referred to hereafter as dB SPL) was measured at a position corresponding to the center of the subject's head (with the subject removed) using a calibrated microphone (Josephson C550H, Josephson Engineering, Santa Cruz, CA) and the same NI hardware and custom software used to generate the test signals. This calibration procedure occurred at the beginning of, and immediately following, each experimental ses-

sion. Prior to the start of testing, the sound field was measured at 27 positions surrounding the chin cup to ensure that the spatial variability of received SPLs did not exceed ± 4 dB of those measured at the calibration position. Background noise levels in the acoustic chamber were measured within the frequency range of tones tested in the current study, as described by [Mulsow and Reichmuth \(2010\)](#).

C. Procedure

A go/no-go procedure was used to determine absolute auditory thresholds for the sea lion subject. A correct response was defined as firmly pressing the response target when a signal was triggered (a hit) and withholding the response during trials when no signal was triggered (a correct rejection). The signal was triggered between 1 and 3 s from the onset of the listening interval. The subject had been previously trained to perform this task in the same environment ([Southall et al., 2003](#)).

The sea lion's responses in the acoustic chamber were monitored in real-time and easily judged by the experimenter in the control room via a surveillance camera. A trial began when the animal positioned her chin appropriately in the chin cup and the trial light was turned on. If a correct response was made, a "bell" sound, which served as a conditioned reinforcer (or bridge), was played through a separate speaker (Advent AV570, Audiovox Electronics Corporation, Hauppauge, NY), the trial light was turned off, and an assistant sitting in the control room delivered a fish reward to the subject via a PVC conduit. Hits and correct rejections were equally rewarded (i.e., a payoff matrix of 1:1 was employed). Incorrect responses, defined as responding in the absence of a signal (false alarm) or failure to respond during a signal presentation (miss), were not reinforced. For most sessions, tones were presented during 50% of the trials. However, in a few sessions, signal-present trials accounted for 60% of all trials in order to maintain a stable false alarm rate throughout the experiment.

Hearing thresholds that were used to determine temporal-summation time constants were obtained using the method of constant stimuli, which requires some knowledge of what the threshold might be ([Stebbins, 1970](#)). At the beginning of testing for each frequency and duration, a minimum of three experimental sessions (40–50 trials each) were conducted using a descending staircase procedure ([Cornsweet, 1962](#)). These sessions were used to obtain an accurate, preliminary estimate of hearing threshold and to ensure that the subject's performance had stabilized for each test stimulus. Once the initial threshold estimate was obtained in this manner, sessions using the method of constant stimuli were run. Usually, five stimulus levels were chosen to surround the predicted threshold in 2 dB increments. Each stimulus level was presented five times, in random order, during each 50 trial, experimental session. Probit analysis ([Finney, 1971](#)) was used for final threshold estimation at the 50% correct detection level, and provided standard errors and 95% confidence limits (dB) of the threshold. A minimum of two sessions was required for probit analysis. If the data pooled from these two sessions showed that the 95% confidence

limits of the threshold was within ± 3 dB, and the false alarm rate was above 0% and below 25%, the calculated threshold was included as a final threshold. If not, additional sessions were conducted until these criteria were met.

Following threshold determination for all of the nine tone durations tested within a frequency, τ was estimated using Eqs. (1) and (2). Threshold data for all durations tested were included in the analysis, as opposed to bracketing data in a way to include only the linear portions of a plot of thresholds as a function of signal duration. This approach was done to avoid arbitrary decisions about which data to include or exclude (see, for discussion, O'Connor *et al.*, 1999). Nonlinear fits were obtained by an iterative process that used the method of Marquardt and Levenberg (Marquardt, 1963). The goal of this method was to minimize the residual sum of squares for each of the parameter estimates [τ for Eq. (1) fit and I_k , τ , and I_∞ for Eq. (2) fit] for all data sets. The two functions were fitted to data separately for each test frequency, in which estimates of R^2 were obtained so that the suitability of the fits could be evaluated and compared quantitatively.

III. RESULTS

The psychometric functions (correct detection plotted as a function of tone SPL) for each frequency and duration tested were sigmoidal in shape. As an example, Fig. 1(left panel) shows the psychometric function for the 100 ms tone at 2.5 kHz. Probit-transformed values of correct detections along with the corresponding interpolated threshold at the 50% detection level at the same frequency and duration are also shown in Fig. 1(right panel). Thresholds, standard errors, testing order and false alarm rates for each test frequency and duration are shown in Table I. The sea lion's hearing thresholds generally decreased in a nonlinear fashion as tone duration increased from 25 to 500 ms at all three frequencies, with most declines in threshold occurring at durations less than 300 ms. Figure 2 shows plots of thresholds (individual points) as a function of tone duration for each test frequency and illustrates this nonlinear relationship. For two of the three frequencies tested, the lowest threshold was

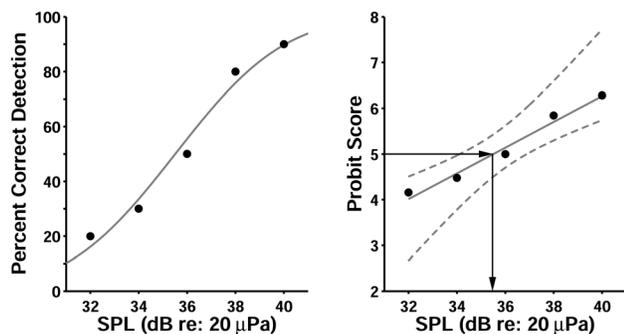


FIG. 1. (Left panel) Sample psychometric function for the sea lion. Percentage of correct detection is plotted as a function of sound pressure level (SPL) for a 100 ms tone at 2.5 kHz. (Right panel) Probit transformed values of the correct detection rates as function of SPL. The solid line is the least squares fit of the data (dotted lines: 5%–95% confidence limits). The threshold for this stimulus, measured at 50% correct detection level (which corresponds to a probit value of 5) is 35.5 dB as indicated by the arrows.

TABLE I. Aerial hearing thresholds (dB SPL re: 20 μ Pa, \pm SE) of a California sea lion to pure-tone stimuli are shown at nine signal durations for each of three signal frequencies; the testing order and false alarm rate (percentage and number of false alarms out of total number of catch trials pooled across experimental sessions) are also provided.

Frequency (kHz)	Duration (ms)	Threshold (dB) \pm SE	Testing order	False alarm rate
2.5	25	38.0 \pm 0.6	24	14% (8/59)
2.5	50	37.8 \pm 0.6	25	7% (4/56)
2.5	100	35.5 \pm 0.7	26	18% (11/60)
2.5	150	35.5 \pm 0.5	21	19% (10/54)
2.5	200	35.1 \pm 0.7	27	16% (9/55)
2.5	250	33.3 \pm 0.5	20	16% (14/88)
2.5	300	34.7 \pm 0.6	23	11% (6/56)
2.5	400	34.7 \pm 0.4	22	10% (6/59)
2.5	500	32.5 \pm 0.5	19	17% (15/88)
5	25	23.6 \pm 0.4	9	16% (43/259)
5	50	23.7 \pm 0.7	8	4% (2/51)
5	100	21.8 \pm 0.6	6	20% (13/64)
5	150	20.9 \pm 0.5	4	19% (9/47)
5	200	18.6 \pm 0.7	7	11% (10/89)
5	250	20.1 \pm 0.4	2	20% (9/46)
5	300	21.9 \pm 0.5	5	15% (14/94)
5	400	20.4 \pm 0.4	3	20% (10/50)
5	500	18.6 \pm 0.6	1	6% (4/64)
10	25	15.5 \pm 0.8	16	12% (7/60)
10	50	14.4 \pm 0.7	13	12% (11/92)
10	100	12.2 \pm 0.9	14	11% (6/54)
10	150	11.5 \pm 0.8	18	12% (19/156)
10	200	12.3 \pm 0.7	12	12% (8/67)
10	250	9.6 \pm 0.5	17	20% (28/140)
10	300	10.7 \pm 0.7	15	7% (4/61)
10	400	8.7 \pm 0.7	11	24% (25/103)
10	500	9.8 \pm 0.6	10	23% (34/150)

measured at the longest duration presented. However, in the case of the 10-kHz tone, the lowest threshold was measured at the second-longest duration tested (Table I). The ambient noise in the acoustic chamber did not exceed -20 dB re: $(20 \mu\text{Pa})^2/\text{Hz}$ within the octave bands surrounding each test frequency. Therefore, all thresholds were at least 28 dB above background noise levels and thus represent absolute (unmasked) hearing sensitivity.

Thresholds for the 2.5 kHz test signal ranged from 33 to 38 dB SPL (Table I), with the highest thresholds measured at 25 ms and the lowest threshold measured at 500 ms. The parameter estimates fitted to the exponential function based on Eqs. (1) and (2) are shown in Table II. Based on Eq. (1), the time constant (τ) was estimated at 141 ms. Based on Eq. (2), τ was estimated at 149 ms and the minimum threshold, I_∞ was estimated at 33 dB SPL. Thresholds of the 5 kHz test signal ranged from 19 to 24 dB SPL, with the highest threshold measured at 50 ms and the lowest thresholds measured at 200 and 500 ms (Table I). The estimate for τ was 120 ms based on Eq. (1), whereas estimates for τ and I_∞ at this frequency were 92 ms and 20 dB SPL, respectively, based on Eq. (2). Thresholds of the 10 kHz test signal ranged from 9 to 16 dB SPL, with the highest thresholds measured at 25 ms and the lowest threshold measured at 400 ms (Table I).

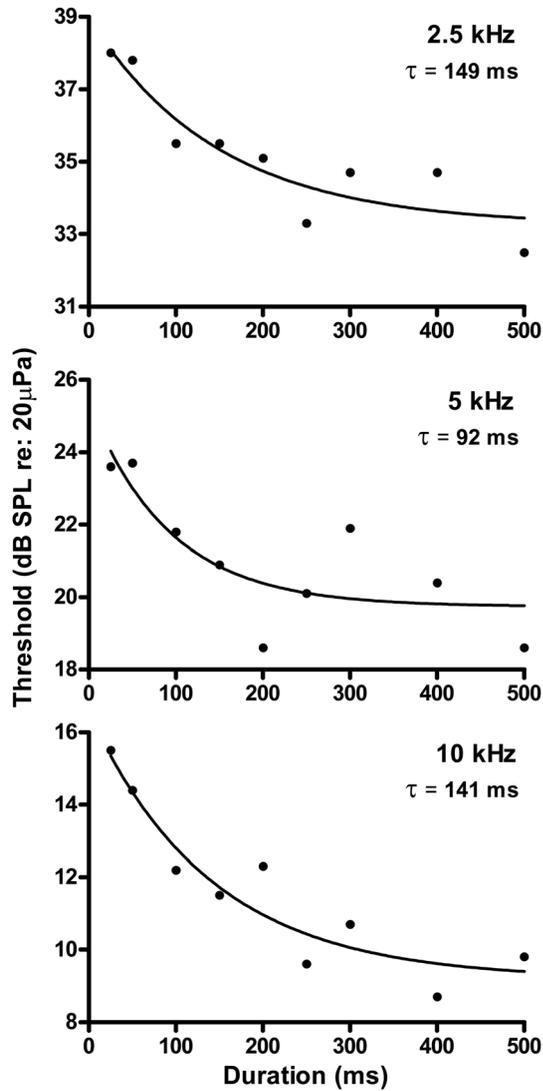


FIG. 2. Aerial hearing thresholds for the California sea lion (*Zalophus*). Thresholds are plotted as a function of signal duration for each the frequencies tested (2.5, 5, and 10 kHz). The curves fitted and time constants (τ) shown are based on an exponential model [Eq. (2)]; see the text for details.

Based on Eq. (1), τ was estimated at 167 ms if the lowest threshold was used to define I_∞ . However, if the threshold at the longest duration was used to define I_∞ instead, τ was estimated at 108 ms. Based on Eq. (2), τ was estimated at 141 ms and I_∞ was estimated at 9 dB SPL at 10 kHz. R^2 values were significant in all cases. The standard errors of τ were lower for fits based on Eq. (1), whereas R^2 values were

TABLE II. Parameter estimates based on two exponential models [Eqs. (1) and (2)] for aerial hearing thresholds of a California sea lion to pure-tone signals, shown as a function of signal duration.^a

Frequency (kHz)	Eq. (1)			Eq. (2)				
	τ	SE_τ	R^2	τ	SE_τ	I_∞	I_k	R^2
2.5	141	27	0.41	149	84	33	5.7	0.83
5	120	28	0.31	92	72	20	5.6	0.67
10	167	24	0.75	141	60	9	7.4	0.89

^aThe standard error (SE_τ) of the time constant (τ) in milliseconds and R^2 values are also shown from the fits of the two exponential models.

higher for fits based on Eq. (2), as shown in Table II. Curve fits based on Eq. (2) are also shown in Fig. 2.

IV. DISCUSSION

The relationship between tone duration and level on aerial hearing sensitivity was examined in the California sea lion using a go/no-go procedure and the method of constant stimuli. Equations (1) and (2) were used to describe the decline in threshold as a function of increasing tone duration. The models used in the current study were chosen as a convenient way to estimate the time constant (τ), which has considerable utility for comparing temporal summation properties of hearing across studies and taxa. Both models provided relatively good fits to the data but R^2 values were higher when Eq. (2) was applied.

Time constants of tones at 2.5, 5, and 10 kHz ranged from 92 to 167 ms, but depended on which version of the exponential model was used. For Eq. (1) fits, the lowest threshold was used to define I_∞ , as in other investigations, whereas for Eq. (2) fits, I_∞ was a free parameter. Parameter estimates of I_∞ based on Eq. (2) seem reasonable, given the psychophysical data (Table I). Estimates of τ were generally consistent regardless of which equation was used, but again, R^2 values were considerably higher in the case of Eq. (2) fits. Further, estimates of τ based on Eq. (1) depended on which datum was used to define I_∞ at 10 kHz. If the threshold at the longest duration was used to define I_∞ , then τ was estimated at 108 ms. If the lowest threshold was used to define I_∞ instead, τ was estimated to be 167 ms—a time constant that is substantially longer. This example illustrates the problem of having to decide which data to include for Eq. (1), whereas no such decisions were necessary for Eq. (2). Given the higher R^2 values, and that no arbitrary decisions regarding which data to include were necessary, Eq. (2) provided key benefits for estimating τ based on data of the current study.

The vast majority of studies on temporal summation, including this one, have employed mathematical models that are descriptive given that the neurophysiological mechanism(s) that underlie this auditory phenomenon are not fully understood. The auditory process is often referred to as temporal integration because early investigators assumed that the ear integrates sound intensity (or a related parameter) over time and operates as an energy detector, at least for signal durations shorter than the time constant (e.g., Plomp and Bowman, 1959). However, other models, that assume that auditory information is collected over short samples or “looks” (Viemeister and Wakefield, 1991) and/or that there is an increased probability of an auditory neural event as stimulus duration increases, are also consistent with the observation that thresholds improve with increasing duration (see, for discussion, Heil and Neubauer, 2003; Krishna, 2006; Meddis, 2006a,b; Meddis and Lecluyse, 2011). The models used in the current study were chosen as a convenient way to estimate the time constant (τ), which is a parameter of interest for comparative purposes.

Time constants reported for the California sea lion in the present study at 2.5, 5, and 10 kHz are well within the

range of 30–800 ms for several mammalian groups (Fay, 1988; O'Connor *et al.*, 1999). Figure 3 shows time constants, based on Plomp and Bouman [1959, (Eq. (1))], for selected terrestrial and marine mammal species that were tested at similar frequencies, along with those of the sea lion tested in the current study. Among pinnipeds, the only comparative data available are for harbor seals (Family Phocidae). Kastelein *et al.* (2010) reported time constants between 14 and 3642 ms for two harbor seals tested over a wide range of frequencies, and concluded that the number of cycles included in a given tone (rather than the overall tone duration) influenced the observed change in time constants as a function of frequency. The authors' determined that a minimum of 780 cycles was required for the seals to achieve stable thresholds with increasing signal duration. Although the measurements made by Kastelein *et al.* (2010) were not conducted at the same frequencies as were used in the current study, we can apply the reported correlation between time constant and frequency to predict what τ might be for harbor seals at 2.5, 5, and 10 kHz. Using 780 cycles as the critical minimum duration (Kastelein *et al.*, 2010), the time constant is predicted to be 312, 156, and 78 ms at 2.5, 5, and 10 kHz, respectively. When compared to the harbor seal, the California sea lion appears to have slightly shorter time constants at 2.5 and 5 kHz, and a slightly longer time constant at 10 kHz, when the same model is used to estimate τ . The time constants reported here did not show clear frequency-dependent effects (i.e., τ did not monotonically decrease with increasing frequency), but only three mid-range frequencies were tested.

In comparing the temporal summation data between pinniped species, it is important to note that testing of the sea lion subject in the current study was conducted in air, whereas testing of the harbor seals in the Kastelein *et al.* (2010) was conducted under water. A variety of other incongruent and likely more important factors might contribute to differences in results. These factors include species, age of subjects, testing environment, experimental procedure, and functions used for threshold estimates. In both the Kastelein *et al.* (2010) report and the current study, experiments were

conducted in quiet conditions and background noise level can be ruled out as a factor contributing to differences in results. In addition, effects of age-related hearing loss (presbycusis), which results in shorter time constants (Corso *et al.*, 1976) and is expected to be most pronounced at higher frequencies (Yost, 2000), are unlikely to influence the comparisons. The 500 ms thresholds at 5 and 10 kHz for the sea lion in the current study (Table I) are within a few decibels of her thresholds at similar frequencies when she was 20 years old—an age before any presbycusis was noted (Reichmuth *et al.*, unpublished data). Further, at the highest frequency tested, the sea lion (of the current study) was older and had a longer time constant compared to those predicted of relatively young harbor seals (Kastelein *et al.*, 2010).

Sample sizes of the pinniped studies were small and individual variation in hearing might also explain some differences in reported results. Unfortunately, only one California sea lion subject was available for testing in the current study and there are no other published time constants for this species in the published literature for comparison. The issue of limited sample size is common in the marine mammal field given the resources required to conduct laboratory studies in these animals. Arguably, we assume that the data presented in this paper is representative of most California sea lions because time constants are well within the range reported for other mammalian taxa (Fay, 1988, Fig. 3).

The aerial auditory thresholds of a California sea lion, at frequencies where hearing is most sensitive, declined as a function of increasing tone duration up to about 300 ms, beyond which little difference in thresholds was observed. These results are consistent with those observed in other mammalian species, despite differences in taxa, methods, and analytical approaches. Such information provides critical data about basic auditory capabilities of sea lions and informs the appropriate design of audiometric experiments conducted with these subjects. Tone durations longer than 300 ms at the frequencies reported here should be used when testing the aerial auditory thresholds of sea lions, in order to avoid underestimating their sensitivity. Conversely, predictions of communication ranges and zones of potential noise impacts for tonal sounds shorter than 300 ms may not be accurate if detection thresholds of longer sounds are applied. For these reasons, studies on the temporal summation properties of a variety of marine mammal species would be useful for policy and management decisions that involve anthropogenic sound exposure. Most sounds produced by pinnipeds, their prey and predators, and humans, are not tonal in nature. Future work could provide information about temporal summation properties of broadband stimuli to inform policy and management.

V. CONCLUSIONS

Auditory temporal summation, which describes the trade-off between a sound's amplitude and its duration on hearing sensitivity, is a fundamental property of hearing. Prior to the current study, the only temporal summation data available for pinnipeds was for the harbor seal. This investigation aimed to describe the temporal summation properties of the California sea lion. Results demonstrated that aerial

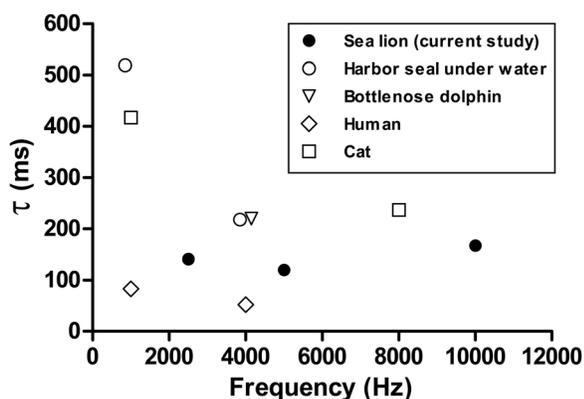


FIG. 3. Time constants, τ , based on Eq. (1) as a function of mid-range test frequency (1–10 kHz) for selected mammal species: California sea lion in air (current study), harbor seal under water (Kastelein *et al.*, 2010), bottlenose dolphin under water (*Tursiops truncatus*; Johnson, 1968 from Fay, 1988), and human (Watson and Gengel, 1969) and domestic cat (*Felis catus*; Costalupes, 1983) in air.

hearing thresholds decreased as tone duration increased up to approximately 300 ms. Time constants derived from two exponential functions for tones at 2.5, 5, and 10 kHz ranged from 92 to 167 ms in the subject. These results are consistent with those observed in other terrestrial and marine mammal species. Such information provides useful data about basic auditory capabilities of the California sea lion to inform auditory studies and predictions of anthropogenic sound impacts in this species.

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