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RESEARCH ARTICLE

Amphibious hearing in spotted seals (*Phoca largha*): underwater audiograms, aerial audiograms and critical ratio measurements

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ABSTRACT

Spotted seals (*Phoca largha*) inhabit Arctic regions that are facing both rapid climate change and increasing industrialization. While little is known about their sensory capabilities, available knowledge suggests that spotted seals and other ice seals use sound to obtain information from the surrounding environment. To quantitatively assess their auditory capabilities, the hearing of two young spotted seals was tested using a psychophysical paradigm. Absolute detection thresholds for tonal sounds were measured in air and under water over the frequency range of hearing, and critical ratios were determined using octave-band masking noise in both media. The behavioral audiograms show a range of best sensitivity spanning four octaves in air, from approximately 0.6 to 11 kHz. The range of sensitive hearing extends across seven octaves in water, with lowest thresholds between 0.3 and 56 kHz. Critical ratio measurements were similar in air and water and increased monotonically from 12 dB at 0.1 kHz to 30 dB at 25.6 kHz, indicating that the auditory systems of these seals are quite efficient at extracting signals from background noise. This study demonstrates that spotted seals possess sound reception capabilities different from those previously described for ice seals, and more similar to those reported for harbor seals (*Phoca vitulina*). The results are consistent with the amphibious lifestyle of these seals and their apparent reliance on sound. The hearing data reported herein are the first available for spotted seals and can inform best management practices for this vulnerable species in a changing Arctic.

KEY WORDS: Spotted seal, Amphibious, Hearing, Arctic, Noise

INTRODUCTION

Recent environmental warming and diminishing sea ice are enabling increased human presence and industrialization in historically undisturbed Arctic regions. Over the past decade, the growth of offshore activities such as oil and gas exploration and commercial shipping has increased low-frequency ambient noise in some areas (Huntington, 2009; Moore et al., 2012). This anthropogenic noise – associated with ship traffic, seismic surveys and drilling – alters acoustic habitats and may disturb or harm marine life. As these activities transform Arctic environments, it is increasingly important to consider and quantify their behavioral and auditory effects on marine mammals.

Among the species of particular concern are ice-dependent ('pagophilic') seals that inhabit northern regions. Ice seals are characterized by a strong association with, and ecological dependence on, sea ice for many important life functions (Boveng et al., 2009; Cameron et al., 2010; Kelly et al., 2010). Although hearing is believed to be a primary sensory modality for all pinnipeds (seals, sea lions and walruses) (Richardson et al., 1995), and ice seals are known to vocalize under water (Wartzok and Ketten, 1999), little is directly known about their reliance on and use of sound in their environment. In terms of sound reception, some auditory data exist for harp (*Pagophilus groenlandicus*) (Terhune and Ronald, 1971; Terhune and Ronald, 1972) and ringed seals (*Pusa hispida*) (Terhune and Ronald, 1975a; Terhune and Ronald, 1975b), but there are few measurements below 1 kHz where industrial and shipping noises typically occur (Wenz, 1962; Richardson et al., 1995). The most comprehensive data exist for the closely related, but more temperate living, harbor seal (*Phoca vitulina*) (Møhl, 1968; Terhune, 1988; Terhune, 1991; Kastak and Schusterman, 1998; Wolski et al., 2003; Southall et al., 2005; Kastelein et al., 2009; Reichmuth et al., 2013). However, because the phylogenetic relationships among the 10 species of northern seals are incompletely resolved (Berta and Churchill, 2012), the validity of extrapolating hearing capabilities across species in this group remains unclear. Characterizing species-typical hearing in Arctic seals is thus important in order to understand their perception of the acoustic environment, their potential susceptibility to anthropogenic noise, and the similarities or differences among related species. To this end, we are conducting a series of audiometric studies to assess basic hearing capabilities and the effects of noise on hearing in ice seals. This paper presents detailed hearing profiles for one species, the spotted seal (*Phoca largha*, Pallas 1811).

Spotted seals inhabit sub-Arctic and Arctic waters including portions of the Beaufort, Chukchi, East Siberian, Bering, Okhotsk and Yellow Seas, and the Sea of Japan (Boveng et al., 2009). Their movements and habitat-use patterns are strongly influenced by the presence of seasonal sea ice, and many of their life history events occur within the transition zone between pack ice and open water (Lowry et al., 1998; Lowry et al., 2000). Because these seals spend much of their time in light-limited, high-latitude environments and forage under water in relatively dark conditions, it is likely that they depend on acoustic cues for orientation, communication, and predator and prey detection. However, no information is currently available regarding sound reception in this species. An examination of hearing in spotted seals can provide insight into their auditory sensitivity and vulnerability to noise exposure, and can inform comparative analyses of auditory anatomy, function and evolution.

The aim of this study is to quantify the hearing abilities of spotted seals above and below the water's surface. Because seals are amphibious, dividing time between land and sea, it is essential to examine their hearing in both media to completely characterize the auditory system. Consequently, underwater and aerial audiograms were measured for two trained subjects in quiet conditions across

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List of symbols and abbreviations

CR	critical ratio
HTP	Hearing Test Program [LabVIEW-based software (Finneran, 2003)]
L_{eq}	equivalent continuous sound pressure level
MCS	method of constant stimuli
SL	sensation level
SPL	sound pressure level

the frequency range of hearing. To directly quantify how noise affects their ability to perceive relevant sounds, hearing was also tested in the presence of controlled background noise. Finally, reaction time measurements were obtained throughout testing to further evaluate the perception of similar sounds detected in quiet and noisy backgrounds. Together, these data allow for meaningful comparisons across frequencies, media, individuals and species, and describe the basic hearing capabilities of spotted seals under different environmental conditions.

RESULTS

Underwater audiograms

The underwater hearing thresholds measured for two spotted seals are provided in Table 1, along with corresponding false alarm rates and ambient noise levels. The mean false alarm rates were 0.15 and 0.20, suggesting that neither subject had an especially conservative response bias. Threshold-to-noise offsets in the testing pool were calculated as the difference between hearing threshold and ambient noise spectral density level at each test frequency. The amount by which thresholds exceeded background noise at a specific frequency was variable (15–74 dB), and greatest at high frequencies. Underwater audiograms and the associated ambient noise profile are shown along with some representative audiograms from related species in Fig. 1. The psychometric functions associated with these hearing thresholds are given as supplementary material Figs S1, S2; these show the relationship between signal sound pressure level (SPL) and detection probability at each frequency, and can be used to infer hearing threshold at the 50% detection level and any other level of interest.

The hearing curves of the two individuals were very similar, with a mean difference of 2 dB between their thresholds at each frequency. The frequency of best sensitivity under water was 25.6 kHz for both seals, whose hearing thresholds at this frequency were 53 and 51 dB re. 1 μPa. The frequency range of best sensitivity within 20 dB of the lowest measured threshold extended over more than seven octaves, from approximately 0.3 to 56 kHz for both subjects. Above this range, sensitivity declined by 40 dB within a half octave. Both audiograms exhibited a general U-shape, with sharper high-frequency roll-offs than those observed at low frequencies.

In-air audiograms

Aerial hearing thresholds are provided in Table 2, along with corresponding false alarm rates, ambient noise levels and reaction times. The mean false alarm rates were 0.18 and 0.13, again suggesting that neither subject had a particularly conservative response bias. Threshold-to-noise offsets in the acoustic chamber were 22–52 dB at frequencies above and below the range of best sensitivity, and 10–25 dB within that range. The audiograms are plotted in Fig. 2, along with the in-air ambient noise profile and existing aerial audiograms for northern seals. The psychometric functions associated with these hearing thresholds are provided as supplementary material Figs S3, S4.

The frequency of best sensitivity in air was 3.2 kHz for both seals, whose hearing thresholds at this frequency were −10 and −13 dB re. 20 μPa. Their 20 dB bandwidth of best sensitivity was much narrower in air than in water, extending across approximately four octaves from 0.6 to 11 kHz. Above this range, sensitivity declined by 20 dB per octave, with a more gradual high-frequency roll-off than that observed for these individuals in water. Similar to their underwater audiograms, however, aerial sensitivity rolled off more sharply at high than at low frequencies. Also of note is the contour of the audiograms, which appear more V-shaped than the underwater curves. The particular shape of the base of the audiogram was confirmed by testing in half-octave increments to either side of 3.2 kHz; both seals showed nearly identical thresholds in this region.

Underwater and in-air critical ratios

Underwater and in-air critical ratios (CRs) for the two seals are given in Table 3, along with masked hearing thresholds, masking noise spectral density levels, false alarm rates and reaction times for each frequency. Mean false alarm rates were 0.17 and 0.16. The CRs are plotted in Fig. 3 with available masking data for northern seals.

CRs measured in this experiment increased monotonically with increasing frequency. Underwater CRs for the spotted seal Amak

Table 1. Underwater hearing thresholds obtained with psychophysical methods for two spotted seals

	Amak		Tunu		Ambient noise
Frequency (kHz)	Threshold (dB re. 1 μPa)	FA rate	Threshold (dB re. 1 μPa)	FA rate	Power spectral density [dB re. (1 μPa)^2 Hz^{-1}]
0.1	93	0.15	92	0.25	74
0.2	76	0.13	75	0.17	58
0.4	71	0.07	68	0.23	48
0.8	66	0.12	65	0.16	44
1.6	63	0.16	62	0.24	41
3.2	56	0.11	52	0.25	37
6.4	56	0.18	54	0.20	33
12.8	60	0.14	51	0.20	31
25.6	53	0.14	51	0.10	30
36.2	57	0.26	56	0.24	28
51.2	63	0.24	64	0.19	28
60.9	81	0.17	80	0.25	29
72.4	102	0.10	101	0.10	28

Fifty percent detection thresholds are reported for each test frequency with corresponding noise levels in the test pool. Noise levels are shown in units of power spectral density determined from 1/3-octave band measurements that included each test frequency. False alarm (FA) rates during the testing phase (pooled across all method of constant stimuli sessions) are also given for each frequency (N≥20). For both subjects, 95% confidence intervals were less than 4 dB for all reported thresholds. The psychometric functions associated with each threshold are provided in supplementary material Figs S1 and S2.

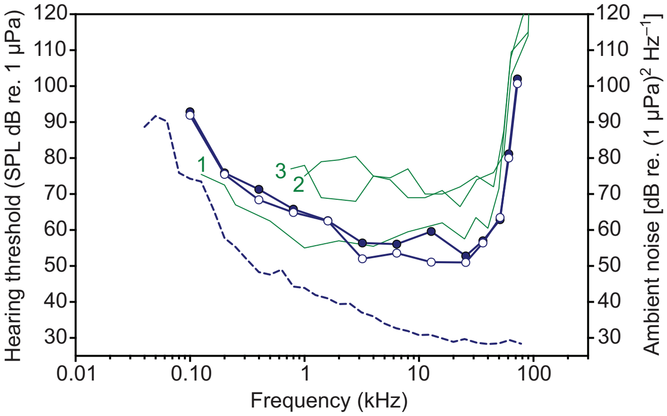

Fig. 1. Underwater audiograms for two spotted seals, Amak (filled circles) and Tunu (open circles), obtained using psychophysical methods. Ambient noise in the underwater testing enclosure is plotted as a dashed line corresponding to the right-hand *y*-axis. The ambient noise profile comprises power spectral density levels [in dB re. (1 μPa)^2 Hz^{-1}] calculated from the median of 1/3-octave band 50th percentile levels measured across all sessions. For comparison, behavioral audiograms are also shown for harbor seals [1, *N*=2 (Kastelein et al., 2009)], ringed seals [2, *N*=2 (Terhune and Ronald, 1975a)] and harp seals [3, *N*=1 (Terhune and Ronald, 1972)]. SPL, sound pressure level.

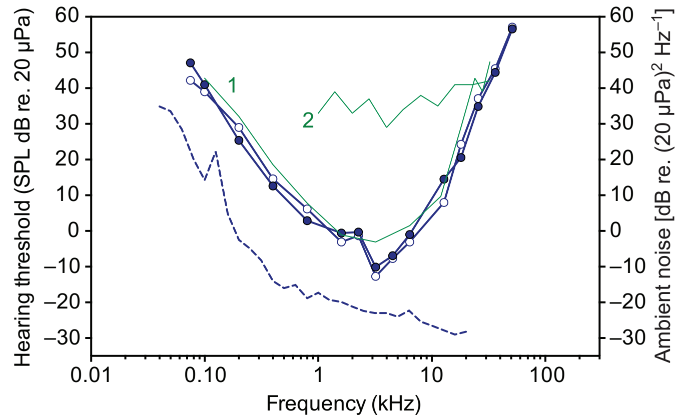

Fig. 2. Aerial audiograms for two spotted seals, Amak (filled circles) and Tunu (open circles), obtained using psychophysical methods. Ambient noise in the acoustic testing chamber is plotted as a dashed line corresponding to the right-hand *y*-axis. The noise profile comprises power spectral density levels [in dB re. (20 μPa)^2 Hz^{-1}] calculated from the median of 1/3-octave band 50th percentile levels measured across all sessions. Previously published thresholds are shown for harbor seals [1, *N*=1 (Reichmuth et al., 2013)] and harp seals [2, *N*=1 (Terhune and Ronald, 1971)]. SPL, sound pressure level.

ranged from 14 dB at 0.2 kHz to 30 dB at 25.6 kHz. Aerial CRs for the spotted seal Tunu ranged from 12 dB at 0.1 kHz to 27 dB at 25.6 kHz. Amak's underwater CRs were not significantly different from Tunu's aerial CRs (t_8=1.77, P=0.11). Furthermore, Tunu's three underwater CRs (14, 20 and 26 dB at 0.2, 3.2 and 12.8 kHz, respectively) were not significantly different either from his own aerial CRs (t_2=1.63, P=0.24) or Amak's underwater CRs (t_2=0.49, P=0.68) at the same test frequencies.

Reaction times

Median reaction times obtained in air under quiet conditions are reported in Table 2 for each frequency at threshold, or 0 dB sensation level (SL), and 20 dB above threshold (20 dB SL). Response times near threshold were typically less than 600 ms, and varied with frequency. Tunu's overall median reaction time at threshold was 475 ms while Amak's was 380 ms. As expected, reaction times were shortest for the loudest sounds presented at a particular frequency. For signals whose levels exceeded threshold by 20 dB, Tunu's median reaction times stabilized at 234 ms and Amak's at 182 ms. Reaction times were different between subjects at both 0 dB SL (t_{14}=2.58, P=0.02) and 20 dB SL (t_{14}=3.29, P=0.01).

The median reaction times obtained in the aerial masking experiment are reported in Table 3 for each frequency at 0 and 20 dB SL. As observed with the aerial audiogram data, reaction times at threshold were longer and more variable than those measured at the higher stimulus level. Under masked conditions, Tunu's reaction

Table 2. In-air hearing thresholds obtained with psychophysical methods for two spotted seals

	Amak				Tunu				Ambient noise
Frequency (kHz)	Threshold (dB re. 20 μPa)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)	Threshold (dB re. 20 μPa)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)	Power spectral density [dB re. (20 μPa)^2 Hz^{-1}]
0.075	47	0.16	289	216	42	0.16	527	230	20
0.1	41	0.28	363	260	39	0.14	565	251	14
0.2	25	0.19	302	182	29	0.20	475	301	−2
0.4	13	0.14	494	185	15	0.13	485	243	−14
0.8	3	0.03	502	306	6	0.08	507	229	−19
1.6	−1	0.03	439	141	−3	0.09	472	265	−20
2.3	0	0.17	421	133	−1	0.12	512	216	−22
3.2	−10	0.25	697	160	−13	0.09	605	282	−23
4.5	−7	0.28	293	171	−8	0.07	529	222	−24
6.4	−1	0.27	409	205	−3	0.21	449	234	−22
12.8	14	0.19	380	196	8	0.07	442	242	−28
18.1	21	0.10	411	227	24	0.03	247	195	−28
25.6	35	0.22	206	150	37	0.21	435	302	–
36.2	44	0.21	204	142	45	0.22	248	191	–
51.2	57	0.19	243	140	57	0.13	367	215	–

Fifty percent detection thresholds are reported for each test frequency with corresponding ambient noise levels in the acoustic chamber. Noise levels are shown in units of power spectral density determined from 1/3-octave band measurements that included each test frequency. False alarm (FA) rates during the testing phase (pooled across all method of constant stimuli sessions) are also given for each frequency (N≥20). Mean reaction times are shown at threshold (0 dB SL) and 20 dB above threshold (20 dB SL) for each frequency. For both subjects, 95% confidence intervals were less than 4 dB for all reported thresholds. The psychometric functions associated with each threshold are provided in supplementary material Figs S3 and S4.

Table 3. Underwater and in-air masked hearing thresholds and critical ratios obtained in the presence of octave-band noise for two spotted seals at nine frequencies

	Underwater critical ratios				In-air critical ratios					
Frequency (kHz)	Masked threshold (dB re. 1 μPa)	Masker level [dB re. (1 μPa)^2 Hz^{-1}]	Critical ratio (dB)	FA rate	Masked threshold (dB re. 20 μPa)	Masker level [dB re. (20 μPa)^2 Hz^{-1}]	Critical ratio (dB)	FA rate	Latency at 0 dB SL (ms)	Latency at 20 dB SL (ms)
0.1	119	103	16	0.06	61	49	12	0.10	414	248
0.2	99	86	14	0.22	63	49	14	0.17	367	222
0.4	96	81	15	0.26	50	35	15	0.16	367	279
0.8	92	76	16	0.12	42	26	16	0.17	622	373
1.6	90	73	18	0.13	36	17	19	0.19	489	308
3.2	87	66	21	0.21	26	7	18	0.06	387	256
6.4	90	66	24	0.16	41	17	24	0.18	586	182
12.8	96	70	27	0.14	55	31	24	0.26	392	162
25.6	93	73	30	0.19	74	47	27	0.16	–	–

Underwater critical ratios were obtained with Amak and in-air critical ratios were obtained with Tunu. Also reported for each frequency are corresponding masker spectral density levels and test phase false alarm (FA) rates (pooled across method of constant stimuli sessions, N≥20). For the in-air data, reaction times at threshold (0 dB SL) and 20 dB above threshold (20 dB SL) are also provided.

time to threshold-level stimuli was 403 ms, and at 20 dB SL his reaction time was 252 ms. The response times of this seal in the presence of masking noise were not significantly different from his response times obtained under quiet conditions, either at threshold (t_7=1.04, P=0.33) or at 20 dB SL (t_7=0.08, P=0.94).

DISCUSSION

Underwater hearing

The spotted seal underwater audiograms obtained in this study agree well with published thresholds for the harbor seal (Møhl, 1968; Terhune, 1988; Kastelein et al., 2009; Reichmuth et al., 2013). However, the spotted seal hearing thresholds are considerably lower than existing underwater data for other Arctic seals. Published thresholds for harp (Terhune and Ronald, 1972) and ringed seals (Terhune and Ronald, 1975a) are elevated across most of the frequencies tested, although there is better agreement with the spotted seal audiograms at the highest frequencies. While this could indicate species differences, more recent auditory data suggest that the hearing capabilities of spotted and ringed seals are actually quite similar (J.M.S., unpublished). When compared with fully aquatic species such as bottlenose dolphins (*Tursiops truncatus*) or harbor porpoises (*Phocoena phocoena*) (Johnson, 1967; Kastelein et al., 2002; Kastelein et al., 2010), spotted seals hear nearly as well in water in their range of best sensitivity, although this range is shifted lower in frequency for the seals. While the cetaceans have higher upper-frequency limits, the seals hear considerably better below 10 kHz, suggesting that they may be more vulnerable to the effects of anthropogenic noise.

An important aspect of any psychoacoustic study is a thorough description of ambient noise in testing environments. Although the time-varying nature of background noise is difficult to characterize, the 50th percentile statistical method used in this experiment more accurately describes temporal variability in noise than do typical methods using L_{eq} values (equivalent continuous SPLs) (Mulsow and Reichmuth, 2010; Reichmuth et al., 2013). Based on the critical ratios obtained for the subjects in this study, frequencies of concern for possible masking of underwater hearing thresholds are 3.2–36.2 kHz. Threshold-to-noise offsets of approximately one CR in this range suggest that masking noise may have marginally influenced these thresholds. Although ambient measurements were obtained in test-ready conditions, they do not represent the exact noise conditions concurrent with each signal presentation. Therefore, the combination of CRs and measured average noise conditions informs the interpretation of these underwater hearing data, but does not allow a definitive analysis given the difficulty of quantifying the effect of temporal fluctuations in noise on thresholds.

The absolute audiograms reported here provide information about the range of frequencies that are detectable by spotted seals, and that may be most relevant in terms of noise exposures. It is important to note that, even if masking of important stimuli is not occurring, the acoustic environment is still altered with the addition of background noise. Such changes may be ecologically significant for acoustically vigilant Arctic seals that utilize auditory cues to orient to features in their environment (Elsner et al., 1989). The broad range of best sensitivity under water suggests that spotted seals may be attending to auditory stimuli across seven or more octaves. This expanded range – relative to the aerial hearing abilities of terrestrial carnivores, and extending upwards toward the high-frequency hearing limits of fully aquatic cetaceans – is likely related to the enhanced role of bone and tissue conduction under water and the operation of different constraints on hearing in each medium (Hemilä et al., 2006; Nummela, 2008). High-frequency hearing supports

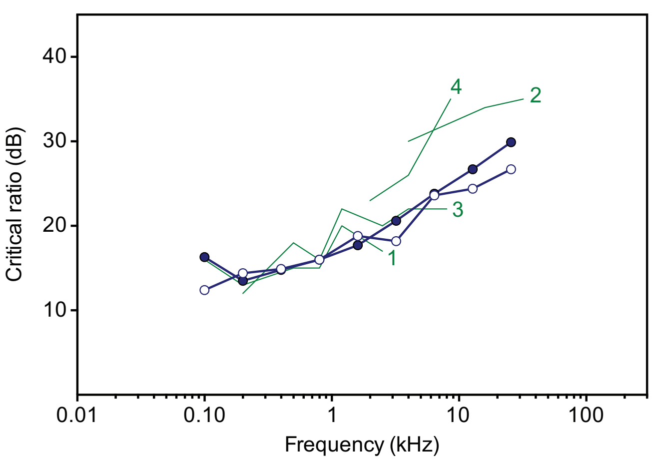

Fig. 3. Underwater and in-air critical ratios for two spotted seals measured in the presence of octave-band masking noise. Underwater critical ratios are shown for Amak (filled circles) and in-air critical ratios are shown for Tunu (open circles) at nine frequencies. Also plotted are underwater critical ratios for harbor [1, N=1 (Southall et al., 2000)] and ringed seals [2, N=2 (Terhune and Ronald, 1975b)], and aerial critical ratios for harbor [3, N=1 (Southall et al., 2003)] and harp seals [4, N=1 (Terhune and Ronald, 1971)].

localization abilities (Heffner and Heffner, 2008; Nummela and Thewissen, 2008), and may allow detection of relevant stimuli such as predator vocalizations. However, while high-frequency hearing sensitivity seems to be a derived characteristic of seals, the ecological and adaptive significance of their wide range of sensitive underwater hearing remains uncertain.

In-air hearing

The spotted seal aerial thresholds measured in this study are the lowest reported for any marine mammal. Compared with available data for seals, Amak and Tunu's thresholds are most comparable to those of harbor seals. The data reported in this experiment are similar to those measured previously for an adult harbor seal tested in the same acoustic chamber (Reichmuth et al., 2013), except at the frequency of best sensitivity, where the spotted seal thresholds are roughly 8 dB lower. The lower thresholds measured for the spotted seals at 3.2 kHz may be attributable to the age of these subjects, who were 15 years younger than the harbor seal at the time of testing. Existing harp seal thresholds (Terhune and Ronald, 1971) – the only aerial data available for ice seals – are substantially elevated across the frequency range of hearing relative to the thresholds measured in this study. While some have suggested that these thresholds were elevated by background noise (Moore and Schusterman, 1987; Watkins and Wartzok, 1985), they were more likely influenced by methodological factors. During testing, the harp seal's head was submerged immediately prior to each trial, which may have impeded the aerial sound conduction pathway (Terhune and Ronald, 1971).

Recent studies have shown that most previously reported hearing thresholds for seals – particularly aerial thresholds – were masked because of inadequate control of the ambient noise background in testing enclosures, leading to underestimates of sensitivity and confounding interpretations of amphibious hearing (Reichmuth et al., 2013). Based on the low aerial thresholds obtained in this study, combined with the CR data, there is some concern for potential masking from 1.6 to 6.4 kHz, where threshold-to-noise offsets are within a few dB of one CR. However, the ambient noise levels in the acoustic chamber approach the limit of detectability for the measurement instrumentation used; threshold-to-noise offsets are therefore conservative at frequencies from 0.8 to 20 kHz, making it difficult to rule out the influence of masking. Regardless, the extremely quiet testing conditions during this experiment enabled the measurement of very low aerial thresholds for both seals, which conservatively estimate hearing sensitivity for this species. In light of thresholds measured for pinnipeds generally that approach or fall below 0 dB re. 20 µPa, and especially the spotted seal audiograms obtained in this experiment, it appears that the effects of airborne anthropogenic noise may be of particular concern for these species.

These results suggest that spotted seals have not lost their acute ability to perceive aerial sounds in their transition to a semi-aquatic lifestyle. In fact, the spotted seal thresholds reported herein describe hearing sensitivity comparable to that of terrestrial carnivores (e.g. Heffner, 1983; Heffner and Heffner, 1985a; Heffner and Heffner, 1985b; Kelly et al., 1986). Although the terrestrial species have higher upper-frequency limits and somewhat broader ranges of best sensitivity, at mid to low frequencies there is a high degree of similarity between the hearing of these marine carnivores and their terrestrial counterparts. For seals that forage at sea but remain tied to sea ice for activities such as whelping and molting, this is not unexpected. Spotted seals are vigilant when hauled out on ice floes and are susceptible to acoustic disturbance (Boveng et al., 2009), which is supported by their sensitivity to airborne sounds.

Amphibious comparison

It is relevant to consider the extent to which the auditory systems of amphibious animals may be adapted for use in one medium or the other. To account for the acoustic impedance difference between media, a basic comparison can be made between underwater and in-air thresholds in terms of energy, given certain assumptions about plane wave propagation in small testing enclosures. An energetic comparison of best hearing sensitivity can be estimated from the measured pressure thresholds for the spotted seals as −131 dB re. 1 W m^{-2} in water and −133 dB re. 1 W m^{-2} in air. These spotted seal data are discussed in terms of pressure rather than intensity because the seal ear is thought to be sensitive primarily to sound pressure, as is true for most mammals; for further discussion of this issue see Kastak and Schusterman (Kastak and Schusterman, 1998), Finneran et al. (Finneran et al., 2002) and Reichmuth et al. (Reichmuth et al., 2013). Regardless of metrics, it is clear that these seals possess efficient sound reception pathways both in water and in air, allowing auditory capabilities comparable to those of hearing specialists in either environment.

Auditory masking

The finding that spotted seal CRs are consistent with those of harbor seals in both air and water (Southall et al., 2000; Southall et al., 2003) provides further evidence for similar hearing between the two species and supports the general trend of low CRs in seals (Reichmuth, 2012). It has been suggested that such low CRs might be an adaptation for detection of signals in relatively noisy marine environments (Southall et al., 2000). Although the spotted seal CRs increase with frequency at a rate similar to that of most mammals (Fay, 1988), their consistently lower CRs indicate that signal detection within background noise is an enhanced capability for these seals. In fact, the CRs measured in this study are among the lowest reported for mammals (Fay, 1988).

Significantly, the spotted seal CRs do not differ across media or subjects. Although underwater and aerial hearing sensitivity are quite different, this finding for CRs is expected and confirms earlier hypotheses. Because sound transmission through the medium and auditory pathway similarly influences signals and noise, CRs – which are based on relative differences between the two – are the same for seals listening above or below water (Renouf, 1980; Turnbull and Terhune, 1990; Southall et al., 2003).

When compared with masking data for other ice seals, these CRs are within 8 dB of those reported in air for one harp seal except at the highest frequency (Terhune and Ronald, 1971); the especially high CR at 8.6 kHz can be explained by the harp seal's behavior during testing (Terhune and Ronald, 1971). The spotted seal CRs are also quite different from those obtained in water for two ringed seals (Terhune and Ronald, 1975b). These differences have implications for our understanding of auditory filtering in ice seals. Based on the CR equal power method (Richardson et al., 1995), estimated masking bandwidths are 2–16% of center frequency in this experiment, with one exception for one subject at 0.1 kHz (40%). Above 0.2 kHz, estimated auditory filter widths are roughly a constant percentage of center frequency. This finding of critical bandwidths of less than one-third of an octave is in contrast to the previous estimates for ice seals reviewed by Richardson et al. (Richardson et al., 1995). It is important to note that these indirect estimates often differ from direct critical bandwidth measurements (Richardson et al., 1995; Southall et al., 2003). Regardless, these data suggest that critical bands in ice seals are narrower than previously believed. Future studies involving direct measurement of critical bandwidth are necessary to characterize auditory filter parameters in ice seals.

In addition to informing cross-species comparisons and providing insight into auditory processing, these CRs can be applied to management decisions. Masking data describe the efficiency with which individuals can extract meaningful signals from noise, as well as their susceptibility to increasing ambient noise levels. The CRs reported herein can be used to quantitatively estimate zones of masking for spotted seals exposed to relevant signals embedded within natural or anthropogenic noise. While these estimates do not account for release from masking due to spatial or other complex factors, they do delineate the outer bounds of masking surrounding a given sound source.

Response latency under different environmental conditions

Comparing reaction time measures across subjects and acoustic testing environments provides additional insight into auditory perception in quiet and noise. In contrast to the measured hearing thresholds, response latencies showed more individual variation. The difference in latencies for the two seals tested under identical conditions underscores the importance of within-individual comparisons when examining the influence of any factor (e.g. background noise) on perception.

In this study, reaction time data for the same individual in the unmasked and masked experiments is a proxy for perceptual loudness under these different signal and noise conditions (Moody, 1970). During the masking experiment, the absolute level of the stimulus was considerably higher than during audiogram testing at the same frequency. Despite 20–50 dB differences in absolute SPL, however, latencies were no different for signals of the same SL across the two noise conditions. This is because sensation level relates the amplitude of the target stimulus to sensory threshold. The different test signals were perceptually equated by the presence of noise in the environment, as expected based on the CR data and confirmed by the equal response times in both cases. Thus it is clear that CRs and reaction times are different metrics for quantifying the same phenomenon: the effects of noise on perception. Both data sets indicate that the addition of anthropogenic noise requires that a relevant sound be of considerably higher amplitude to achieve the same perceptual loudness as a sound received in quiet conditions.

Conclusions

Little is known about the acoustic ecology of spotted seals, with no prior studies describing their hearing and few assessing their acoustic communication or behavior (Beier and Wartzok, 1979; Gailey-Phipps, 1984; Xiao-mei et al., 2012). The present study provides auditory profiles for two young spotted seals, addressing a significant knowledge gap. Comparisons of underwater and in-air data demonstrate acute sensitivity in each medium, suggesting a need to consider anthropogenic noise effects both above and below the water's surface for these amphibious animals. Furthermore, these data reveal hearing capabilities comparable to those of the closely related harbor seal, suggesting that the larger knowledge base available for the harbor seal may be applied as a good first approximation for spotted seal auditory processing and ecology. Of special relevance to the present study is the remarkable similarity in data obtained for the two subjects in matched conditions. The high degree of agreement between thresholds measured with young, well-trained animals in controlled conditions lends confidence to the conclusion that these data represent species-typical hearing in spotted seals. Finally, the auditory data presented in this paper support the claim that seals have not traded their aerial hearing capabilities for superior underwater sound reception (Reichmuth et al., 2013). Rather, these spotted seals have retained acute hearing sensitivity in both media, consistent with an amphibious existence.

As human presence at high latitudes increases, it is necessary to assess the capacity of northern species to cope with changing environments. Anthropogenic noise is one of many threats facing pagophilic seals, and the ultimate persistence of these seals will depend on resilience in the face of multiple simultaneous stressors. Effective conservation depends first on an understanding of the potential impacts. Careful assessments of hearing for individual species can quantify both perceptual capabilities and the potential effects of increasing noise levels. This psychoacoustic study thoroughly describes the amphibious hearing capabilities of spotted seals, and informs best management practices for this vulnerable species in a rapidly shifting environment.

MATERIALS AND METHODS

General experimental methods

Test subjects

The subjects were two young male spotted seals, *Phoca largha*, identified as Amak (NOA0006675) and Tunu (NOA0006674). Both subjects were 1 year old at the start of testing. These seals stranded as pups and were subsequently transferred to Long Marine Laboratory at the University of California at Santa Cruz. Neither seal had a known history of ear injury, exposure to ototoxic medication, or other complication that might affect their hearing capabilities. Their body masses at the start of testing were 42 and 34 kg, respectively, and their interaural distances were 15 and 14 cm. As true seals lack external pinnae, the interaural distance was measured as the curvilinear length between the meatal openings, measured dorsally.

The seals were housed outdoors at Long Marine Laboratory in free-flow seawater tanks with adjacent haul-out space. Both subjects were trained via operant conditioning methods using fish reinforcement to voluntarily participate in husbandry and research sessions. They underwent extensive training for the signal detection task prior to audiometric testing, which occurred from 2011 to 2013. Throughout this period, the seals received one-third to one-half of their daily diets (freshly thawed capelin) during experimental sessions. Their diets were established to maintain a healthy body mass and were not constrained for experimental purposes. Each seal generally participated in experimental sessions once per day for 5 days per week.

All research was conducted with the approval and oversight of the University of California at Santa Cruz Institutional Animal Care and Use Committee, with authorization from the Ice Seal Committee and the National Marine Fisheries Service of the United States (research permit 14535).

Test environments

Testing took place in two environments. The underwater environment comprised a circular, partially in-ground pool 1.8 m deep and 7.6 m in diameter. This concrete, epoxy-lined test pool was filled with seawater that ranged from 10 to 14°C. Aerial testing took place in a modified hemi-anechoic acoustic chamber (Eckel Industries, Cambridge, MA, USA) that contained a 3.3×2.3×2.2 m testing room with double-paneled stainless steel walls and ceiling lined with sound-attenuating, fiberglass-filled aluminium wedges. The solid floor of the acoustic chamber was covered with a 4 cm thick foam mat. The experiments were controlled remotely from an adjacent, sound-isolated room where the experimenter could monitor surveillance cameras in the test enclosure while remaining out of view.

Psychoacoustic procedures

Hearing thresholds were determined using similar behavioral methods for all experimental conditions. Each seal was trained to perform a go/no-go procedure with single-response audiometry, in which he touched a response target upon detecting an acoustic signal or withheld this response when he did not (Stebbins, 1970). To begin an experimental session, a trainer unaware of the individual trial conditions cued the subject to enter the test enclosure and place his head on a chin station positioned within a calibrated sound field. This station precisely controlled head position and ensured consistency across trials and sessions. A small light, placed in front of this station at eye level, was illuminated by the experimenter to define the 4 s duration of each individual trial. The response target – which the subject could press upon detection of a signal – was a PVC plate located 20 cm to the left of station. Each trial began when the subject was settled in the chin station and the trial light was turned on, and ended when the subject touched the response target or when the 4 s interval was complete and the light was extinguished.

Trials had two possible types – signal present or signal absent – and four possible outcomes. A correct detection occurred on signal-present trials when the subject touched the response target. A correct rejection occurred on signal-absent trials when the subject remained on station for the entire trial interval. Both correct responses were marked with a conditioned acoustic reinforcer (buzzer) triggered by the experimenter. The trainer, wearing a headset linked to the experimenter, was then instructed to deliver primary reinforcement (one fish) to the seal. Conversely, if the subject withheld a response when a signal was presented (miss) or touched the response target when no signal was generated (false alarm), he did not receive conditioned or primary reinforcement, and was allowed to progress to the subsequent trial. The trial sequence for each session was pseudorandomly predetermined according to a set ratio of signal-present to signal-absent trials. This sequence was constrained such that there were never more than four in a row of a given trial type; this further reduced the likelihood of the subject predicting the trial type over a typical Gellermann (Gellermann, 1933) series. Testing sessions included 40–60 trials. The frequencies for each experiment were tested successively in random order to avoid learning effects.

Two psychoacoustic procedures were used to determine hearing thresholds. An adaptive staircase method (Cornsweet, 1962) was used to estimate a preliminary threshold, followed by the method of constant stimuli (MCS) (Stebbins, 1970) for final threshold determination. Within a single testing session of either type, frequency was held constant while signal amplitude was varied. The absolute threshold at each frequency was defined as the SPL in dB r.m.s. re. 1 μPa (under water) or dB r.m.s. re. 20 μPa (in air) at which there was a 50% correct detection rate.

Adaptive staircase testing was conducted over multiple sessions at the start of each frequency to allow the subject to acclimate to the test signal and to establish the preliminary estimate of threshold. These sessions began with a signal level easily detected by the subject, after which the amplitude was decreased by 4 dB following each correct detection until the first miss. The experimenter would then adjust the signal amplitude up in 4 dB steps after each miss and down by 2 dB steps after each correct detection, until five descending misses within 6 dB of each other were obtained. These five misses made up the test phase. Finally, a cool-down phase concluded each session, consisting of four to six trials at a more salient level – approximately 20 dB above the estimated threshold – to ensure stimulus control on the signal detection task. Once testing performance had stabilized, the preliminary threshold was estimated as the mean of three individual session thresholds within 3 dB of one another.

Subsequent MCS testing served to determine the final hearing threshold and proceeded as follows. Five signal levels were selected in 2 dB increments centered on the preliminary threshold obtained from adaptive staircase testing [+4, +2, +0 (preliminary threshold), −2 and −4 dB]. Each SPL was presented five times per session, distributed evenly into randomized blocks to eliminate any effect due to predictable changes in level. Final threshold was calculated using Probit analysis (Finney, 1971). This involved fitting the psychometric function to the proportion of correct responses obtained at each signal level, and using an inverse prediction to determine threshold at the 50% correct detection level. A minimum of two MCS sessions were used for this analysis, with additional sessions run until 95% confidence intervals were less than 4 dB.

Response bias was evaluated by monitoring false alarm rates, quantified as the percentage of signal-absent trials in which subjects reported a detection. To maintain a stable response bias (Schusterman, 1974), the proportion of signal-present trials was varied between 0.50 and 0.70 and the reinforcement ratio for correct detections to correct rejections was varied between 1:1 and 2:1. [A 2:1 reinforcement ratio was used for Amak at 72.4 kHz under water. Amak exhibited a conservative response bias at this frequency, with a false alarm rate of 0 for five sessions with a 70:30 signal to catch ratio, until the reinforcement ratio was adjusted.] Adjustment of these parameters occurred between but not within sessions. False alarm rates during each session's test phase were deemed acceptable if they were above 0 and below 0.3.

Stimulus generation and calibration

These experiments were conducted using the Hearing Test Program (HTP) virtual instrument (Finneran, 2003) built from LabVIEW software (National Instruments Corp., Austin, TX, USA). Signals were sent from HTP through an NI USB-6259 BNC M-series data acquisition module with an update rate of 500 kHz. For all experiments, test stimuli were 500 ms frequency-modulated sweeps with 10% bandwidth (±5% from the test frequency) and 5% rise and fall times on the signal. These narrow-band sweeps were used rather than pure tones to minimize variability in the received sound field (Kastelein et al., 2002; Finneran and Schlundt, 2007). The outgoing test stimuli were bandpass filtered as an added measure to ensure signal integrity, using a Krohn-Hite 3364 anti-aliasing filter (Krohn-Hite, Brockton, MA, USA). Subsequently, signals were sent through a TDT PA5 digital attenuator (Tucker-Davis Technologies, Alachua, FL, USA) and, in some cases, a Hafler P1000 power amplifier (for underwater audiogram testing at 6.4 kHz and below, and for the masking experiment at all frequencies; Hafler Professional, Tempe, AZ, USA) prior to reaching the transducer.

Stimulus calibration was performed daily. Immediately prior to each session, calibration tones at the test frequency were generated at various levels and transmitted into the test enclosure. Received signals were returned from a hydrophone or microphone (see below) through the same filter, NI hardware and HTP software used for signal generation. The update rate on the incoming signal was 500 kHz. Calibration signals were measured, compared with expected SPLs and examined in the frequency domain using fast Fourier transform analysis to ensure that the subject was receiving clean signals without harmonics. Sound level calibrations were conducted at the listening station in the absence of the subject.

Ambient noise characterization

Ambient noise measurements were taken daily at the center position of the seal's head during testing, using a battery-powered Brüel & Kjær 2250 sound analyzer (Brüel & Kjær A/S, Nærum, Denmark) with a calibrated Reson TC4032 low-noise hydrophone (0.01–80 kHz, ±2.5 dB; Reson A/S, Slangerup, Denmark) under water and a calibrated Brüel & Kjær 4189 free-field microphone (0.006–20 kHz) in air. One-minute, unweighted noise samples were recorded prior to each session and percentile statistics of 1/3-octave band levels were calculated from 1 min L_{eq} values for frequencies from 0.04 to 20 kHz. For frequencies from 20 to 78 kHz under water, a battery-powered Fostex FR-2 Field Memory Recorder (Fostex Company, Tokyo, Japan) was used in conjunction with the Reson TC4032. These high-frequency noise measurements were made on several days under testing conditions. In air, equipment limitations prevented absolute noise measurements lower than 0 dB re. 20 μPa above 20 kHz.

Underwater audiograms

Underwater auditory thresholds for the two subjects were measured across the hearing range at 13 frequencies: 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4, 12.8, 25.6, 36.2, 51.2, 60.9 and 72.4 kHz.

Stimulus generation and calibration

In addition to the hardware described above, three underwater transducers were used to project stimuli into the test enclosure. These transducers were a National Undersea Warfare Center J-11 speaker (Newport, RI, USA) for 0.1–0.2 kHz signals, a Lubell Labs 1424 HP projector (Columbus, OH, USA) for 0.4–6.4 kHz, and an ITC 1042 projecting hydrophone (International Transducer Corporation, Santa Barbara, CA, USA) for 12.8–72.4 kHz. These transducers were decoupled from the underwater testing apparatus and suspended into the pool 5–6 m behind the subject, a distance that exceeded the theoretical near-field boundary (Siler, 1969) at all frequencies. The precise position of the transducer was frequency specific and based on spatial mapping of the received sound field. Prior to testing, mapping was conducted at each frequency to ensure acceptable variability (±3 dB) in the test stimulus recorded at 25 positions on a 14×14×14 cm grid centered at the daily calibration position (i.e. the depth of the seal's ears in the center of the head). We used the Reson TC4032 hydrophone with a Reson EC6073 input module, or a calibrated ITC 1042 hydrophone (0.01–100 kHz, ±2.5 dB), as a receiver for both mapping and calibration. During mapping, the speaker was moved around the testing enclosure until criteria were met, which determined the speaker's testing location for each frequency.

The underwater experimental apparatus consisted of a water-filled PVC frame with a mounted chin cup designed to position each animal's ears at a depth of 1 m, 0.75 m from the edge of the pool. This apparatus was located in the same position for all testing configurations with all subjects.

In-air audiograms

Aerial auditory thresholds were measured across the hearing range at 15 frequencies: 0.075, 0.1, 0.2, 0.4, 0.8, 1.6, 2.3, 3.2, 4.5, 6.4, 12.8, 18.1, 25.6, 36.2 and 51.2 kHz.

Stimulus generation and calibration

In addition to the hardware described above, four aerial transducers were used to project stimuli. These speakers were the JBL 2245H (JBL Incorporated, Northridge, CA, USA) for 0.075, 0.1 and 0.8 kHz; the JBL 2123H for 0.2, 0.4 and 1.6–3.2 kHz; the Fostex FT96H for 4.5–36.2 kHz; and the Avisoft Vifa (Avisoft Bioacoustics, Berlin, Germany) for 51.2 kHz. A calibrated Josephson C550H microphone (0.02–20 kHz, ±2 dB; Josephson Engineering, Santa Cruz, CA, USA) or a calibrated Microtech MK301 microphone capsule (0.005–100 kHz, ±2 dB; Microtech Gefell GmbH, Gefell, Germany) with an ACO Pacific 4016 preamplifier and PS9200 power supply (ACO Pacific Incorporated, Belmont, CA, USA) was used for stimulus calibration and sound field mapping. The speakers were mounted in the acoustic chamber 0.6–1.2 m directly in front of the subject, at a frequency-specific distance determined by spatial mapping of the sound field. The near-field boundary was exceeded at every test frequency (Siler, 1969). The received sound field was measured at each frequency at 11 positions within a 12×12×12 cm grid surrounding the position of the animal's head during testing, in order to ensure acceptable variability (±3 dB). The grid points included locations coincident with the seal's left and right auditory meatus. The daily calibration position depended on frequency and was at the position of the left or right meatus, based on which location had a higher received level during sound field mapping.

The in-air experimental apparatus consisted of a U-shaped chin station that positioned the seal's ears 0.3 m above the floor of the chamber. The station included a plexiglass latency switch that the animal was trained to depress with his nose to initiate each trial. This enabled the measurement of time between signal onset and release of the switch as the subject moved to touch the response target.

Underwater and in-air CRs

Underwater and aerial masked hearing thresholds were obtained in the presence of octave-band noise centered on the frequency of the test signal. CRs – defined as the difference (in dB) between the SPL of the masked threshold and the spectral density level of the octave-band noise masker at the center frequency of the masking band (Fletcher, 1940; Scharf, 1970) – were obtained for each subject at nine frequencies: 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4, 12.8 and 25.6 kHz. Amak completed testing at these nine frequencies under water, and Tunu completed the same testing in air. In addition, Tunu completed testing at three frequencies (0.2, 3.2 and 12.8 kHz) under water to cross-validate these data.

The masking task was similar to audiogram testing in each medium, the exception being that calibrated noise was paired with the duration of the trial light. Masking noise was presented only during the trial interval as a precaution to avoid loudness adaptation (Gelfand, 1981; Southall et al., 2000).

Stimulus generation and calibration

Test stimuli for the masking experiment were generated, calibrated and projected using the same hardware as that used for the audiograms. Noise stimuli were gated (500 ms rise time) octave-band white noise maskers, generated and filtered using AVS Audio Editor 7.1 (Online Media Technologies Limited, London, UK) or Adobe Audition CS6 (Adobe Systems Incorporated, San Jose, CA, USA) and analyzed using SpectraPLUS (Pioneer Hill Software LLC, Poulsbo, WA, USA). These maskers were produced (sampling rate 44.1 kHz, 16 bit resolution) and passed from the sound card of a computer to a Hafler P1000 power amplifier – where they were mixed with the test signals – prior to reaching the speaker. The only exception was the 25.6 kHz masker, which was generated and filtered using MATLAB (MathWorks, Natick, MA, USA) and transmitted from the computer through a Roland Quad-Capture USB 2.0 Audio Interface (sampling rate 192 kHz; Roland Corporation US, Los Angeles, CA, USA) and a Reson VP1000 voltage preamplifier (in air only) before reaching the amplifier. Test signals and masking noise were projected from the same speaker to avoid spatial release from masking (Terhune and Turnbull, 1989; Turnbull, 1994; Holt and Schusterman, 2007). For in-air CR determination, the speakers used were the same as for the in-air audiogram. For underwater testing, the J-11 was used at frequencies from 0.1 to 12.8 kHz and the ITC 1042 at 25.6 kHz.

The masking noise was filtered to ensure that spectral density levels were relatively flat (±3 dB in air; ±5 dB under water) across the central 1/3-octave band at the daily calibration position. [At the two highest frequencies under water – 12.8 and 25.6 kHz – variability in spectral density levels was ±9 and ±7 dB, respectively. This resulted from narrowband peaks or troughs in the noise that were unable to be filtered. The primary 1/3-octave band criterion was met for both frequencies.] Noise stimuli were mapped prior to testing, across a subset of the mapping positions used for the test signals. Under water, 1 min noise samples were projected and received across nine positions in a 14×14 cm plane at the depth of the subject's ears. In air, 1 min noise samples were recorded across six positions in a 12×12 cm plane at the height of the subject's ears. Each of the three 1/3-octave band levels across the entire octave-band masker was measured at every position, and acceptable variability was ±3 dB between all 1/3-octave bands across all positions in the mapping grid.

Before each testing session, both signal SPL and masking noise spectral density level were calibrated. The masker level was invariant throughout audiometric testing at a particular frequency. Masking noise spectral density levels [dB re. $(1\ \mu Pa)^2\ Hz^{-1}$ underwater and dB re. $(20\ \mu Pa)^2\ Hz^{-1}$ in air] were either 10 or 20 dB (determined by hardware limitations) above the hearing threshold measured for each frequency for the same subject. Because CRs are independent of masker level (Fay, 1988), this difference was unlikely to affect measurements. Noise stimuli were calibrated using SpectraPLUS to ensure that the 1/3-octave band centered on the test frequency was within 1 dB of the target level, and that the 1/3-octave bands above and below this central band were within 3 dB of the target level.

Reaction times

Reaction times (in ms, between tone onset and release of latency switch) were automatically recorded in HTP on all signal-present trials correctly detected during aerial testing, in both quiet and noisy conditions. Data from MCS testing only were pooled across sessions to generate latency–intensity functions at each frequency for each condition. A least-squares power function (Moody, 1970) was used to fit these data and to interpolate reaction times at threshold and 20 dB SL. A comparison of median latencies across subjects in quiet conditions was conducted using a paired *t*-test. A direct comparison was also made between Tunu's audiogram latencies at 0 and 20 dB SL and those obtained at the same frequencies and sensation levels during CR testing.

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Competing interests

The authors declare no competing financial interests.

Author contributions

J.M.S. was involved in all aspects of this study and responsible for manuscript preparation. B.L.S. was involved in design, measurement and analysis. C.R. was involved in all aspects and responsible for funding and animals.

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Supplementary material

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