Spatial release from masking of aerial tones in pinnipeds

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In most masking experiments, target signals and sound intended to mask are located in the same position. Spatial release from masking (SRM) occurs when signals and maskers are spatially separated, resulting in detection improvement relative to when they are spatially co-located. In this study, SRM was investigated in a harbor seal, who naturally lacks pinnae, and California sea lion, who possesses reduced pinnae. Subjects had to detect aerial tones at 1, 8, and 16 kHz in the presence of octave bands of white noise centered at the tone frequency. While the masker occurred in front of the subject (0°), the tone occurred at 0, 45, or 90° in the horizontal plane. Unmasked thresholds were also measured at these angles to determine sensitivity differences based on source azimuth. Compared to when signal and masker were co-located, masked thresholds were lower by as much as 19 and 12 dB in the harbor seal and sea lion, respectively, when signal and masker were separated. Masked threshold differences of the harbor seal were larger than those previously measured under water. Performance was consistent with some measurements collected on terrestrial animals but differences between subjects at the highest frequency likely reflect variations in pinna anatomy. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2404929]

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I. INTRODUCTION

The directional hearing systems of many vertebrates have been shown to enhance the reception of relevant acoustic signals in the presence of noise (NRC, 2003). For example, when a target signal and masker have separate spatial locations, detection and identification of the target signal is improved relative to the condition when the signal and masker are located in the same place. This phenomenon has been termed spatial release from masking (SRM) or spatial unmasking and can significantly increase the detection range of signals such as those of conspecifics, prey, or predators.

In both air and water, pinnipeds (seals, sea lions, and walruses) are often faced with the challenge of detecting socially and reproductively important sounds in a background of ambient noise. Auditory masking in pinnipeds has been relatively well documented in a few species given appreciable concerns regarding ocean noise, human activity, and their potential negative effects on free-ranging marine mammals (Terhune and Ronald, 1975; Turnbull and Terhune, 1990; Turnbull, 1994; Southall et al., 2000; Southall et al., 2003a). In all but one pinniped masking study (Turnbull, 1994), the auditory signals and maskers were spatially coincident despite the fact that in everyday experiences, signals and maskers may take on a vast number of different spatial configurations relative to each other. In fact, only a handful of masking studies in nonhuman subjects have investigated the effects of SRM.

The earliest work on masking and spatial hearing documented this effect in human subjects wearing earphones by presenting a low frequency signal 180° out of phase between the two ears while the noise masker remained in phase (e.g., Hirsh, 1948; Jeffress et al., 1962). Because interaural phase differences are the dominant spatial cues for azimuth localization at low frequencies, the assumption followed that detection would improve if the signal is spatially separated from the masker (Yost, 1997). Other interaural disparities projected through earphones that resulted in release from masking include onset time and level differences (Colburn and Durlach, 1965; Zerlin, 1966) as well as frequency differences (Robinson, 1971). Thus, from these early studies with humans, a binaural system seemed to have advantages over a monaural one not only for sound localization in the horizontal plane but also for the detection of signals in the presence of noise.

Subsequent investigations have shown that SRM in humans also occurs in “free-field” environments at most frequencies (Santon, 1987; Terhune and Turnbull, 1989; Saberi et al., 1991; Gilkey and Good, 1995). While interaural time cues are important for SRM at azimuth in the case of low frequency signals, monaural spectral cues, which also govern localization in the vertical plane, are the predominant cues necessary for release from masking for high frequency target signals (Gilkey and Good, 1995; Gilkey et al., 1997; Zurek et al., 2004). Furthermore, SRM has been observed for signal and masker configurations spatially separated in the vertical...
plane, although the effects tend to be smaller in magnitude than those measured in the horizontal plane (Saberi et al., 1991; Gilkey and Good, 1995). These monaural cues are created by differences in signal to (masking) noise level ratios in frequency dependent ways from both near or “better ear” effects as well as binaural input differences (Shinn-Cunningham et al., 2005).

Measures of spatial release from masking in nonhuman mammals are limited to a few studies including those conducted in air in ferrets (Mustela putorius; Hine et al., 1994) and mice (Mus musculus; Ison and Agrawal, 1998), and under water in a dolphin (Tursiops truncatus; Au and Moore, 1984) and harbor seal (Phoca vitulina; Turnbull, 1994). In these studies, when the signal source and masker were located at different points in either the horizontal or vertical plane, masked thresholds were lower in most conditions relative to the condition in which the signal and masker were either spatially co-located or heard monaurally. In the Hine et al. (1994) investigation, SRM for low frequencies was due to binaural processing given that monaural conditions abolished the detection advantages of spatially separating the signal and masker. On the other hand, release from masking occurred with high but not low frequencies in mice subjects (Ison and Agrawal, 1998). Likewise, these animals have been shown to localize high but not low frequencies in the horizontal plane, indicating that they cannot use interaural time differences for either auditory process (Ison and Agrawal, 1998). In the underwater marine mammal investigations, it is unclear whether or not performance was influenced by monaural spectral cues, binaural cues, or some combination of both. Turnbull (1994) found that spatial release from masking (threshold differences for co-located versus separated sources) generally grew with increasing spatial separation by up to 4 dB but depended on both test frequency and masker location. Although these threshold differences measured under water were small, those based on interaural cues would likely be greater in air. Given the faster travel time and longer wavelengths of sound in water relative to air, the magnitude of interaural differences as well as monaural spectral cues created by the shadowing effects of the body are diminished in an aquatic medium. For example, pinniped localization acuity, which is based on these two binaural cues, is worse under water than in air by a factor that is predicted based on these propagation differences (Terhune, 1974; Moore and Au 1975; Holt et al., 2004).

Localization performance of most pinnipeds tested in azimuth, including harbor seals and California sea lions (Zalophus californianus), is consistent with the duplex theory (low frequencies are localized by interaural time differences and high frequencies by interaural level differences; Strutt, 1907; Terhune, 1974; Moore and Au 1975; Holt et al., 2005). If SRM in the horizontal plane is governed by the same binaural cues that dictate localization performance then it is expected that the effects of SRM will be comparable at the lower and higher frequencies in the harbor seal and California sea lion. Additionally, these effects are expected to be reduced at intermediate frequencies in which both binaural cues are reduced in magnitude. On the other hand, if monaural filtering effects of the external ears, head, and body are responsible for SRM at higher frequencies, differences in performance and the extent of SRM between seals and sea lions are expected at these frequencies given that there are considerable variations in the presence and configurations of the external ears between the two pinniped taxa. Figure 1 shows that the harbor seal lacks pinnae while the sea lion possesses pinnae which are considerably reduced in size compared to most terrestrial mammals. Thus, it is hypothesized that if the monaural effects of the external ears (as well as the head and body) rather than interaural level differences are responsible for SRM at high frequencies, then the size of the observed SRM will differ between the two subjects at higher frequencies.

Spatial release from masking in free-ranging animals has important implications for understanding how masking interferes with the reception of important signals, such as intraspecific vocalizations. This is relevant for considering detection in noise from both natural and anthropogenic sources, particularly for directional maskers (see Zurek et al., 2004). For example, masking effects of noise from oil-spill cleanup vessels on the reception of killer whale (Orcinus Orca) vocalizations was investigated in two trained killer whales. Results showed that masking was reduced when signal and noise sources were separated (Bain and Dahlheim, 1994). Furthermore, spatial release from masking may result in larger detection ranges of calls (e.g., of those enabling female and offspring to reunite) which in turn may have significant consequences for survival and fitness.

In this study, spatial release from masking was investigated in air in two pinniped subjects (a female California sea lion and a male harbor seal) to determine potential detection advantages that might be afforded by free-ranging pinnipeds from this type of auditory process. Both masked and unmasked thresholds were measured for all signal locations to determine what contribution azimuth-dependent hearing sensitivity had on SRM.

II. METHODS

A. Subjects

The subjects were a 17-year-old male harbor seal (Sprouts) and a 20-year-old female California sea lion (Rio). Both subjects were resident animals at Long Marine Laboratory in Santa Cruz, CA and had extensive previous experi-

FIG. 1. External ears of the (A.) harbor seal on the left and (B.) California sea lion on the right (see text for discussion).
ence performing sound detection tasks in the presence and absence of masking noise in air (Southall et al., 2003a; Reichmuth Kastak et al., 2004). For the current study, subjects received up to 50% of their daily food totals (2.5–5.5 kg of mixed herring and capelin) during experimental sessions. This study followed the protocols approved by the University of California Chancellor’s Animal Research Committee.

In a previous localization investigation, both subjects could localize 1 and 16 kHz tones with equal proficiency, indicating that they both possess comparable abilities to utilized interaural time and level differences. However, both had more difficulty localizing a 8 kHz tone (Holt et al., 2005). Thus, these frequencies were used in this study to determine, if like localization, there exists predictable frequency-dependent effects on SRM performance.

**B. Apparatus**

Testing occurred in a custom-built 4.0×2.8×2.4 m double-walled hemi-anechoic chamber (Eckel Industries) as described in Holt et al. (2004). All surfaces of the test chamber were lined with acoustic foam wedges except the concrete floor and stainless steel door, which were covered with 2.6 cm neoprene mats. A stationing chin cup made of polyvinyl chloride (PVC) was mounted to the floor and placed 1 m from the sound sources mounted to the wall in front of the chin cup. One rectangular PVC response target (each 11.4×8.9 cm) was also mounted to the floor and spaced to the left side of the chin cup.

**C. Stimulus production and equipment**

All equipment was controlled by the experimenter in a 1.3×2.8×2.4 m control room adjacent to the test chamber. The signals were pure tones at 1, 8, and 16 kHz generated and triggered by the experimenter using custom designed LABVIEW™ 6 software and operated by a National Instruments PXI 1010 Chassis and National Instruments 6070E multifunction input/output (I/O) board. The signal duration was 500 ms and was shaped with a linear rise and fall time of 20 ms. The signal was routed to a stepwise attenuator (Hewlett-Packard 350D) and then to a speaker (Morel MDT37 horn tweeter for 1 and 8 kHz or Fostex FT96H horn tweeter for 16 kHz tone) placed at 0°, 45°, or 90° relative the subject’s head.

The masker was an octave band of white noise in which the center frequency was set to the target signal. The masker was generated (sampling rate 48 000 Hz, 16 bit resolution) and filtered on a PC laptop using Cool Edit Pro software (Syntrillium). A six second sample of the masker was fed from the sound card output of the laptop to the input channel of a 20 W power amplifier (Radio Shack MPA-40). The masker source was always placed at 0° and was only presented during the trial interval to prevent potential confounding effects of loudness adaptation (Southall et al., 2000). When the signal was projected at 0°, the signal and masker were mixed into the power amplifier and broadcast through the same speaker.

Signal and masker levels were determined using a calibrated free-field microphone (C550H, Josephson Engineering, Santa Cruz, CA) and a spectrum analyzer (SpectraPlus). The sound pressure level of the signal (dB rms re: 20 μPa) and noise spectral density level of the masker (dB re: μPa²/Hz) were determined at a position corresponding to the center of the subject’s head (with the subject removed) for each of the test angles at the beginning and end of each experimental session. Acoustic mapping was performed prior to experimental testing in which received masker and signal levels were measured for each possible location. For each azimuth location, received levels were mapped at 27 separate positions within a 20×20×20 cm area surrounding the chin cup of the test apparatus to ensure that signal and masker level variation fell between ±3 dB. Unmasked sound detection thresholds for each signal location were determined using methods described below. The average masker spectral density level was approximately 5–20 dB above the un-masked threshold for both subjects, a value set by hardware limitations of the experimental setup. These differences were not likely to affect the measured masked thresholds because the signal to noise ratio at masked threshold is generally independent of the masker level (i.e., critical ratios are independent of the masker level, see Fay, 1988).

**D. Procedure**

A go/no-go procedure was used to determine unmasked and masked thresholds for each subject. A correct response was defined as pressing the response target when a signal was triggered (a hit) and withholding response during trials when no signal was triggered (a correct rejection). During data collection, subject responses were monitored by the experimenter in the control room via a surveillance camera. Once the animal stationed itself in the chin cup, the trial began with the experimenter illuminating the trial light and, in the case of masked threshold testing, the masking noise was presented. Trial durations were 5 s and signal presentations randomly varied between 1 and 4 s during the trial interval. If a correct response occurred, a digitized whistle bridge was broadcast through a separate speaker (placed on 0° azimuth on the floor), the trial light was turned off, and an assistant sitting in the control room delivered a fish reward via a PVC conduit in front of the subject. Both types of correct responses were given an equal proportion of fish (i.e., a payoff matrix of 1:1). Incorrect responses [responding in the absence of a signal (false alarm) or withholding response during a signal presentation (miss)] were not reinforced. The overall and first order conditional probabilities of signal-present and signal-absent (catch) trials were 0.5 within a testing session. Catch trials were used to monitor false alarm rates in order to maintain comparable response criteria between experimental sessions. Data from sessions were only used if the false alarm rate fell between 5 and 25%. Approximately eight warm-up and cooldown trials were given at the beginning and end of each experimental session in which the signal was approximately 25 dB above
threshold. Warm-up and cooldown trials were used to ensure good stimulus control over the subject’s go/no-go behavior but were not included in data analysis.

Two types of psychophysical approaches were used to estimate detection thresholds. To determine a preliminary estimate of both unmasked and masked thresholds, approximately two sessions were conducted using the staircase method (Cornsweet, 1962). For these sessions, signal levels were initially attenuated in 4 dB steps after each correct detection until the first miss. The following signal levels were then adjusted in 2 dB steps (either decreased after a correct detection, or increased after a miss) until nine reversals between misses and hits were conducted. Once a threshold estimate using the staircase method was obtained for a given frequency and signal-masker configuration, method-of-constant stimuli sessions (Stebbins, 1970) were then conducted.

Both unmasked and masked thresholds reported here were estimated only from method-of-constant stimuli sessions. In these sessions, five to six signal levels separated by 2 dB steps around the predicted threshold were presented in random order within the test phase of an experimental session. Performance was pooled across these sessions for each signal level and a 50% correct detection threshold was estimated from signal trial performance using Finney’s probit analysis (Finney, 1971). Threshold testing for a particular frequency and condition was completed when the 95% confidence limit of a threshold estimate fell within a ±3 dB range. This typically required data from two to three experimental sessions, each consisting of approximately 50 trials. Critical ratios were defined as the difference in dB of the masking noise spectrum level at the center frequency of the noise band, measured from the spectral density level of the masker, and the masked threshold sound pressure level.

Testing order for frequencies and locations were randomized to measure thresholds. Unmasked thresholds for each of these signal source locations were first determined. Masked thresholds for each of the signal source locations were then measured. The difference in unmasked and masked thresholds (in dB re: 20 µPa) for each signal source location was calculated and masking level differences (MLDs) were computed as defined in Saberi et al. (1991):

\[
\text{MLD} = [(M_\theta - M_{0\theta}) - (U_\theta - U_{0\theta})],
\]

where \(U_{0\theta}\) is the unmasked threshold with the signal projected at 0°, \(U_\theta\) is the unmasked threshold with the signal projected at angle \(\theta\), \(M_{0\theta}\) is the masked threshold with the signal projected at 0°, and \(M_\theta\) is the masked threshold with the signal projected at angle \(\theta\). These differences were compared to the condition in which the signal and masker were both at 0°. In this way, the effects of varying the spatial configuration of the signal relative to the masker were directly compared to the condition in which the signal and masker were coincident in space while controlling for sensation level effects (Saberi et al., 1991). Note that the sign of MLDs reported here was reversed as in other investigations (e.g. Saberi et al., 1991) and thus, a positive MLD indicates spatial release from masking.

III. RESULTS

Unmasked and masked thresholds and critical ratios for each subject are shown in Table I. Thresholds referenced to those at 0° for each test frequency of the harbor seal and the sea lion are shown in Fig. 2. For the harbor seal, differences of unmasked thresholds at azimuth relative to 0° ranged from −0.6 to −13.1 dB, with the largest differences occurring at the highest test frequency. Differences of masked thresholds at azimuth relative to 0° of this subject ranged from −7.5 to −19.0 dB and were lowest at 90° for all frequencies tested. In contrast, unmasked threshold differences of the sea lion relative to 0° ranged from +5.0 to −7.7 dB, with the largest differences occurring at the lowest test frequency. For the sea lion, masked threshold differences relative to 0° ranged from +1.3 to −11.7 dB. These differences were lowest at 90° for the 1 and 8 kHz test tones and at 45° for the 16 kHz test tone. For both subjects, Table I shows that critical ratios at 0° for each frequency were in close agreement with those of an earlier study in which the signal and masker were spatially coincident (Southall et al., 2003a).

Masking level differences (MLDs) for each test frequency of the harbor seal and the sea lion are shown in Fig. 3. MLDs of the harbor seal ranged from 0.3 to 6.9 dB and were largest at 90° for the 1 and 16 kHz test tone and at 45° for the 8 kHz tone. In contrast, MLDs of the sea lion ranged from 2.1 to 8.2 dB and were largest at 45° for all three test frequencies, although MLDs at 45° and 90° at 1 kHz were approximately the same.

IV. DISCUSSION

In real world cases, the detection advantages with spatial separation of the signal and the masker are fully described by considering the differences in masked thresholds for co-located versus separated sources. This is because increased sensitivity of a signal from free-field SRM includes both “better ear” effects, that is larger signal to noise ratios at the near ear (Kopco and Shinn-Cunningham, 2003), and monaural and binaural effects that are generated by the relative spatial positions of the signal and masker. Better ear effects may include level gain from filtering mechanisms of the head, torso, and external ears as well as resonance of the ear canal and middle ear structures (Shaw, 1974). These factors may act separately or in combination with one another.

In all conditions in the harbor seal and all but one condition in the sea lion, masked thresholds were lower with spatial separation of signal and masker compared to when they were co-located. Based on previous studies conducted on humans and animals, the largest differences in masked thresholds were expected to occur for the largest separations between signal and masker (i.e., a 90° separation). In most cases, this was observed in both pinniped subjects of this investigation. The average difference in masked threshold from 0° for all frequencies was −10.3 dB for the harbor seal and −6.4 dB for the sea lion. These masked threshold differences were within the range of previous results on humans and other mammals although in some of these studies methodological differences do not justify direct comparisons (Santon, 1987; Terhune and Turnbull, 1989; Saberi et al.,
1991; Hine et al., 1994; Gilkey and Good, 1995). As expected, the harbor seal’s threshold differences of the present study were larger in air than those previously measured under water when the signal was projected at 0° and the masker azimuth varied between 0° and 90° (Turnbull, 1994). Even relatively small masking level differences resulting from different signal-masker configurations can have significant effects on intraspecific communication ranges. For example, the detection range of a pup call may change on the order of tens of meters or more with a 5 dB detection advantage assuming a source level around 87 dB and spherical 20 log R spreading loss in ideal conditions; Southall, 2002; 2003b. Because separated pups are more likely to be attacked by other females and even die of starvation if they are orphaned (Reiter et al., 1981), such effects have important fitness consequences on individual pinnipeds.

Masking level differences, as defined in this study (from Saberi et al., 1991), take into account spatial separation of the signal relative to the masker while subtracting out the sensation level effects of the signal varying in azimuth. For example, unmasked human thresholds of broadband signals are generally lowest at approximately 50° in the horizontal plane (Saberi et al., 1991). In the case of pure tones, unmasked threshold differences relative to 0° vary in azimuth in frequency-dependent ways. These threshold differences tend to be relatively small (less than 5 dB) below 1 kHz but may be as large as −15 dB at higher frequencies (Sivian and White, 1933). In the harbor seal of this study, unmasked as well as masked threshold differences relative to 0° were also largest at the highest test frequency. This was not the case in the sea lion subject, for whom the largest negative unmasked and masked threshold differences occurred at the lowest test frequency. MLDs at the lowest frequency of both subjects were comparable further indicating a similar ability to utilize interaural time cues (Holt et al., 2005). In this study, the masker was always positioned at 0° and thus the differences in relative amplitude spectra of the masker between the two ears are likely to be small in the absence of anatomical asym-

### Table I. Unmasked and masked thresholds, threshold differences from 0°, masking level differences (MLDs), and critical ratios of each subject for each test condition.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Frequency (kHz)</th>
<th>Type</th>
<th>Angle (degrees)</th>
<th>Threshold (dB SPL)</th>
<th>Difference from 0° MLD</th>
<th>Critical ratio</th>
</tr>
</thead>
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<tr>
<td>Harbor seal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Phoca)</td>
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<tr>
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<td>−3.9</td>
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<tr>
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<tr>
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<td>−0.6</td>
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<td>−5.0</td>
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<td>0</td>
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<td></td>
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<td>−9.3</td>
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<td>Unmasked</td>
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<td>11.5</td>
<td>−13.1</td>
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<td>−7.8</td>
<td>3.9</td>
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<td>−9.3</td>
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<td>50.3</td>
<td>−7.1</td>
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<td>1.3</td>
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</table>
metry. However, despite subtracting out the unmasked detection advantages of a signal projected to the closer ear, MLDs of both pinniped subjects were generally larger than zero, indicating release from masking that was not solely explained by sensation level effects in azimuth. This was also observed in human subjects detecting broadband signals in which MLDs were as large as approximately 10 dB when the masker was presented at 0° and the signal at 90° (Saberi et al., 1991).

Based on the assumption that release from masking at higher frequencies is primarily governed by monaural filtering effects of the pinna (as well as the head), it was expected that SRM would differ between the harbor seal and sea lion at higher frequencies. While there were considerable differences between the two subjects' unmasked and masked thresholds (referenced to 0°) as well as MLDs at 16 kHz, masked thresholds (referenced to 0°) at 8 kHz were similar. This was the case even though the resulting MLDs of the sea lion were almost half of those of the harbor seal at this frequency. It remains in question whether or not the sea lion pinna functions in similar ways to those of terrestrial mammals for spatial auditory processing. The sea lion pinna is assumed to be primarily adapted to reduce drag for swimming and diving but it is likely that the structure along with the head and torso would provide some filtering effect at both 8 and 16 kHz. Furthermore, differences in body position, head shape, and pinna configuration between the two subjects would likely result in substantial differences in head related transfer functions (i.e., the way that these structures filter sound from source to ear drum). Because performance between the two subjects at 16 kHz showed the most variation, it is likely that SRM at higher frequencies in the horizontal plane is influenced by monaural cues created by these anatomical structures. However, it is possible that differences between the SNRs between the two ears can be quite substantial at high frequencies. It remains unclear at this point what influence binaural effects may have on high frequency SRM in pinnipeds given that monaural masked thresholds were not determined in this investigation to make comparisons with binaural performance.

FIG. 2. Unmasked (dashed lines) and masked (solid lines) thresholds relative to those measured at 0° as a function of signal azimuth of the harbor seal (Phoca) on the left and the California sea lion (Zalophus) on the right.

FIG. 3. Masking level differences relative to those measured at 0° as a function of signal azimuth of the harbor seal (Phoca) on the left and the California sea lion (Zalophus) on the right.
The results of this study illustrate that when signal and masker are spatially separated, hearing sensitivity of pinnipeds in the presence of simultaneous masking noise is enhanced. This improvement in sensitivity was as much as 19 dB in the harbor seal and 12 dB in the sea lion. Signals and maskers may take on an almost infinite number of different spatial configurations relative to each other in the everyday world. Accordingly, this study extends earlier masking work in pinnipeds to more complex auditory scenes and provides results that are important for considering the challenges of detecting biologically significant sounds in a background of noise including those from anthropogenic sources.

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