Corrigendum

Four-choice sound localization abilities of two Florida manatees, *Trichechus manatus latirostris*

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This Corrigendum relates to *J. Exp. Biol.* **212**, 2105-2112.

The authors misunderstood JEB's policies on citing non-peer-reviewed literature and failed to cite the dissertation of Gerstein (Gerstein, 1999), who measured the ability of one manatee to localize tones.

Gerstein used pulsed test tones with a 20 ms duration and a repetition rate of 10 Hz for either 200 or 500 ms. Signals were presented in azimuth from –90 to +90 deg (with 0 deg facing directly in front of the manatee). The manatee was able to localize with above-chance performance, from 55 to 90% accuracy. In our study we used either 3 s tonal signals or broadband noise with four signal durations (200 ms, 500 ms, 1 s and 3 s). Accuracy for the tonal signals was 32 to 49%, but much higher (65–90%) for the broadband signals. The results of Gerstein suggest that pulsed tonal signals are intermediate in localizability between tonal and broadband signals.

The authors apologise to Dr Gerstein, the journal editors and the readership for any inconvenience this may have caused but assure readers that it does not affect the data, results, interpretations or conclusions of the paper.

Publisher's note

The journal received a letter of concern relating to a lack of acknowledgement of a previous body of research in *J. Exp. Biol.* **212**, 2105-2112. After contacting the authors of the paper, the journal asked The University of South Florida, USA, to carry out an investigation. The outcome of this investigation indicated no evidence of misconduct.

Reference

Gerstein, E. R. (1999). Psychoacoustic evaluations of the West Indian manatee. PhD dissertation, Florida Atlantic University, Boca Raton, FL, USA.

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Four-choice sound localization abilities of two Florida manatees, *Trichechus manatus latirostris*

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SUMMARY

The absolute sound localization abilities of two Florida manatees (*Trichechus manatus latirostris*) were measured using a four-choice discrimination paradigm, with test locations positioned at 45 deg., 90 deg., 270 deg. and 315 deg. angles relative to subjects facing 0 deg. Three broadband signals were tested at four durations (200, 500, 1000, 3000 ms), including a stimulus that spanned a wide range of frequencies (0.2–20 kHz), one stimulus that was restricted to frequencies with wavelengths shorter than their interaural time distances (6–20 kHz) and one that was limited to those with wavelengths longer than their interaural time distances (0.2–2 kHz). Two 3000 ms tonal signals were tested, including a 4 kHz stimulus, which is the midpoint of the 2.5–5.9 kHz fundamental frequency range of manatee vocalizations and a 16 kHz stimulus, which is in the range of manatee best-hearing sensitivity. Percentage correct within the broadband conditions ranged from 79% to 93% for Subject 1 and from 51% to 93% for Subject 2. Both performed above chance with the tonal signals but had much lower accuracy than with broadband signals, with Subject 1 at 44% and 33% and Subject 2 at 49% and 32% at the 4 kHz and 16 kHz conditions, respectively. These results demonstrate that manatees are able to localize frequency bands with wavelengths that are both shorter and longer than their interaural time distances and suggest that they have the ability to localize both manatee vocalizations and recreational boat engine noises.

Key words: audition, Sirenian, hearing, spatial hearing.

INTRODUCTION

The Florida manatee (*Trichechus manatus latirostris* L.) is an endangered species that lives in an environment where conspecifics are often out of visual range and recreational boats are found in high numbers. Manatee vocalizations, categorized as chirps, squeaks and squeals, are characteristically short tonal complexes that contain several harmonics and have fundamental frequencies that range from 2.5 to 5.9 kHz but can extend up to 15 kHz (Nowacek et al., 2003). Recreational boat engine noise, composed of bands of sound, has a typical dominant frequency range of 0.01–2 kHz (Richardson et al., 1995). Although it seems likely that the manatee's auditory system plays an important role in finding conspecifics and avoiding boats, little is known about the manatee's ability to localize auditory stimuli within these frequency ranges.

Behavioral testing of sound localization abilities has typically been investigated by measuring the species' minimum audible angle (MAA) (Brown and May, 1990; Brown, 1994). This method determines the smallest detectable angular difference between two sound source locations positioned in front of the subject in the azimuth plane (Mills, 1958) and has been used with California sea lions (Gentry, 1967; Moore, 1974; Moore and Au, 1975), harbor seals (Terhune, 1974), northern fur seals (Babushina and Poliakov, 2004), northern elephant seals, harbor seals and California sea lions (Holt et al., 2004), harbor porpoises (Anderson, 1970) and bottlenose dolphins (Renaud and Popper, 1975; Moore and Pawloski, 1993; Moore and Brill, 2001). More recently, absolute in-water sound localization investigations, which require subjects to identify sound sources relative to different locations surrounding their bodies, have been conducted with a harbor seal (Bodson et al., 2006) and a harbor porpoise (Kastelein et al., 2007). Absolute localization measures compared with the relative measures provided by MAAs are often more ethologically appropriate because they involve natural orienting responses (Moore et al., 2008).

Sound localization for animals in water using interaural time delays (ITD) and interaural level differences (ILD) may be more difficult than in air, because the speed of sound in water is approximately five times faster than in air. Thus, the ITD for the same ear spacing is five times shorter for sound underwater than in air, and the wavelength for the same sound frequency is five times longer underwater than in air leading to reduced head shadowing. Ketten et al. calculated the manatee intermeatal distance as 278 mm with a maximum in-water acoustic travel time of 258 μs, and the intercochlear distance as 82 mm with a maximum in-water acoustic travel time of 58 μs (Ketten et al., 1992). ILD cues have been found to be most effective with wavelengths that are shorter than a species' interaural distance (Brown and May, 1990; Brown, 1994; Blauert, 1997). The frequency of a sound with a 278 mm wavelength (corresponding to the intermeatal distance) in water is 5.5 kHz (for a 1520 $\mathrm{m\,s^{-1}}$ sound speed), and for an 82 mm wavelength (corresponding to the intercochlear distance) in water is 18.5 kHz. This raises the question as to whether manatees may be able to localize sound underwater, especially at low frequencies typical of boat sounds, using the same types of interaural cues as other mammals (terrestrial and marine). Manatees have been shown to respond to actual boat approaches and playbacks of boat noise by retreating to deeper water (Nowacek et al., 2004; Miksis-Olds et al., 2007); however, it is not known how accurately they are able to localize the boats.

Gerstein et al. obtained a behavioral audiogram for two manatees, which showed sensitivity from 0.5 to 38 kHz for one subject and from 0.4 to 46 kHz for the other (Gerstein et al., 1999). The frequency range of best hearing was between 10 and 20 kHz and maximum sensitivity was ~50 dB (re. 1 μPa at 16 kHz and 18 kHz), decreasing by ~20 dB per octave from 0.8 to 0.4 kHz and by 40 dB per octave above 26 kHz. Evoked-potential techniques have also been used to measure the manatee's range of frequency detection. Bullock et al. (Bullock et al., 1980; Bullock et al., 1982) and Popov and Supin (Popov and Supin, 1990) found that the highest frequency detection reached 35 kHz when tested in air and Klishen et al. (Klishen et al., 1990) found it reached 60 kHz when tested in water. More recently, Mann et al. (Mann et al., 2005) found that detection with the same subjects used in the present study reached 40 kHz when tested in water, results consistent with those found by Gerstein et al. (Gerstein et al., 1999), Bullock et al. (Bullock et al., 1980; Bullock et al., 1982) and Popov and Supin (Popov and Supin, 1990).

This absolute sound localization study was designed to measure the manatee's capacity to localize frequencies that are both shorter and longer than their interaural time distances, as well as those that are typical of manatee vocalizations and boat engine noise. Acoustic parameters were varied systematically across dimensions of bandwidth and duration to determine their effects on localization ability. Two tonal signals were used: a 4 kHz tone that was midway between the 2.5–5.9 kHz fundamental frequency range of typical manatee vocalizations (Nowacek et al., 2003), and a 16 kHz tone that was in the 10–20 kHz range of manatee best hearing (Gerstein et al., 1999). Broadband stimuli were also tested and included a 0.2–20 kHz signal that spanned a wide range of frequencies, a 6–20 kHz signal that was composed of frequencies shorter than manatee interaural time distances and a 0.2–2 kHz signal that contained frequencies longer than their interaural time distances.

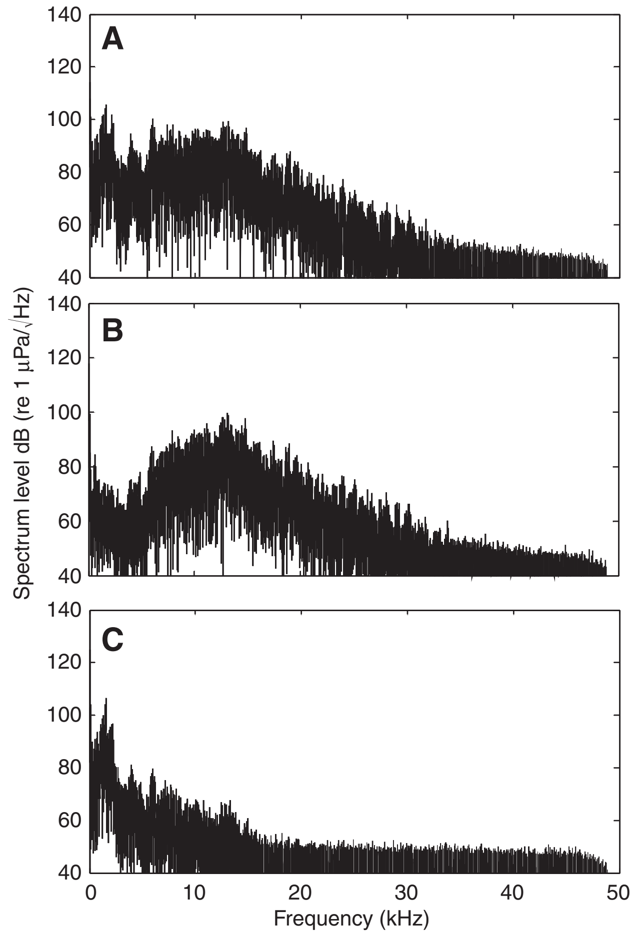

Fig. 1. Power spectra comparison of the 0.2–20 kHz (A), 6–20 kHz (B) and 0.2–2 kHz (C) broadband test signals played at the 3000 ms duration (sample rate of 97,656 Hz).

MATERIALS AND METHODS

Subjects

Experiments were conducted with two male captive-born Florida manatees at Mote Marine Laboratory and Aquarium (MML) in Sarasota, FL, USA (USFWS Permit Number MA837923-6). All procedures were approved by the MML Institutional Animal Care and Use Committee. At the inception of this study, Subject 1 was 17 years old, 3.3 m long and 773 kg, and Subject 2 was 20 years old, 3.1 m long and 547 kg. Both were in good health, had an extensive training history and were subjects in an earlier auditory evoked potential study (Mann et al., 2005). They were housed in a 265,0001 cement pool, consisting of three connecting sections: a 3.6×4.5×1.5 m medical pool, a 4.3×4.9×1.5 m shelf area and a 9.1×9.1×3 m exhibit area. Training and testing was conducted in the shelf area, which was located between the medical pool and exhibit area.

Experimental design

A four alternative forced-choice discrimination paradigm was used to test 14 experimental conditions, including three broadband signals ranging from 0.2–20 kHz, 6–20 kHz and 0.2–2 kHz (Fig. 1) with 3000, 1000, 500 and 200 ms durations and two tonal signals at 4 kHz and 16 kHz with 3000 ms durations. Signals were digitally generated by a real-time processor (TDT RP2.1 with a 97,656 Hz sample rate) [Tucker-Davis Technologies (TDT), Gainesville, FL, USA], attenuated with a programmable attenuator (TDT PA5), amplified with a Hafler power amplifier (Tempe, AZ, USA) and switched through a power multiplexer (TDT PM2R) that was capable of switching the signal to one of the four underwater test speakers (Aquasonic AQ 339, Littleton, CO, USA). All test signals were played at a 100 dB (re. 1 μPa spectrum level), and sound levels were randomized ±1.5 dB to obscure any intensity differences between speakers and included a 100 ms $\cos^2$ rise–fall time to eliminate transients. To generate the noise bands, a Gaussian noise signal was run through a digital biquad Butterworth low-pass filter followed by a biquad Butterworth high-pass filter using the RP2. No attempt was made to flatten the frequency response of the speakers. To ensure that speaker artifacts were not present and/or used as cues, the speakers were removed from their original locations and re-positioned in the location diagonally across after half of the testing had been completed for each condition. A separate digital to analog channel was used to generate an individualized stationing signal (10–20 kHz, repeated at a rate of 1.5 s for Subject 1 and 5 s for Subject 2) from a speaker positioned on the stationing apparatus located at the center of the test speaker array.

All test signals were recorded from each of the four speakers in their different locations *via* a Reson hydrophone (TC4013, Slangerup, Denmark; sensitivity –212 dBV μPa^{-1} from 1 Hz to 170 kHz) with the TDT hardware at a sample rate of 96 kHz. Power spectra were made of all recordings and examined for frequency or intensity cues that might occur at either a specific location or from a specific

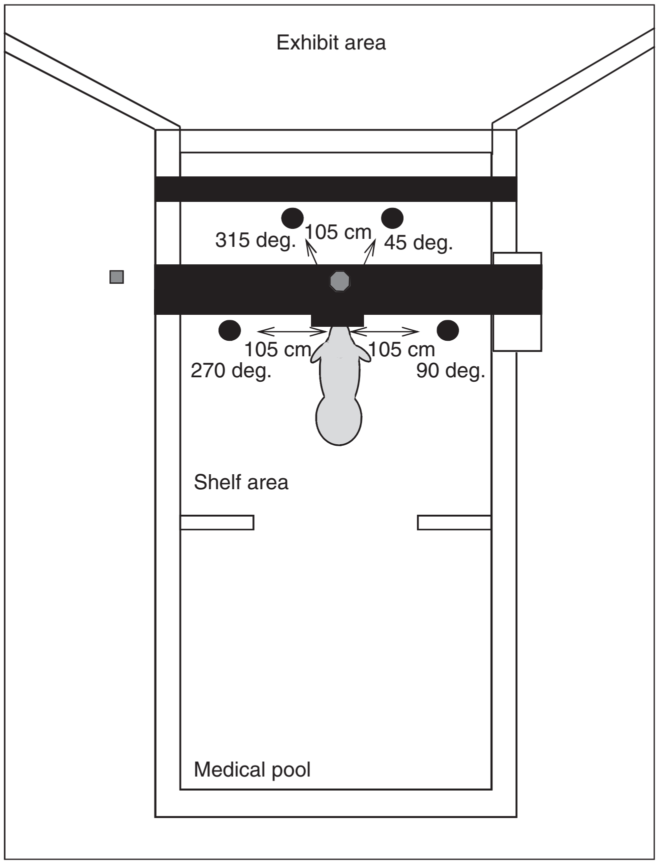

Fig. 2. Testing configuration with four test speakers located 105 cm from the center of the stationing bar and 75 cm below the surface. The test speakers are represented as the black circles. The gray octagon represents the 'test trainer's' position and the gray square represents the 'data recorder's' position.

speaker. Spectrograms were made and examined for temporal cues within the signals tested. No obvious patterns or harmonic distortions were observed with either the broadband or tonal signals.

Testing was conducted in the center of the shelf area of the exhibit (Fig. 2). Each subject was trained to position the crease on the top of its rostrum, ~10 cm posterior to the nostrils, up against a water-filled 2.54 cm diameter polyvinyl chloride (PVC) stationing bar positioned at mid-water depth (75 cm) in response to a stationing signal. The subject remained stationed facing 0 deg. until a test signal was played from one of four underwater test speakers positioned at 45 deg., 90 deg., 270 deg. and 315 deg. angles, 105 cm from the center of the stationing bar and 75 cm below the surface (Fig. 2). Upon hearing the test signal, the subject was trained to swim to and push the speaker from which the sound originated. If correct, a secondary reinforcer signal was emitted from the test speaker and the subject returned to the stationing device to be fed a primary reinforcement of food (apples, beets and carrots). If incorrect, the stationing tone was played from the stationing apparatus speaker, the subject would re-station correctly with no reinforcement given and await a minimum of 30 s before the initiation of the next trial. Video analyses demonstrated that the subjects did not move their heads for more than two seconds after the initiation of a signal. Therefore, 3000 ms signals allowed the subjects to use behavioral adjustments (e.g. head movements) to guide the localization response. The shorter sounds, 1000 ms and less, did not permit time for behavioral accommodation to assist sound localization.

Six blocks of 12 trials were run per subject for each of the 14 conditions. The order of presentation was as follows: 0.2–20 kHz, then 6–20 kHz and finally 0.2–2 kHz, tested at the 3000 ms duration. This order was followed throughout each of the sound duration conditions, which were tested in descending order. The tonal signals, 4 kHz and 16 kHz, were only tested at the 3000 ms duration. Trials were counterbalanced between speakers and presented in a quasi-random order using a random number table, with no more than two trials in a row run from the same location. A Dell Latitude D505 computer (Round Rock, TX, USA) that controlled the TDT hardware was used to run the signal generation equipment, which was interfaced to a button box to control the trials and enter the subject responses. The test parameters and results of each trial were automatically saved into a text file.

Two people were required to run the experiment to avoid inadvertent cuing. The 'test trainer', who was 'blind' to the test stimulus locations, wore noise-masking headphones. The 'test trainer' ensured that the subject stationed properly, initiated trials, indicated which speaker the subject selected and provided reinforcement when the subject selected the correct speaker location. The 'data recorder' was unable to view the subjects' position in the testing set-up and informed the 'test trainer' if the subject was correct or incorrect.

Table 1. Overall accuracy (%) for each subject by frequency (broadband and tonal) and duration conditions

	Frequency					
	Broadband signals (kHz)				Tonal signals (kHz)	
Duration (ms)	0.2–20	6–20	0.2–2		4	16
Subject 1						
200	93%	89%	85%	**89%**		
500	85%	92%	86%	**88%**		
1000	93%	79%	92%	**88%**		
3000	88%	82%	92%	**87%**	44%	33%
Mean	**90%**	**86%**	**89%**			
Subject 2						
200	64%	51%	58%	**58%**		
500	71%	63%	57%	**64%**		
1000	74%	71%	65%	**70%**		
3000	93%	86%	81%	**87%**	49%	32%
Mean	**76%**	**68%**	**65%**			

Mean values are indicated in bold.

All testing was conducted between 07:00–10:00 h. Each session consisted of three blocks of 12 trials, started with eight warm-up trials and finished with four cool-down trials using the 0.2–20 kHz, 3000 ms signal, which is an easily localized signal (Table 1) to control for motivation. In addition, eight practice trials were completed directly after the warm-up trials using same signal stimulus that was to be tested in that session. Blocks were considered potentially unrepresentative and dropped if motivation was measurably compromised as indicated by performance under 75% on warm-up or cool-down trials. Blocks were also dropped if any combination of three or more interruptions from the non-test manatee and/or departures or attempted departures from the test subject per block occurred. If a block was dropped, the experimental condition was repeated in the next session.

RESULTS

Training was initiated on 6 January, 2005 and completed on 11 July, 2005. Testing was initiated on 12 July, 2005 and completed on 26 August, 2005. Nine 12-trial blocks with Subject 1 and 13 blocks with Subject 2 were not included because they met the drop criteria. Video analysis of all trials indicated that neither subject made head movements prior to the termination of the 200 ms, 500 ms or 1000 ms signals. Orientation head movements were observed only during the 3000 ms trials.

Performance accuracy is summarized in Table 1. Percentage correct was calculated for each subject based upon 72 trials per condition with a total of 1008 trials per subject. Both subjects performed well above the 25% chance level for all of the broadband frequency conditions. Subject 2 showed a drop in percentage correct as the broadband signal duration decreased but this result was not observed with Subject 1.

The broadband error rate derived from the complete data set (excluding tonal results) collapsed across all conditions was only 11% for Subject 1 and 22% for Subject 2. Frequency selection distributions (percentage of location selections by frequency, collapsed across duration) revealed that although differences in performance accuracy were found between subjects within the broadband signal conditions, their errors were generally

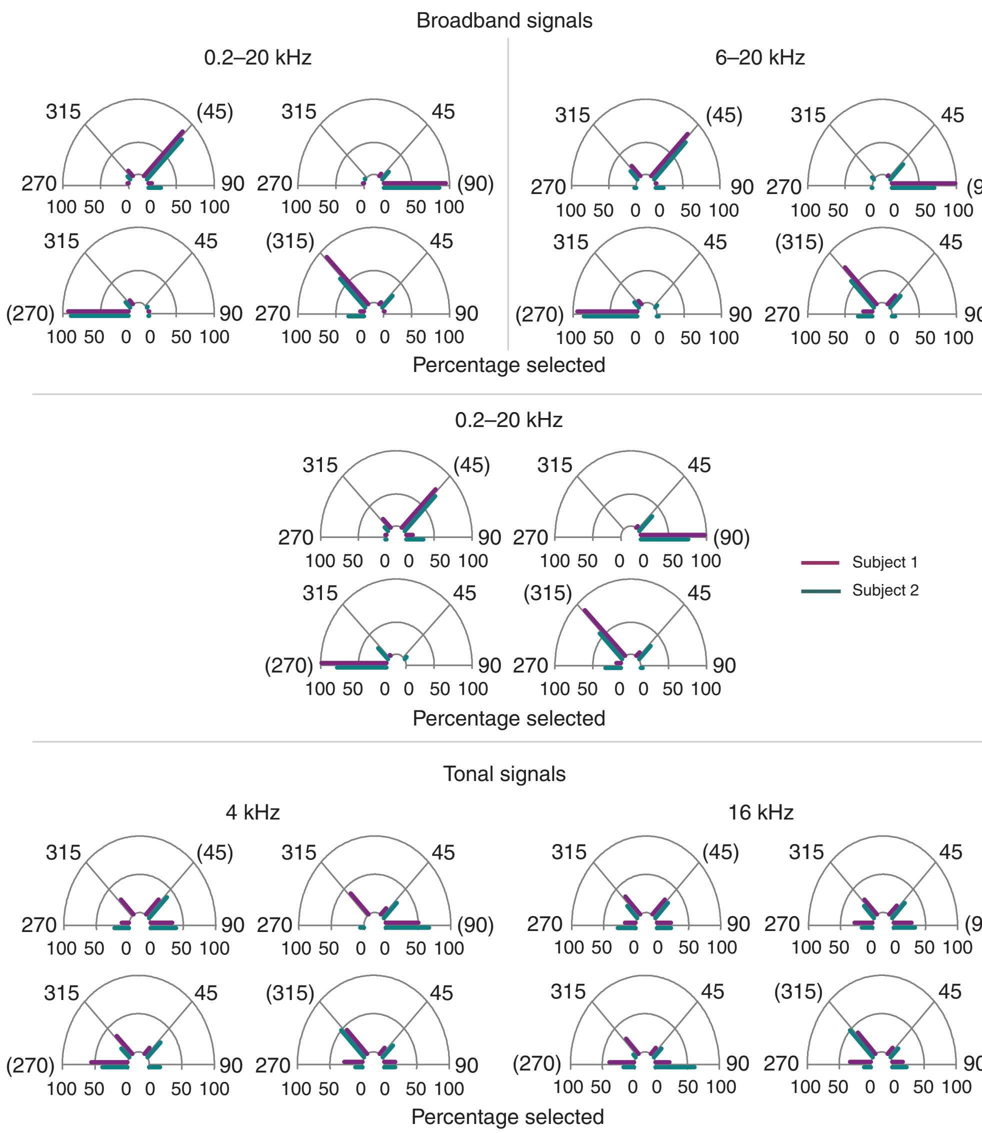

Fig. 3. Percentage correct and distribution of errors by frequency collapsed across duration (top two rows). Tonal conditions are presented in the bottom row. Correct speaker location is notated by parentheses. Subject 1's results are presented above the grid lines and Subject 2's are presented below.

consistent, with most equally distributed to the locations adjacent to the correct location (Fig. 3). Similar results were found for duration selection distributions (percentage of location selections by duration, collapsed across frequency) (Fig. 4). Selection distributions were also calculated for each of the individual broadband conditions (percentage of location selections within the 12 individual broadband conditions). Errors again were generally consistent and distributed to the locations adjacent to the correct location (Fig. 5).

Both animals performed above chance levels with the tonal signals but at a much lower accuracy rate than with the broadband signals. The selection distribution for the tonal signal conditions was almost equally scattered among the four locations (Fig. 3). Tonal signals were only tested at the 3000 ms duration because the subjects performed at a low accuracy level and demonstrated behaviors consistent with frustration such as multiple departures from the testing set-up and breaking equipment.

DISCUSSION

The results from the present study indicate that manatees have the ability to localize frequencies that are both shorter and longer than their interaural time distances, as well as those typical of manatee vocalizations and boat engine noise. Subjects were better able to localize the broadband signals compared with the tonal signals, as is typical with many species (Stevens and Newman, 1936; Marler, 1955; Casseday and Neff, 1973). Although psychoacoustic studies often use relatively simple sound stimuli in a controlled setting, natural environments contain a multitude of complex sounds that are primarily broadband and have rapid amplitude, frequency and bandwidth fluctuations on an ongoing basis. The fact that these highly trained manatees (Colbert et al., 2001; Kirkpatrick et al., 2002; Bauer et al., 2003; Manire et al., 2003; Bauer et al., 2005; Mann et al., 2005) had difficulty localizing the tonal signals while being quite proficient with the broadband signals indicates a challenging sensory task rather than a learning problem.

The fundamental frequencies of manatee vocalizations, ranging from 2.5 kHz to 5.9 kHz, closer to the 4 kHz test signal used, are characteristically short tonal complexes but they typically contain several harmonics. The subjects' decreased accuracy with tonal signals as compared with broadband signals might suggest that localization of manatee tonal vocalizations would be difficult; however, the harmonics of different frequencies contained within these vocalizations may provide additional cues to aid in this capacity. Some vocalizations transition from a tonal harmonic complex to more strongly modulated calls covering a greater frequency range that are often produced by calves, probably making it easier for localization (Nowacek et al., 2003; Mann et al., 2006; O'Shea and Poche, 2006).

Recreational boat engine noise is characterized as broadband with a typical dominant frequency range of 0.01–2 kHz although it can reach over 20 kHz with the 1/3-octave source levels at 1 m for small motorboats estimated at 120–160 dB (re. 1 μPa). Personal watercrafts, such as jet-skis, are approximately 9 dB quieter than small motorboats (Buckstaff, 2004). The subjects' ability to localize the 0.2–2 kHz test signals at the 100 dB (re. 1 μPa) spectrum level indicates that they are able to localize typical recreational boat engine noise but also suggests a need to investigate directional hearing in more natural or complex acoustic environments.

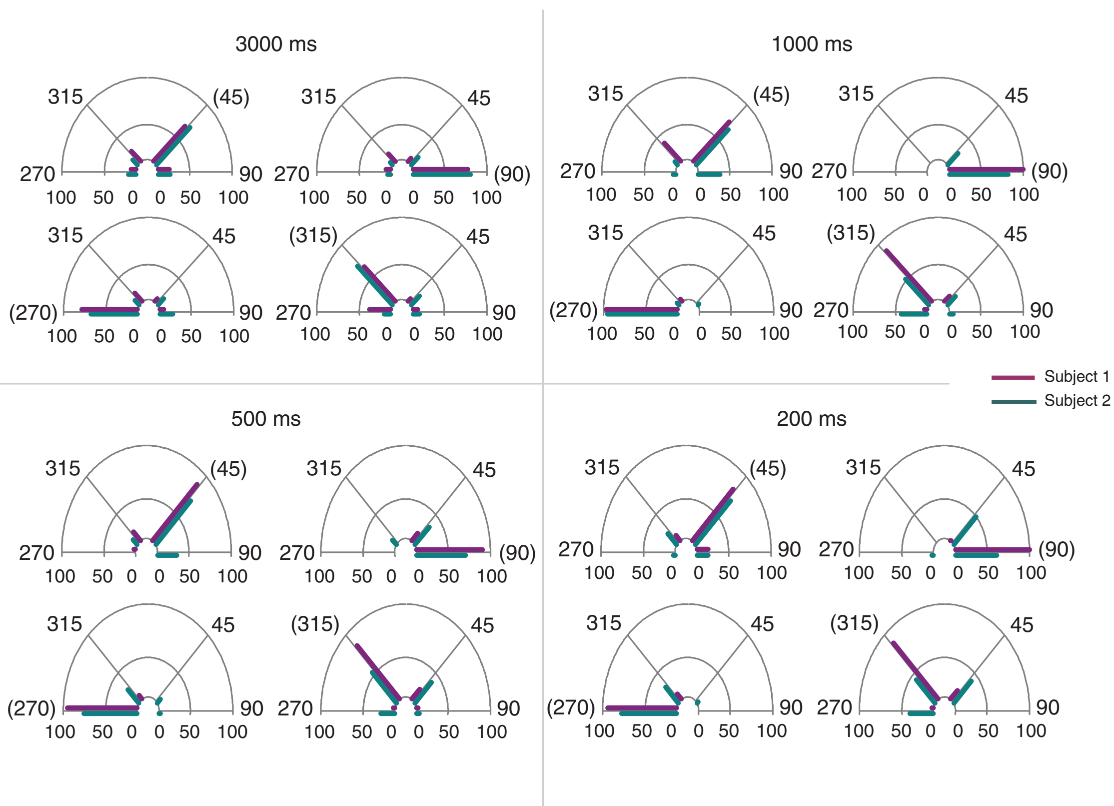

Fig. 4. Percentage correct and distribution of errors by duration using only the results from testing with the broadband signals. Correct speaker location is notated by parentheses. Subject 1's results are presented above the grid lines and Subject 2's are presented below.

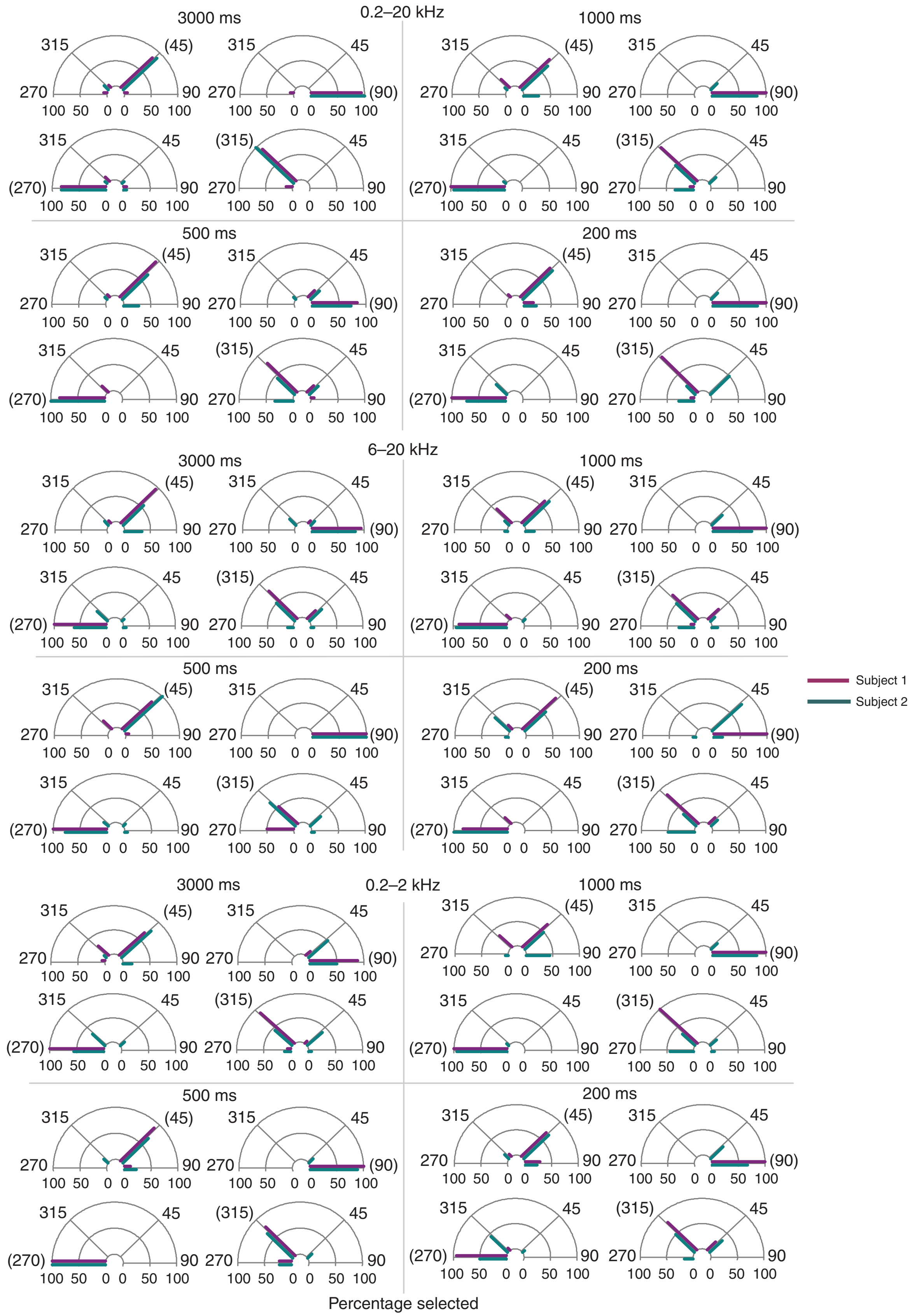

Fig. 5. Percentage correct and distribution of errors by duration within the 0.2–20 kHz, 6–20 kHz and 0.2–2 kHz broadband conditions. Correct speaker location is notated by parentheses. Subject 1's results are presented above the grid lines and Subject 2's are presented below.

The ability to localize sounds varies among species and requires the interpretation of one or any combination of binaural differences of time of arrival, level and phase cues (Brown, 1994). Heffner and Heffner (Heffner and Heffner, 1982; Heffner and Heffner, 1992) have shown that some species use a combination of two cues, such as the Indian elephant, which utilizes time of arrival and level differences whereas some depend on only one cue, such as the hedgehog, which utilizes level differences or the horse, which utilizes time of arrival differences. Some animals do not seem to be able to utilize any cues and are incapable of sound localization, such as the pocket gopher. The present study does not determine which cues are used by manatees; however, it does show that the manatees were able to localize a short high-frequency band of noise, which suggests the use of ITD's and/or ILD's for high frequencies.

Power spectra were made of all the test signals and no consistent frequency or amplitude cues were observed from specific locations or speakers. As all signals were tested at the 100 dB (re. 1 μPa spectrum level), we expected that the subjects would perform better with the 16 kHz signals because of their greater sensitivity at this level (Gerstein et al., 1999; Mann et al., 2005). Interestingly, both subjects demonstrated greater accuracy with the 4 kHz tone, which has a longer wavelength (wavelength=0.38 m) than the 16 kHz tone (wavelength=0.09 m). When considering which potential interaural cues might be used to localize the test signals, interaural level differences would likely to be larger with the shorter 16 kHz signal whereas interaural phase differences would be better utilized for the 4 kHz signal.

Duration was manipulated within the broadband conditions and included short signal lengths of 1000 ms and less, which precluded head movement, as well as the 3000 ms signal that allowed orienting behavior. Accuracy did not decline as duration decreased with Subject 1 but it did with Subject 2. Although the performance of Subject 2 might have been adversely affected by his inability to move his head at shorter stimulus durations, it more likely reflects his less sensitive detection levels found in previous sensory studies of these subjects, including studies of visual acuity (Bauer et al., 2003), vibrissae tactile sensitivity (Bauer et al., 2005) and auditory evoked potentials (Mann et al., 2005), and is assumed to represent normal variation (Ridgway and Carder, 1997; Brill et al., 2001). It is likely that manatees would be better able to localize sounds in their natural environment considering most stimuli are repetitive and/or of longer duration than the test signals used in this investigation. This would provide increased opportunities to alter head or body orientation to better utilize interaural cue differences.

Although the error rates within the broadband conditions were low, error distribution was consistent and most errors were equally distributed at the locations adjacent to the correct location. For the tonal signals, errors were scattered among the locations and no obvious strategy could be discerned. This pattern suggests that for broadband sounds the subjects' errors were ones of resolution, i.e. on error trials they were able to localize within a quadrant (90 deg.) but not within 45 deg. By contrast, the random pattern of errors to tonal sounds suggests guessing and a reduced capacity to localize.

Environmental noise during testing was a factor that should be considered. Exhibit background noise was continuous and typically below 500 Hz, indicating the possibility of masking at lower frequencies. The subjects were tested in an area that was only 1 m in depth and where there would be multiple reflections. These reflections could provide additional cues for the noise signals, although this would be less likely for the tonal signals. Construction of a 3-story building, located less than 200 feet (61 m) from the manatee exhibit, caused intermittent noise of different frequencies, including subsonic vibrations, intensities and amplitudes, to be present throughout the course of the study but did not appear to have an effect on the manatees' performance. If the exhibit or construction noise were factors that interfered with the subject's localization ability, the results presented in the current study might actually portray an underestimation of the manatee's abilities.

Understanding how the endangered manatee perceives its environment is a crucial component in making competent conservation management decisions. The results of the present study have increased our understanding of the manatee's absolute sound localization abilities and demonstrate their ability to localize test signals that are both shorter and longer than their interaural time distances and are within the frequency ranges of conspecifics and recreational boat engine noises. Future MAA investigations, which measure the smallest detectable angular difference between two sound source locations or absolute localization investigations, which measure the subject's ability to determine the directionality of sounds as they originate from different horizontal and vertical angles surrounding their bodies, would be of great value.

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REFERENCES

Anderson, S. (1970). Directional hearing in the harbor porpoise, *Phocoena phocoena*. In *Investigations on Cetacea*, vol. 2 (ed. G. Pilleri). Berne: Benteli AG.

Babushina, E. S. and Poliakov, M. A. (2004). The underwater and airborne sound horizontal localization by the northern fur seal. *Biophysics* **49**, 723-726.

Bauer, G. B., Colbert, D. E., Gaspard, J. C., Littlefield, B. and Fellner, W. (2003). Underwater visual acuity of Florida manatees (*Trichechus manatus latirostris*). *Int. J. Comp. Psychol.* **16**, 130-142.

Bauer, G. B., Gaspard, J. C., 3rd, Colbert, D. E., Leach, J. B. and Reep, R. (2005). Tactile discrimination of textures by Florida Manatees, *Trichechus manatus latirostris*. Presented at the 12th Annual International Conference on Comparative Cognition, http://www.pigeon.psy.tufts.edu/ccs/proceedings2005/Talks.htm, Melbourne, FL, USA.

Blauert, J. (1997). *Spatial Hearing: The Psychophysics of Human Sound Localization*. Cambridge, MA: MIT Press.

Bodson, A., Miersch, L., Mauck, B. and Dehnhardt, G. (2006). Underwater auditory localization by a swimming harbor seal (*Phoca vitulina*). *J. Acoust. Soc. Am.* **120**, 1550-1557.

Brill, R. L., Moore, W. B. and Dankiewicz, L. A. (2001). Assessment of dolphin (*Tursiops truncatus*) auditory sensitivity and hearing loss using jawphones. *J. Acoust. Soc. Am.* **109**, 1717-1722.

Brown, C. H. (1994). Sound localization. In *Comparative Hearing: Mammals* (ed. R. R. Fay and A. N. Popper), pp. 57-97. New York: Springer-Verlag.

Brown, C. H. and May, B. J. (1990). Sound localization and binaural processes. In *Comparative Perception*, vol. 1 (ed. M. A. Berkley and W. C. Stebbins), pp. 247-284. New York: John Wiley.

Buckstaff, K. C. (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay Florida. *Mar. Mamm. Sci.* **20**, 709-725.

Bullock, T. H., Domning, D. P. and Best, R. C. (1980). Evoked potentials demonstrate hearing in a manatee (*Trichechus inunguis*). *J. Mammal.* **61**, 130-133.

Bullock, T. H., O'Shea, T. J. and McClune, M. C. (1982). Auditory evoked potentials in the West Indian manatee (Sirenia: *Trichechus manatus*). *J. Comp. Physiol.* **148**, 547-554.

Casseday, J. H. and Neff, W. D. (1973). Localization of pure tones. *J. Acoust. Soc. Am.* **54**, 365-372.

Colbert, D. E., Fellner, W., Bauer, G. B., Manire, C. and Rhinehart, H. (2001). Husbandry and research training of two Florida manatees, *Trichechus manatus latirostris*. *Aquat. Mamm.* **27**, 16-23.

Gentry, R. L. (1967). Underwater auditory localization in the California seal lion (*Zalophus californianus*). *J. Aud. Res.* **7**, 187-193.

Gerstein, E., Gerstein, L., Forsythe, S. and Blue, J. (1999). The underwater audiogram of the West Indian manatee (*Trichechus manatus*). *J. Acoust. Soc. Am.* **105**, 3575-3583.

Heffner, R. S. and Heffner, E. H. (1982). Hearing in the elephant (*Elephas maximus*): absolute sensitivity, frequency discrimination, and sound localization. *J. Comp. Physiol. Psychol.* **96**, 926-944.

Heffner, R. S. and Heffner, E. H. (1992). Evolution of sound localization in Mammals. In *The Biology of Hearing* (ed. D. Webster, R. Fay and A. Popper), pp. 691-715. New York: Springer-Verlag.

Holt, M. M., Schusterman, R. J., Southall, B. L. and Kastak, D. (2004). Localization of aerial broadband noise by pinnipeds. *J. Acoust. Soc. Am.* **115**, 2339-2345.

Kastelein, R., Haan, D. and Verboom, W. (2007). The influence of signal parameters on the sound source localization ability of a harbor porpoise (*Phocoena phocoena*). *J. Acoust. Soc. Am.* **122** (2), 1238-1248.

Ketten, D. R., Odell, D. K. and Domning, D. P. (1992). Structure, function, and adaptation of the manatee ear. In *Marine Mammal Sensory Systems* (ed. J. A. Thomas, R. A. Kastelein and A. Y. Supin), pp. 77-79. New York: Plenum Press.

Kirkpatrick, B., Colbert, D. E., Dalpra, D., Newton, E. A. C., Gaspard, J., Littlefield, B. and Manire, C. A. (2002). Florida red tides, manatee brevetoxicosis, and lung models. In *10th International Conference on Harmful Algae* (ed. K. A. Steidinger, J. H. Landsberg, C. R. Tomas and G. A. Vargo). St Petersburg, FL: Florida Fish and Wildlife Conservation Commission and Intergovernmental Oceanographic Commission of UNESCO.

Klishen, V. O., Diaz, R. P., Popov, V. V. and Supin, A. Y. (1990). Some characteristics of hearing in the Brazilian manatee, *Trichechus inunguis*. *Aquat. Mamm.* **16**, 139-144.

Manire, C. A., Walsh, C. J., Rhinehart, H. L., Colbert, D. E., Noyes, D. R. and Luer, C. A. (2003). Alterations in blood and urine parameters in two Florida manatees, *Trichechus manatus latirostris*, from simulated conditions of release following rehabilitation. *Zoo Biol.* **22**, 103-120.

Mann, D., Colbert, D. E., Gaspard, J. C., 3rd, Casper, B., Cook, M. L. H., Reep, R. L. and Bauer, G. B. (2005). Temporal resolution of the Florida manatee (*Trichechus manatus latirostris*) auditory system. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**, 903-908.

Mann, D. A., O'Shea, T. and Nowacek, D. P. (2006). Non-linear dynamics in manatee vocalizations. *Mar. Mamm. Sci.* **22**, 548-555.

Marler, P. (1955). Some characteristics of animals calls. *Nature*, **176**, 6-8.

Miksis-Olds. J. L., Donaghay, P. L., Miller, J. H., Tyack, P. L. and Reynolds, J. E., 3rd (2007). Simulated vessel approaches elicit differential responses from manatees. *Mar. Mamm. Sci.* **23**, 629-649.

Mills, A. W. (1958). On the minimum audible angle. *J. Acoust. Soc. Am.* **30**, 127-246.

Moore, J. M., Tollin, D. J. and Yin, T. C. T. (2008). Can measures of sound localization acuity be related to the precision of absolute location estimates? *Hear. Res.* **238**, 94-109.

Moore, P. W. B. (1974). Underwater localization of click and pulsed pure-tone signals by the California sea lion (*Zalophus californianus*). *J. Acoust. Soc. Am.* **57**, 406-410.

Moore, P. W. B. and Au, W. L. (1975). Underwater localization of pulsed pure tones by the California sea lion (*Zalophus californianus*). *J. Acoust. Soc. Am.* **58**, 721-727.

Moore, P. W. B. and Brill, R. L. (2001). Binaural hearing in dolphins. *J. Acoust. Soc. Am.* **109**, 2330-2331.

Moore, P. W. B. and Pawloski, D. A. (1993). Interaural time discrimination in the bottlenose dolphin. *J. Acoust. Soc. Am.* **94**, 1829-1830.

Nowacek, D. P., Casper, B. M., Wells, R. W., Nowacek, S. M. and Mann, D. A. (2003). Intraspecific and geographic variation of West Indian manatee (*Trichechus manatus spp.*) vocalizations. *J. Acoust. Soc. Am.* **114**, 66-69.

Nowacek, S. M., Wells, R. S., Owen, E. C. G., Speakman, T. R., Flamm, R. O. and Nowacek, D. P. (2004). Florida manatees, *Trichechus manatus latirostris*, respond to approaching vessels. *Biol. Conserv.* **119**, 517-523.

O'Shea, T. J. and Poche, L. B. (2006). Aspects of underwater sound communication in Florida manatees (*Trichechus manatus latirostris*). *J. Mammal.* **87**, 1061-1071.

Popov, V. V. and Supin, A. Y. (1990). Electrophysiological studies on hearing in some cetaceans and a manatee. In *Sensory Abilities of Cetaceans: Laboratory and Field Evidence* (ed. J. A. Thomas and R. A. Kastelein). New York: Plenum Press.

Renaud, D. L. and Popper, A. N. (1975). Sound localization by the bottlenose porpoise *Tursiops truncatus*. *J. Exp. Biol.* **63**, 569-585.

Richardson, W., Greene, C., Malme, C. and Thompson, D. (1995). *Marine Mammals and Noise*. San Diego, CA: Academic Press.

Ridgway, S. H. and Carder, D. A. (1997). Hearing deficits measured in some *Tursiops truncatus*, and discovery of a deaf/mute dolphin. *J. Acoust. Soc. Am.* **101**, 590-594.

Stevens, S. S. and Newman, E. B. (1936). The localization of actual sources of sound. *Am. J. Psychol.* **48**, 297-306.

Terhune, J. M. (1974). Directional hearing of a harbor seal in air and water. *J. Acoust. Soc. Am.* **56**, 1862-1865.