

Localization of aerial pure tones by pinnipeds

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In this study, minimum audible angles (MAAs) of aerial pure tones were measured in and compared between a northern elephant seal (*Mirounga angustirostris*), a harbor seal (*Phoca vitulina*), and a California sea lion (*Zalophus californianus*). Testing was conducted between 0.8 and 16 kHz in the elephant seal and 0.8 and 20 kHz in the harbor seal and sea lion in a hemi-anechoic chamber using a left/right psychophysical procedure. Performance for the same frequencies was also quantified for discrete speaker separation of 5° from the mid-line. For all subjects, MAAs ranged from approximately 3° to 15° and were generally equal to or larger than those previously measured in the same subjects with a broadband signal. Performance at 5° ranged from chance to 97% correct, depending on frequency and subject. Poorest performance in the sea lion and harbor seal occurred at intermediate frequencies, which is consistent with the duplex theory of sound localization. In contrast, the elephant seal's poorest performance occurred at higher frequencies. The elephant seal's result suggests an inferior ability to utilize interaural level differences and is perhaps related to best hearing sensitivity shifted toward lower frequencies in this species relative to other pinnipeds. © 2005 Acoustical Society of America. [DOI: 10.1121/1.2126931]

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I. INTRODUCTION

Many pinnipeds produce loud, stereotyped, repetitive calls in air. In land breeding species, including elephant seals, sea lions, and fur seals, aerial vocalizations are produced regularly during the breeding season by all age classes. For example, mothers and pups exchange calls to facilitate contact and/or reunions during the lactation period (Insley *et al.*, 2003) while males produce threat vocalizations during male-male competitive behaviors (Bartholomew and Collias, 1962; Peterson and Bartholomew, 1969; Fernandez-Juricic *et al.*, 2001). Thus, detection and localization of conspecific aerial vocalizations in pinnipeds apparently have direct implications for reproductive success. Furthermore, these auditory processes are also likely important in detecting land predators (Stirling and Archibald, 1977) and may contribute to fitness by enhancing survival. Thus, the need to localize a variety of airborne acoustic signals has likely been a significant source of selective pressure in these marine mammals.

Most mammals rely on both monaural and binaural input for localizing sounds in a three-dimensional space. The auditory mechanisms involved in azimuth (horizontal plane) localization are best described by the duplex theory of sound localization (Strutt, 1907) which states that low frequencies are localized by interaural time differences (ITDs) while high frequencies are localized by interaural level differences (ILDs). The duplex theory has been supported by studies conducted with human subjects (Stevens and Newman,

1936; Mills, 1958; Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002) and several other terrestrial mammals (see Heffner and Heffner, 1992, for review). However, not all mammals have demonstrated the ability to utilize both of these binaural cues. For example, hedgehogs (*Paraechinus hypomelas*) have a limited ability to utilize ITDs (Masterton *et al.*, 1975) while horses (*Equus caballus*) have a limited ability to utilize ILDs (Heffner and Heffner, 1986). In pinnipeds, pure tones at intermediate frequencies (between 2 and 4 kHz) of the audible range were poorly localized by both a harbor seal (*Phoca vitulina*) listening in air (Terhune, 1974) and a California sea lion (*Zalophus californianus*) listening under water (Gentry, 1967; Moore and Au, 1975). The general interpretation of these results is that, according to the duplex theory, there are significantly reduced ITDs and ILDs for the intermediate frequencies, resulting in poorer localization ability.

Accordingly, there have been several attempts to predict the intermediate frequencies at which the auditory system of a given species might shift between the utilization of time-based to level-based interaural cues for localization in the horizontal plane. One consideration is phase ambiguity that occurs when a particular phase cycle of a sound does not reach the far ear before the next phase cycle reaches the near ear (Brown *et al.*, 1978). Assuming a simplified spherical head, the frequency of phase ambiguity for a given interaural distance, azimuth, and medium may be estimated by the following equation:

$$F = 1/[6(r/c)\sin \theta], \quad (1)$$

where r is the head radius, c is sound speed, and θ is azimuth in degrees (Kuhn, 1977; Brown *et al.*, 1978). This relationship predicts the upper frequency limit at which ITD cues are physically available for azimuth sound localization. The frequency of phase ambiguity will occur at higher frequencies as head size decreases. Neurophysiologically, ITD cues are also dictated by the limits of phase locking. Phase locking has typically not been found to be robust in the auditory nerve fibers of mammals at frequencies higher than 2500 Hz (Kuwada *et al.*, 1997; Taberner and Liberman, 2005).

Investigators have commonly measured sound localization ability using the minimum audible angle (MAA). The MAA is most often defined as half the angle between two sound sources bisected by an observer's midline that are acoustically discriminated as separate in space (Mills, 1958). By this definition, smaller MAAs indicate better sound localization performance. In mammals, horizontal plane MAAs for broadband signals range from a few degrees in humans (Mills, 1958), elephants (*Elephas maximus*; Heffner and Heffner, 1992), and dolphins (*Tursiops truncatus*; Renaud and Popper, 1975) to over 30° in cows (*Bos taurus*; Heffner and Heffner, 1992) and gophers (*Geomys bursarius*; Heffner and Heffner, 1990a).

MAAs are typically estimated by varying the angle of projection. However, according to Eq. (1), the frequency of phase ambiguity is not only dependent on the speed of sound and head size, but also on the azimuth relative to a listener. Thus, attempts to determine the frequencies in which neither ITDs nor ILDs are salient for sound localization using MAA estimates will vary depending on the test angles employed. This may lead to inconsistency in the data and nonmonotonic performance functions (e.g., see Brown *et al.*, 1978). To address this potential limitation, some investigators have opted to fix the angle of sound projection and measure performance across a number of frequencies of the audible range to determine at which frequencies performance declines. These frequencies are interpreted as the region in which the auditory system shifts from using ITDs at low frequencies to ILDs at high frequencies at the given test angle (e.g., Heffner *et al.*, 2001).

For this study, two experiments were conducted to measure and compare the abilities of three pinnipeds, a northern elephant seal (*Mirounga angustirostris*), a harbor seal, and a California sea lion, to localize a range of aerial pure tones. These species have anatomical, behavioral, and phylogenetic differences that are potentially relevant to sound localization. For example, the elephant seal and harbor seal are phocids (true seals) and lack external ears while the sea lion is an otariid and has vestigial external ears. Furthermore, the elephant seal and sea lion are land breeders and primarily call in air (Bartholomew and Collias, 1962; Peterson and Bartholomew, 1969) while the harbor seal is an aquatic breeder and adult males primarily call under water (Hanggi and Schusterman, 1994), although pups vocalize in air and water during their dependence period to maintain contact with their mothers (Renouf, 1984). These pinniped species have been shown to resolve the spatial location of aerial broadband sig-

nals within 5° from the midline (Terhune, 1974; Holt *et al.*, 2004). Previous studies on localization of airborne pure tones have been conducted on harbor seals between 0.5 and 8 kHz (Møhl, 1964; Terhune, 1974). MAAs measured in these studies ranged from approximately 5° at the lowest and highest frequencies to an undefined MAA estimate at the intermediate frequencies due to very poor performance (Møhl, 1964; Terhune, 1974).

In the first experiment of this study, MAAs were measured in the horizontal plane at frequencies ranging from 0.8 to 16 kHz in the elephant seal and from 0.8 to 20 kHz in the sea lion and harbor seal. MAAs across these frequencies were then compared within and between subjects and between previous pinniped results including MAAs measured with a broadband signal in the same subjects using the same methods (Holt *et al.*, 2004). It was expected that pure tone MAAs would be equal to or larger (i.e., performance would be worse) than MAAs for broadband signals because localization performance is typically better with a wider signal bandwidth that contains both ITD and ILD cues (Brown *et al.*, 1980). It was also expected that MAAs at the intermediate frequencies tested would be larger than those at the extreme frequencies. This is based on the observation that pinnipeds tested thus far have demonstrated evidence of utilizing both ITDs and ILDs and ambiguity of these two cues is expected to occur at intermediate frequencies (Terhune, 1974; Moore and Au, 1975).

In the second experiment, performance at a fixed angle of 5° at the same test frequencies and subjects as in experiment 1 was assessed to determine at which frequencies performance was reduced to chance and how this correlated with the predicted frequency of phase ambiguity given by Eq. (1) for each subject. Preliminary results from experiment 1 indicated that a relatively small test angle would be necessary to obtain chance performance at least at some of the test frequencies and thus a fixed angle of 5° was used. Equation (1) predicts that the highest frequency available for ITD cues will be lower for a larger head. Hence, the elephant seal was expected to show a shift between the two binaural cues at a lower frequency relative to both the sea lion and the harbor seal subjects.

This study extends the previous pure tone localization work on pinnipeds in the left/right plane (Møhl, 1964; Gentry, 1967; Terhune, 1974; Moore and Au, 1975). The results of this comparative investigation provide further information regarding the use of binaural cues for sound localization in air while considering physical and species-related factors that may influence this auditory ability in pinnipeds.

II. METHODS

A. Subjects

The subjects were an 11-years-old female Northern elephant seal (Burnyce), a 14-years-old male harbor seal (Sprouts), and a 17-years-old female California sea lion (Rio). All subjects were resident animals at Long Marine Laboratory in Santa Cruz, CA, and had experience performing sound localization tasks of a broadband signal in air (Holt *et al.*, 2004). For the current study, subjects received up

to 50% of their daily food totals (3–15 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 (CARC).

B. Experimental apparatus

Testing occurred in a custom-built $4.0 \times 2.8 \times 2.4$ m³ 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 PVC was mounted to the floor and placed 1 m from the sound sources mounted to the wall in front of the chin cup. Two rectangular PVC response targets (11.4×8.9 cm) were also mounted to the floor and spaced equidistant (11.7 cm) from either side of the chin cup. All subjects were tested with stimuli projected at ear level. A small light, placed 1 m in front of the subjects, was used to ensure that the subject was attentive to the auditory signal during the trial interval.

All equipment was controlled by the experimenter in a $1.3 \times 2.8 \times 2.4$ -m³ control room adjacent to the test chamber. The signals were pure tones at 0.8, 1, 2, 4, 8, 16, and 20 kHz that were generated and triggered by the experimenter using custom-designed LabVIEW software and a National Instruments PXI-6070E multifunction I/O board. Due to limitations of the equipment and a lower sensitivity at higher frequencies, the elephant seal could not be tested above 16 kHz. The signal duration was 100 ms, which was short enough to minimize any performance improvement due to head motion during its presentation (Heffner *et al.*, 2001). Additionally, the signal was shaped with a linear rise and fall time of 10 ms and, when necessary, the signal was low-pass filtered (Krohn-Hite 3550 filter) to remove or reduce harmonics below the sensation level of the subject. The signal was routed to a speaker selector (Acoustic Research 1108) that allowed one of six connected speakers (Morel MDT37 horn tweeters) to be manually selected by the experimenter. In the case of testing the elephant seal at 16 kHz, an amplifier was connected from the output of the filter to the input of a 20-W amplifier (Radio Shack MPA 40). The output of the amplifier was fed to the input of the speaker selector. Background noise emitted from a selected speaker was maintained below the absolute detection threshold of all subjects. Each speaker was housed in a PVC cup and mounted on a 2.4-m linear track that was placed 1 m away from and at 0° elevation relative to the subject's ears. This allowed the speakers to be placed anywhere between 45° to the left and 45° to the right of the subject's midline (with $\pm 0.5^\circ$ of accuracy).

For experiment 1, three speakers were always placed to the right and the left of the subject's midline. The speaker positions were manually changed in azimuth relative to the subject's midline between experimental sessions using a modified method of constant stimuli to determine horizontal plane MAAs for each subject. In experiment 2, test speakers were placed at 5° to the left and the right of the subjects' midline, along with another pair of speakers placed at wider angles for "warm-up" and "cool-down" trials.

The average sound pressure level of the stimuli ($\text{dB}_{\text{RMS}} \text{ re: } 20 \mu\text{Pa}$) was determined at a position corresponding to the center of the subject's head (with the subject removed) using a calibrated free-field microphone (C550H, Josephson Engineering, Santa Cruz, CA) and a spectrum analyzer (using LabVIEW software and National Instruments PXI-6070E multifunction I/O board) for each of the test angles at the beginning of each experimental session. Acoustic mapping was performed in which received signal levels were measured at every 2° within 10° of azimuth and at every 5° between 10° and 45° of azimuth. For each azimuth location, received levels were measured at ten separate positions within a $10 \times 10 \times 10$ -cm³ area surrounding the chin cup of the test apparatus. Differences of up to 10 dB in sound pressure levels were observed between stimuli projected from different speaker locations during acoustic mapping. Therefore, the stimulus level was randomly varied from trial to trial over a 10-dB range surrounding the average level so that the subjects could not use intensity discrimination between speakers or speaker positions to improve performance. Sound detection thresholds for the 100-ms signal at each frequency were determined prior to localization testing for each subject using methods described in Kastak and Schusterman (1998). The average signal level was 25–30 dB above threshold depending on the test frequency. Based on the results of studies involving terrestrial mammals, it has been shown that these differences in sensation levels have only marginal effects (within the average range of error) on the ability of some terrestrial mammals to localize the signal (Heffner *et al.*, 2001; Inoue, 2001; Su and Recanzone, 2001).

C. Procedure

For both experiments, the procedure was similar to those reported in Holt *et al.* (2004). Only one frequency was presented within an experimental session. Subject responses were monitored by the experimenter in the control room via a surveillance camera. A trial began when the animal stationed properly in the chin cup and the trial light was manually illuminated. A correct response was defined as pressing the left target when a left speaker was activated and pressing the right target when a right speaker was activated. If a correct response was made, a digitized "whistle" was played through a separate speaker (0° azimuth), the trial light was turned off, and an assistant in the control room delivered a fish reward via a PVC conduit to the subject. Both types of correct responses were given an equal proportion of fish. Additionally, one or two no-go trials in which the animal was reinforced for not responding to "blank" trials were randomly incorporated within each experimental session. Responses made before the stimulus presentation or to an incorrect target were not reinforced. The overall and first-order conditional probabilities of left and right trial presentations were 0.5 within a testing session (Holt and Schusterman, 2002). Approximately six warm-up and cool-down trials were given at the beginning and end of each experimental session in which the stimulus was projected at angles $\geq 25^\circ$. These trials were incorporated to ensure good stimulus con-

TABLE I. Minimum audible angles (MAAs), standard errors, performance at 5° relative to the midline, and testing order for each subject at each test frequency.

Subject	Test frequency (kHz)	MAA (deg)	Standard error	Performance at 5°	Testing order
Harbor seal (<i>Phoca</i>)	0.8	4.3	0.25	97%	6
	1	4.1	0.23	84%	1
	2	5.4	0.19	92%	3
	4	7.9	0.18	67%	2
	8	12.7	0.23	52%	4
	16	3.8	0.20	83%	5
	20	6.9	0.18	74%	7
Sea lion (<i>Zalophus</i>)	0.8	4.7	0.20	91%	6
	1	6.0	0.19	84%	1
	2	11.9	0.21	92%	3
	4	8.0	0.19	58%	2
	8	11.1	0.20	63%	4
	16	3.9	0.17	75%	5
	20	8.7	0.23	70%	7
Elephant seal (<i>Mirounga</i>)	0.8	3.3	0.19	83%	1
	1	4.8	0.19	77%	2
	2	3.7	0.19	87%	4
	4	3.9	0.18	80%	3
	8	15.0	0.23	49%	5
	16	14.2	0.23	66%	6

control over the subject's behavior but were not used for data analysis. An experimental session typically contained approximately 60 trials.

1. MAA estimates

For experiment 1, 30 trials for each left and right test angle were pooled across approximately 12 experimental sessions for each frequency tested. Performance for left and right angles were plotted separately rather than pooling performance across angles of symmetry (Mills, 1958). Based on previous work (Holt *et al.*, 2004), it was expected that data from the resulting plots would follow a sigmoidal psychometric function. Probit analysis (Finney, 1971) was used to transform the data linearly and interpolate MAAs from a linear regression analysis as the azimuth value corresponding to 75% correct performance averaged from both left and right angles (see Holt *et al.*, 2004).

2. Fixed angle performance

For experiment 2, the results of 50 trials collected at both 5° to the left and the right were pooled and used to quantify performance relative to chance. Based on preliminary results of experiment 1 and a previous investigation (Holt *et al.*, 2004), subjects may develop a bias toward one response within an experimental session, particularly as discrimination becomes more difficult. To address this potential bias and to justify pooling the data, only data from sessions in which there was no significant difference in performance (as determined using a Fisher's exact test and an alpha level of 0.05) across the two angles of symmetry were used in the analysis.

III. RESULTS

Localization data collected during experiment 1 for all subjects were best described as sigmoidal psychometric functions similar to those obtained with broadband signals for the same subjects (Holt *et al.*, 2004). MAAs, standard errors of the estimate, performance at 5°, and testing order for all three subjects at each frequency are given in Table I. MAAs were generally smaller and performance was better at the two lowest frequencies tested for all subjects and at 16 and 20 kHz for the harbor seal and sea lion (see Fig. 1).

In the elephant seal subject, MAAs ranged from 3.3° to 15.0° and were smallest below 4 kHz. In the harbor seal subject, MAAs ranged from 3.8° to 12.7° and increased with increasing frequency up to 8 kHz, beyond which perfor-

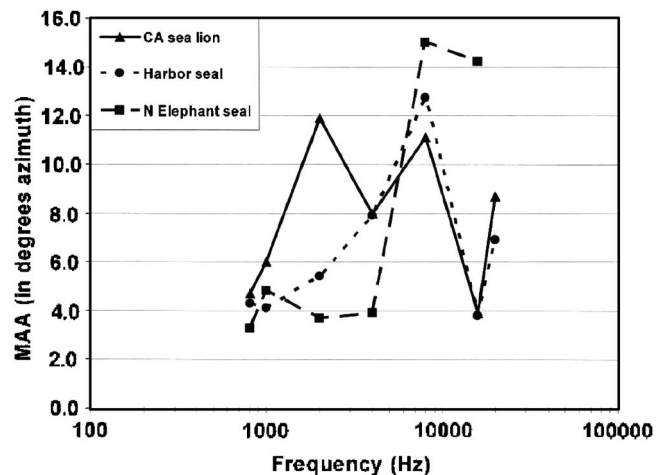


FIG. 1. Minimum audible angles for each subject at each test frequency of this study.

TABLE II. Head size and predicted frequency of phase ambiguity for each subject of this study at a test angle of 5° from the midline using the equation from Kuhn (1977).

Subject	Head radius (m)	Frequency of ambiguity (kHz)
Harbor seal	0.083	7.9
Sea lion	0.080	8.2
Elephant seal	0.154	4.3

mance improved at the two highest frequencies tested and resulted in smaller MAAs. In the sea lion subject, MAAs ranged from 3.9° to 11.9° and increased with increasing frequency up to 2 kHz. At 4 kHz, performance improved relative to the 2-kHz data point, declined at 8 kHz, and then improved at the two highest frequencies tested. The smallest MAAs measured for each subject of this study were within a degree of those previously measured for a broadband signal in the same subject (Holt *et al.*, 2004).

Head radius (m) for each subject and the predicted frequency of phase ambiguity for 5° angular separation are shown in Table II. Figure 2 shows performance at 5° for each subject along with the predicted frequency of phase ambiguity given by Eq. (1) and indicated by the coded legend. The shaded section of Fig. 2 indicates chance performance. For the elephant seal and harbor seal, performance was significantly above chance for all frequencies except 8 kHz. For the sea lion, performance was significantly above chance for all frequencies except 4 kHz, although performance at 8 kHz was only marginally above chance.

IV. DISCUSSION

As expected, pure tone MAAs were generally equal to or larger (i.e., performance was worse) than broadband MAAs within a subject (Holt *et al.*, 2004). MAAs for both the harbor seal and sea lion were largest at the intermediate frequencies tested, supporting the duplex theory of sound

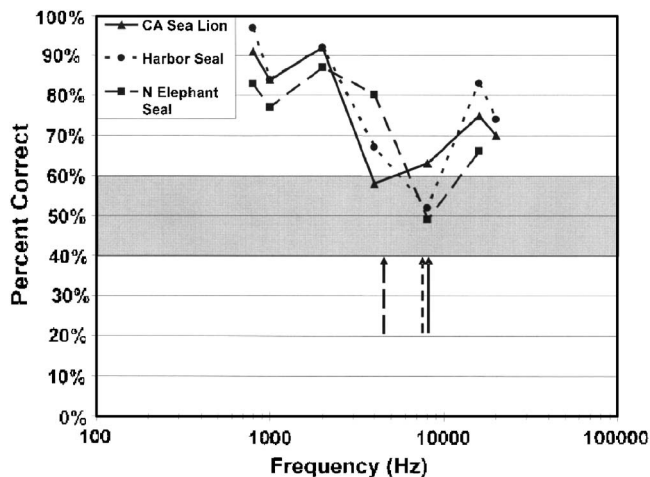


FIG. 2. Performance for each subject at 5° from the midline. Shaded section of the graph indicates chance performance using a binomial test and an alpha level of 0.05. Arrows indicate predicted frequency of phase ambiguity using the equation from Kuhn (1977) for each subject as indicated by the legend.

localization in these animals while the elephant seal MAAs were smallest at only the lowest frequencies tested.

The MAA of a harbor seal measured in air at 1 kHz by Terhune (1974) agreed closely with the MAA estimate at the same frequency for the harbor seal of this study. The worst performance of the harbor seal of this study was found at 8 kHz. The worst performance in the Terhune (1974) study was found between 2 and 4 kHz. It is likely that differences in testing environment, signal design, angles tested, and procedure contributed to the differences found between the two studies as well as the small sample sizes ($n=1$ for both studies).

Performance at a fixed angle (5°) for the harbor seal agreed well with the predictions based on Eq. (1). The highest frequency that phase cues should be available for this angle was 7.9 kHz and performance was at chance for only the 8-kHz data point. The MAAs for this subject measured in the first experiment agreed closely with these results. In the sea lion, the predicted frequency of phase ambiguity was at 8.2 kHz. In experiment 2, performance of the sea lion was at chance at 4 kHz and slightly above chance at 8 kHz. While these results are somewhat consistent with the prediction, it is possible that using a model that assumes a spherical head is not as accurate for a sea lion. Furthermore, in experiment 1, the worst performances (largest MAAs) of this subject occurred at 2 and 8 kHz (see Table II for a comparison of MAAs estimates and performance at 5°). Although the ITD cue by itself should be physically unambiguous at 4 kHz, the relatively poor performances of both the harbor seal and sea lion at this frequency is likely explained by the limits of phase locking. For experiment 2, the predicted frequency of phase ambiguity for the elephant seal was 4.3 kHz and this subject performed above chance at all frequencies except 8 kHz. Although this subject had a larger head size and interaural distance relative to the two other subjects, the frequency of chance performance did not occur at a lower frequency. The fixed angle performances of both true seals were in closer agreement to each other compared to those of the sea lion.

Results from this study demonstrate that these pinnipeds can localize both low- and high-frequency pure tone signals in air proficiently, although the elephant seal had more difficulty at higher frequencies. Neither the presence of external ears nor the medium in which acoustic displays occur correlated with this ability. Other large mammals such as the horse, elephant, pig (*Sus scrofa*), goat (*Capra hircus*), and cow have also shown relative difficulty localizing high-frequency pure tones (Heffner and Heffner, 1992). The elephant seal's range of best hearing sensitivity is shifted toward the lower frequencies relative to the other two pinniped subjects tested in this study, although, as in the other pinniped subjects of this study, the upper frequency cutoff of aerial hearing sensitivity (defined at 60 dB *re*: 20 μ Pa) extends beyond 16 kHz (Kastak and Schusterman, 1999; Schusterman, unpublished data). Performance suggests that the elephant seal has a reduced ability to utilize ILDs for sound localization in the horizontal plane; the first and largest pinniped tested thus far that has not demonstrated an equal proficiency to localize both low- and high-frequency

tones, at least at the frequencies tested in this study. Heffner and Heffner (1990b) discuss the possibilities of why some large mammals have limited or absent abilities to localize high frequencies even though these mammals do possess high-frequency hearing abilities. They suggest that sensitivity to high frequencies is probably not a vestigial ability but necessary rather to utilize monaural cues for vertical plane and front/back sound localization (Heffner and Heffner, 1990b). These monaural cues are primarily created by the diffraction of sound around the pinna (Musicant and Butler, 1984; Heffner *et al.*, 1996) and hoofed mammals typically possess large, mobile pinnae. As with all true seals, northern elephant seals lack pinnae, and this does not adequately explain the retention of some high-frequency hearing in elephant seals. Other selective pressures placed on elephant seals such as the reception of communicative signals, specifically of pups and juveniles, may better explain the need to detect higher-frequency signals, although these animals most likely rely on the lower-frequency components of conspecific calls for localization.

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