Localization of aerial broadband noise by pinnipeds

Marla M. Holt, Ronald J. Schusterman, Brandon L. Southall, and David Kastak

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

Although many pinnipeds (seals, sea lions, and walruses) emit broadband calls on land as part of their communication system, few studies have addressed these animals' ability to localize aerial broadband sounds. In this study, the aerial sound localization acuities of a female northern elephant seal (*Mirounga angustirostris*), a male harbor seal (*Phoca vitulina*), and a female California sea lion (*Zalophus californianus*) were measured in the horizontal plane. The stimulus was broadband white noise that was band pass filtered between 1.2 and 15 kHz. Testing was conducted in a hemi-anechoic chamber using a left/right forced choice procedure to measure the minimum audible angle (MAA) for each subject. MAAs were defined as half the angular separation of two sound sources bisected by a subject's midline that corresponded to 75% correct discrimination. MAAs were 4.7°, 3.6°, and 4.2° for the northern elephant seal, harbor seal, and California sea lion, respectively. These results demonstrate that individuals of these pinniped species have sound localization abilities comparable to the domestic cat and rhesus macaque. The acuity differences between our subjects were small and not predicted by head size. These results likely reflect the relatively acute general abilities of pinnipeds to localize aerial broadband signals. © *2004 Acoustical Society of America.*
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I. INTRODUCTION

Pinnipeds are a group of carnivorous mammals that comprise three families: Phocidae (true seals), Otariidae (sea lions and fur seals), and Odobenidae (walruses). These amphibious animals typically forage and navigate under water but are tied to land or ice for molting and at least some components of their reproductive cycle. Pinnipeds rely on a variety of acoustic signals in both media to coordinate important life history events. In general, pinniped airborne calls are stereotyped and broadband (Bartholomew and Collias, 1962; Peterson and Bartholomew, 1969; Perry and Renouf, 1988) and contain directional components that are dependent on the orientation of the caller (Schusterman, 1978; Southall, 2002). Sound emissions are largely used for communicative purposes particularly in the context of reproductive activities. In general, calls are produced under water in odobenids and aquatically breeding phocids and in air in otariids and land or ice breeding phocids. For example, mutual calling in air functions in the maintenance of contact between mothers and offspring during the lactation period in otariids (Trillmich 1981; Gisiner and Schusterman, 1991; Insley, 2001) and elephant seals (Bartholomew and Collias, 1962; Petrinovich, 1974). Furthermore, studies have shown that otariid mothers and pups are capable of recognizing each others calls on land (e.g., Insley 2001; Charrier *et al.*, 2002, 2003). Males produce aerial vocalizations while delineating territorial or hierarchical status during the breeding season (Bartholomew and Collias, 1962; Peterson and Bartholomew, 1969). In addition to intraspecific signaling, aerial sounds may also be important for detecting and avoiding land predators [e.g., bears and foxes (Stirling and Archibald, 1977)]. Thus, sounds serve important biological functions in pinnipeds and the ability to determine the accurate location of these sounds can have significant consequences on an individual's fitness.

Several investigations on hearing in marine mammals have recently been conducted, in part due to concerns about increased levels of noise in the ocean (Richardson *et al.*, 1995; Andrew *et al.*, 2002). These studies describe aerial hearing abilities of several pinniped species and demonstrate that hearing in some species can be affected by exposure to noise (Turnbull and Terhune, 1990; Kastak and Schusterman, 1996, 1998; Kastak *et al.*, 1999; Southall *et al.*, 2000, 2003). While these studies have contributed to a larger understanding of the peripheral mechanisms involved in pinniped hearing, little is known about other auditory abilities of pinnipeds such as sound localization. Sound localization capabilities have been measured in only three pinniped species: northern fur seals in air and under water (Babushina, 1998; Babushina and Yurkevich, 1994), two California sea lions under water (Gentry, 1967; Moore, 1975; Moore and Au, 1975), and two harbor seals in air and under water (Møhl, 1964; Terhune, 1974). A comparative assessment of pinniped aerial and underwater sound localization revealed that localizing broadband sounds under water is more difficult for harbor seal subjects (Terhune, 1974). Despite the social importance of localizing broadband signals in air by all land breeding pinnipeds, only two studies (Terhune, 1974; Babushina, 1998) have measured this ability in the horizontal plane in these animals.

The typical mammalian auditory system primarily utilizes two types of binaural cues for sound localization in the horizontal plane: interaural phase differences and interaural level differences (Yost, 2000). Interaural phase differences (IPDs) are generally important for localizing low frequency sounds given phase ambiguity at higher frequencies. Interau-

ral level differences (ILDs), primarily created by the shadowing effects of the head, are generally important for localizing high frequency sounds (for review, see Heffner and Heffner, 1992a). The dual processing of these two binaural cues describes the duplex theory of sound localization (Strutt, 1907) and has been supported by several studies conducted in humans (Mills, 1958; Wightman and Kistler, 1992; Macpherson and Middlebrook, 2002) and in other mammals (Heffner and Heffner, 1992a) including a harbor seal in air and a California sea lion under water (Moore and Au, 1975; Terhune, 1974).

The most common metric for measuring sound localization ability is the minimum audible angle (MAA). The MAA is most often defined as half the angle between two identical sound sources bisected by a subject's midline that are acoustically discriminated as separate in space (Mills, 1958), with smaller MAAs representing better localization ability. Because the ability to localize sound in the horizontal plane is generally dependent on both time and intensity based binaural cues, testing is often conducted using broadband signals that contain both IPDs and ILDs. In mammals, horizontal plane MAAs for broadband signals range from a few degrees in humans (Mills, 1958), elephants (Heffner and Heffner, 1992a), and dolphins (under water, Renaud and Popper, 1975) to over 30° in cows (Heffner and Heffner, 1992b) and gophers (Heffner and Heffner, 1990). Because binaural cues are theoretically enhanced by a larger head, some investigators have hypothesized a negative correlation between MAA and head size in mammals. While some of the available data suggest such a correlation, there are numerous exceptions. For instance, cows have relatively large heads but are poor sound localizers (Heffner and Heffner, 1992b). Thus, head size alone does not comprehensively account for the variations of sound localization abilities measured in mammals tested thus far (see Heffner and Heffner, 1992a). Furthermore, not all mammals have demonstrated the ability to utilize both binaural cues for horizontal plane sound localization. For example, evidence from behavioral testing indicates that hedgehogs have a limited ability to utilize IPDs (Masterton et al., 1975) while horses have a limited ability to utilize ILDs (Heffner and Heffner, 1986).

In this study, we determined aerial MAAs in the horizontal plane using a broadband white noise signal in trained individuals representing three pinniped species: a northern elephant seal (*Mirounga angustirostris*), a harbor seal (*Phoca vitulina*), and a California sea lion (*Zalophus californianus*). The elephant seal and California sea lion are land breeders and primarily call in air and the harbor seal is an aquatic breeder and primarily calls under water. This allowed us to investigate the overall sound localization abilities of these pinnipeds given the possible ecological and physical factors that may influence this auditory ability (e.g., head size).

II. METHODS

A. Subjects

The pinniped subjects were a 9-year-old female northern elephant seal (Burnyce), a 13-year-old male harbor seal (Sprouts), and a 16-year-old female California sea lion (Rio).

All subjects were kept at Long Marine Laboratory in Santa Cruz, CA in free-flowing saltwater pools with adjacent haul-out sites. All subjects had previous experience performing sound detection tasks in air and under water and appeared to have normal hearing (Kastak and Schusterman, 1998; Kastak et al., 1999; Southall et al., 2000). In the current study, subjects received approximately 30%–50% of their daily food total (3–15 kg of mixed herring and capelin) during experimental sessions. Additionally, one 22-year-old female human subject (KAJ) was tested under identical conditions so that her results could be compared with previously published data on human subjects. Prior to localization testing, this subject was tested to ensure that her absolute hearing sensitivity was typical for her age group (ANSI 3.6-1996). This study followed the protocols approved by the University of California Chancellor's Animal Research Committee (CARC) and the University of California Human Subjects Institutional Review Board (IRB), and was conducted under National Marine Fisheries Services (NMFS) permit #259-1481-00.

B. Apparatus

Testing occurred in a custom-built $4.0 \times 2.8 \times 2.4$-m double-walled hemi-anechoic chamber (Eckel Industries). The surfaces were lined with acoustic foam wedges except the concrete floor, which was covered with 2.6-cm-thick neoprene mats, and the stainless steel door in the rear of the chamber. The testing chamber was lit with two 75-W light bulbs and was ventilated with a remote quieted fan during testing. 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 (each 11.4×8.9 cm) were also mounted to the floor and spaced equi-distance (11.7 cm) to either side of the chin cup. All subjects were tested with stimuli projected at ear level. Given the height differences between the subjects, the height of the chin cup was 33.0 cm for the harbor seal and sea lion and 38.1 cm for the elephant seal. The height of the response targets was 33.0 cm for all subjects. A small light was placed 1 m in front of the subjects and was manually turned on and off during each trial by the experimenter. This was done to ensure that the subject was attentive to the auditory signal during the trial interval.

C. Stimulus production and equipment

All equipment was controlled by the experimenter in a $1.3 \times 2.8 \times 2.4$-m^3, control room adjacent to the test chamber. The signal was a single noise burst that was generated and triggered by the experimenter using custom designed LabVIEW™ 6i software and operated by a National Instruments PXI 1010 Chassis and National Instruments 6070E multi-function I/O board. Unrepeated samples of white noise were produced on each trial with a rise and fall time of 0.1 ms to avoid switching transients when the signal was triggered. The signal was 100 ms in duration, which was short enough to minimize any performance improvement due to head motion during its presentation (Heffner et al., 2001). The signal was band pass filtered between 1.2 and 15 kHz and thus included frequencies that spanned most of the aerial hearing
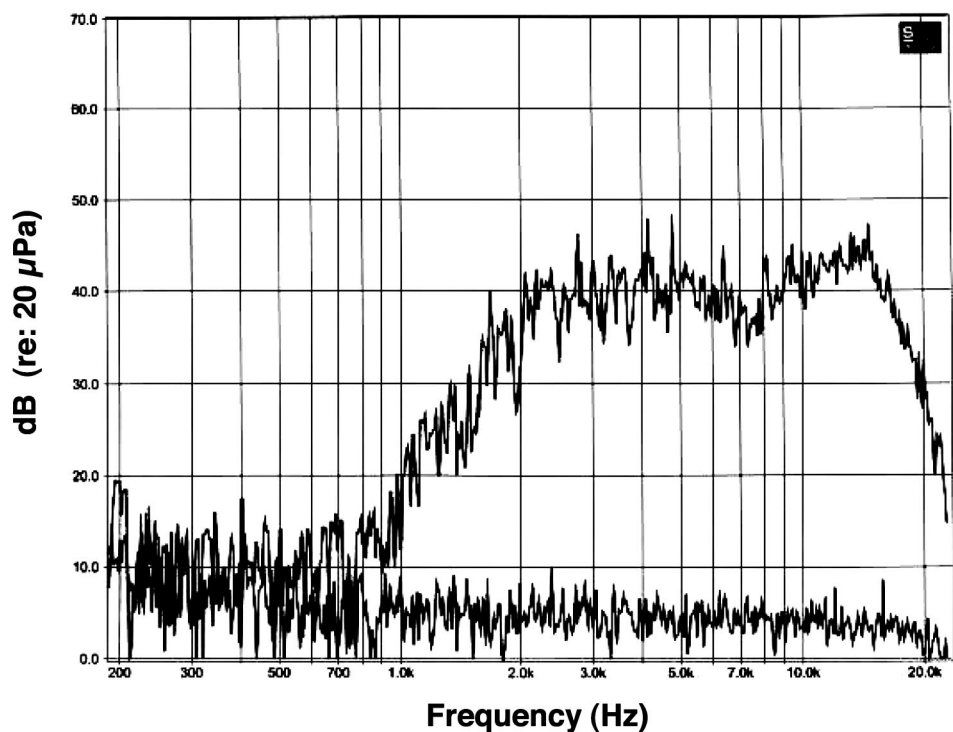
FIG. 1. Spectrum of the noise stimulus used in this study (based on 1.5-Hz analysis bandwidth). The top curve represents the stimulus and the bottom curve represents the position of the noise floor relative to the stimulus.

range of all subjects (Kastak and Schusterman, 1998). Figure 1 shows a plot of the noise spectrum (at 0° azimuth) used during experimental testing. 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. Before each trial, two speakers were always selected, one from the left and one from the right and then one of these two speakers was made inactive before the beginning of a trial. This was done to prevent possible cuing from any switching transients produced during the intertrial period. Inside the test chamber, 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 subjects' ears. This allowed the speakers to be placed anywhere between 45° to the left and 45° to the right of the subjects' midline (with $\pm 0.5°$ of accuracy). Within a session, three speakers were always placed to the right and three speakers were always placed to the left of the subject's midline. The speaker positions were manually changed in azimuth relative to the subject's midline between experimental sessions. A modified method of constant stimuli was used to determine horizontal plane MAAs for each subject.

The average sound pressure level of the stimuli (dB re: 20 μPa) was determined at a position corresponding to the center of the subject's head (with the subject removed) using a calibrated microphone (Etymotic Research ER-7C) and a spectrum analyzer (SpectraPlus®) using narrow-band analysis (48 000 Hz sample rate, 32 768 FFT size, 1.5-Hz analysis bandwidth) for each of the test angles at the beginning of each experimental session. Acoustic mapping was performed prior to testing in which received noise stimulus 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 on each trial over a 12-dB range surrounding the average level (in 2-dB steps) so that the subjects could not use intensity discrimination between speakers or speaker positions to improve performance. Plots of the noise spectrum for both left and right angles at 2°, 4°, 6°, 8°, and 10° were compared against each other and at 0° using the overlay function on SpectraPlus® and showed that the spectra measured for each location were essentially identical, especially between symmetrical angles. Small differences between spectra likely resulted from generating new samples of noise on each trial (i.e., the signal was not a fixed sample of white noise that was repeated over and over again). Additionally, the position of any one speaker was periodically switched between sessions relative to other speakers in the array so that any differential performance between speakers was not systematically correlated with a position in the horizontal plane.

Sound detection thresholds for the signal were determined prior to localization testing for each subject using methods described in Kastak and Schusterman (1998). The average signal level was 60 dB above threshold for the California sea lion, harbor seal and human, and 35 dB above threshold for the northern elephant seal. The perceived signal level was lower for the elephant seal due to a lower sensitivity to the stimulus and limitations of the equipment. Based on the results of studies involving terrestrial mammals, it has been shown that differences in sensation level had little or no effect on the ability of the subjects to localize the signal (e.g., see Heffner et al., 2001).

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D. Procedure

A left/right forced choice procedure was used to determine the MAAs for each subject. A correct response was defined as pressing the left target when the left speaker was activated and pressing the right target when the right speaker was activated. This procedure was novel to all subjects of this study and each had extensive prior experience performing sound detection tasks using a go/no-go procedure (Southall *et al.*, 2003). A spontaneous orienting response to a nearby sound source was used to train the left/right discrimination procedure for this investigation. For the first phase of training, the two response targets were placed directly next to either side of the subject with a speaker located directly behind each target. Training consisted of approximating a left/right response by rewarding the subject for orienting towards, then approaching and then eventually nose-touching the correct target when the speaker played from behind it. In this phase of training, all three subjects showed a spontaneous orienting and then responding to targets associated with spatially disparate speakers. Then the speakers were moved successively away from the targets and towards the speaker track until eventually the responses were under good stimulus control using test speakers placed at ≤45° relative to the subject's midline on the track. All subjects achieved performance criterion of ≥90% correct responses at angles wider than 15° by the ninth training session (each approximately 25 trials per session).

During data collection, 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 by the experimenter. If a response was made to the left target after a left sound presentation or to the right target after a right sound presentation, a digitized whistle bridge was played through a separate speaker (placed on 0° azimuth) indicating to the subject that a correct response was made, 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). 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 and the trial light was extinguished by the experimenter, indicating the end of the trial. 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 six cool-down trials were given at the beginning and end of each experimental session, respectively, in which the stimulus was projected at 25° to the right and the left of the subject's midline. Warm-up, cool-down, and no-go trials were incorporated to ensure good stimulus control over the subject's behavior and were not used in the analysis to calculate MAAs.

E. Statistical analysis

After the initial training phase for each subject was completed, 25 trials at each test azimuth (between 1° and 12°, in 1° increments) were collected in random order in approximately 30 experimental sessions. The resulting data were pooled across all sessions for each subject and the percentages of right target responses were plotted against both left and right test angles (Mills, 1958). Performance for left and right test angles was plotted separately rather than pooling performance across test angles of symmetry to determine if any of the subjects had measurable biases to one side. All of the data from the resulting plots followed a sigmoidal psychometric function. Finney's (1971) probit analysis was used to linearize the data and interpolate MAAs from a linear regression analysis as the azimuth value corresponding to 75% correct performance for both left and right angles. Because performance for left and right angles were plotted separately, this average corresponds to the 75% right target responses for the right sound presentations (positive angles on the *x*-axis) and the 25% right target responses for the left sound presentations (negative angles on the *x*-axis) since 100 minus percent right target response on this plot corresponds to the percent left target response and thus correct performance for left angles. Probit analysis was used as opposed to assuming a purely linear model for the raw data because the decreasing slope of the psychometric functions at larger angles would otherwise inflate the estimated MAAs [for a brief discussion see Mills (1958)].

III. RESULTS

Subjects sometimes developed a bias towards one response within an experimental session, especially with smaller test angles (i.e., when discrimination was difficult). However, any biases observed within an experimental session were averaged out between sessions because none of the subjects developed long-term biases. Figure 2 shows the psychometric function for each subject plotted as the percentage of right target responses against both left and right test angles. Note that the proportion of left target responses is one minus the proportion for right target responses. Minimum audible angles, head radii and maximum interaural distance for each subject are shown in Table I. The maximum interaural distance was calculated for each subject as the time in microseconds it would take airborne sound to travel from one side of the head to the other using head diameter as the distance and the speed of sound in air equal to 343 m/s. Of the three pinniped subjects of this study, the harbor seal had the smallest MAA (3.6°, s.d.=0.12), followed by the California sea lion (4.2°, s.d.=0.10) and then the northern elephant seal (4.7°, s.d.=0.11), although the differences between subjects were small. Interpreting interspecific differences is problematic given the small sample size and likelihood that interindividual differences exist within a species.

Figure 3 shows the relationship between sound localization acuity in the horizontal plane and interaural distance for the pinnipeds that we tested in this study as well as other selected terrestrial mammals which are shown for comparison.
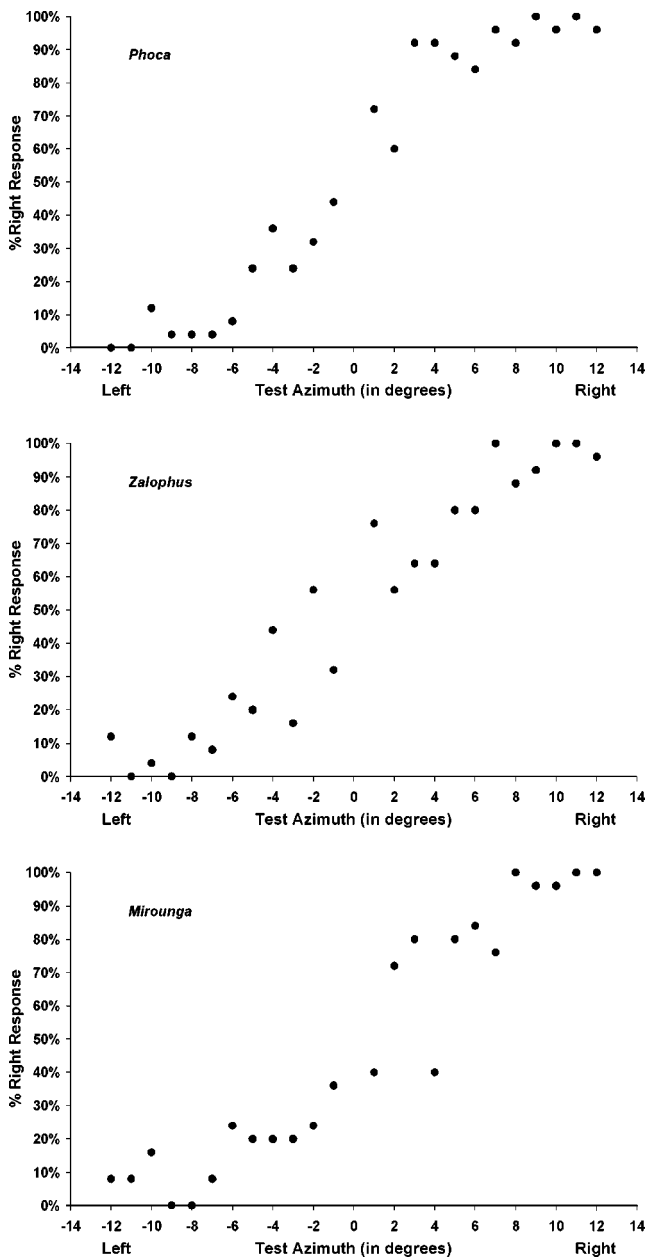
FIG. 2. Psychometric function for each animal tested in this study. For test angles presented to the right of the subjects' midline, correct responses correspond directly to the percent right target responses while for the left angles (negative angles on the *x*-axis), correct responses are 100 minus the percent right target response on the plot. Minimum audible angles were estimated by averaging the left and right test angles corresponding to 75% correct performance.

IV. DISCUSSION

In this study, MAAs were determined using a left/right forced choice procedure and the subjects sometimes developed response biases to one side within an experimental session. This bias was noted from differential performances between left and right azimuths of symmetry. This type of bias was also noted in previous studies with harbor seal subjects (Møhl, 1964; Terhune, 1974). Despite this caveat, a left/right procedure was used in this study for two reasons. First, the spontaneous orienting response of the subject to a sound source could be utilized for efficient training of the task. Second, all subjects had performed sound detection tasks us-

ing a go/no-go procedure prior to the sound localization task and training a left/right procedure seemed to enable the subjects to differentiate the two tasks more easily. Because the stimulus was presented on every trial, the subjects rarely made responses before the sound presentation. MAAs were statistically determined by plotting the proportion of right target responses against both left and right test azimuths in this study [as in Mills (1958)]. Investigators of other localization studies have taken a variety of different procedural and statistical approaches and thus methodological differences between this study and others should be carefully considered while making data comparison across studies.

As shown in Table I, the 0.6° MAA measured in the human subject is consistent with previously reported broadband MAAs in humans (Heffner and Heffner, 1992b). This suggests that there was nothing experimentally unusual in the testing conditions of this study. Furthermore, the human subject was interviewed after the completion of data collection and reported that no switching transients or background noise was detectable from any speaker during testing. The harbor seal MAA of this study closely matches those previously reported broadband MAAs measured in air for the same species [3° for click train stimulus, 75% correct for a left/right procedure; 2° for broadband noise, 50% correct for a center/left procedure, (Terhune, 1974)].

Head size alone did not account for the small MAA differences between the subjects of this study given that the subject with the largest head size (the northern elephant seal) had the largest MAA as shown in Table I. As can be seen from Fig. 3, some mammals with relatively large interaural distances are generally poor sound localizers (e.g., cows and goats). Heffner and Heffner (1992b) have addressed a number of other variables such as predation, domestication, and vision as possible correlates of sound localization acuities measured in mammals. They have shown that sound localization acuity is inversely correlated with the width of the visual field such that mammals with broad visual fields have relatively poor sound localization acuities and vice versa (Heffner and Heffner, 1992a; Heffner *et al.*, 2001). This supports the hypothesis that one of the main roles of sound localization in terrestrial mammals is to orient the subject to the sound source for visual purposes (Heffner and Heffner, 1992a). Such a spontaneous orienting response to a nearby sound source was observed in all three pinnipeds of this study and utilized for training the left/right procedure. Furthermore, such an orienting response not only directs the visual field of the subject toward the source but it also positions the subject so that sound is projected relatively closer to the midline. This may be advantageous, particularly in low-light conditions because localization acuity in the horizontal plane, at least in humans, is best at the midline compared to acuity measured with sources projected at wider angles (e.g., Mills, 1958). With the exceptions of walruses, pinnipeds have eyes directed forward and probably have good binocular vision (Riedman, 1990). However, quantitative measurements of the widths of the visual field for the species of this study are not currently available. Such information would allow us to determine if this variable predicts the MAAs measured in this investigation.

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TABLE I. Aerial minimum audible angles (in degrees azimuth), standard deviations, head radii (in meters), and interaural distance (in microseconds) for each subject of this study.

Subject	MAA (degrees)	s.d.	Head radius (m)	Interaural distance (in μsec)
Phoca vitulina (Sprouts) 13-year-old male	3.6	0.12	0.083	760
Zalophus californianus (Rio) 16-year-old female	4.2	0.10	0.080	733
Mirounga angustirostris (Burnyce) 9-year-old female	4.7	0.11	0.154	1411
Human subject (KAJ) 22-year-old-female	0.6	0.01	0.090	824

Given the importance of localizing conspecific calls on land and the small MAA differences between the subjects of this study, horizontal plane sound localization of broadband signals in most pinniped species is probably relatively acute. This study illustrates the aerial localization ability of three pinnipeds including two phocid and one sea lion species. Of the two phocid subjects of this study, one is a land breeder and primarily calls in air (the Northern elephant seal) while the other is an aquatic breeder and primarily calls under water (the harbor seal). The sound localization abilities of these two subjects were not considerably different despite environmental differences in their vocal reproductive behavior. Of the mammalian data available, broadband sound localization abilities for all pinniped subjects of this study are compa-

rable to pigs, opossums, cats, and rhesus macaques with only humans, elephants, and dolphins having better acuity (Renaud and Popper, 1975; Heffner and Heffner, 1992a). It is very likely that the pulsed, broadband, directional and repetitive nature of pinniped calls in air aids in both the detection and localization of these sounds in naturally noisy environments (Schusterman *et al.*, 2000). A few studies have measured localization of a broadband signal under water in a California sea lion and a harbor seal and results show that localization is more difficult in this medium than in air (Terhune, 1974; Moore, 1975). This is an important finding considering the amphibious nature of pinnipeds and suggests that the faster travel time of underwater sounds may constrain this auditory ability. Other sensory modalities such as
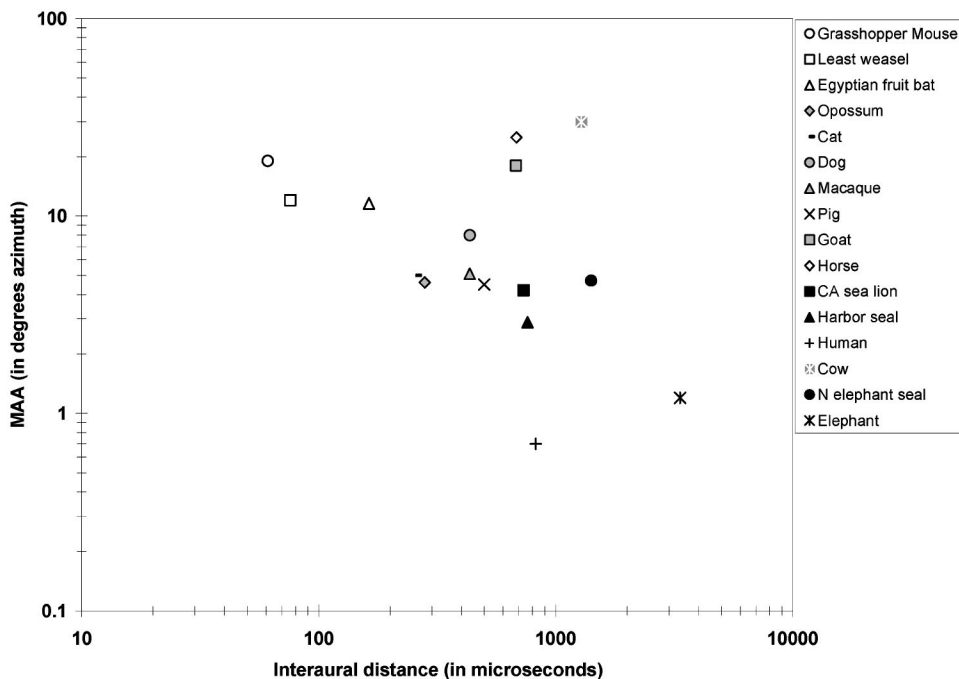

FIG. 3. Aerial minimum audible angles of broadband stimuli plotted against interaural distance (in microseconds) for selected land mammals and pinnipeds. Legend lists species in increasing order of interaural distance (note log-log scale). Grasshopper mouse, $n=2$ (Heffner and Heffner, 1992a); least weasel, $n=3$ (Heffner and Heffner, 1992a); Egyptian fruit bat, $n=3$ (Heffner *et al.*, 2001); cat, $n=5$ (Heffner and Heffner, 1992a); opossum, $n=6$ (Ravizza and Masterton, 1972); dog, $n=4$ (Heffner and Heffner, 1992b); macaque, $n=6$ (Brown *et al.*, 1980); pig, $n=3$ (Heffner and Heffner, 1992a); goat, $n=2$ (Heffner and Heffner, 1992b); horse, $n=2$ (Heffner and Heffner, 1992a); California sea lion, $n=1$ (this study); harbor seal, $n=2$ (this study; Terhune, 1974); human, $n=4$ (this study, Heffner and Heffner, 1992b); cow, $n=3$ (Heffner and Heffner, 1992b); northern elephant seal, $n=1$ (this study); and elephant, $n=1$ (Heffner and Heffner, 1992a).

vision may be more important for underwater activities involving traveling and foraging (see Schusterman *et al.*, 2000). Additional localization investigations involving pure tone and underwater signals would provide further insight regarding the use of binaural cues and differences in localization abilities in air versus under water in these amphibious animals.

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