Hearing in alpacas (*Vicugna pacos*): Audiogram, localization acuity, and use of binaural locus cues

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Behavioral audiograms and sound localization abilities were determined for three alpacas (*Vicugna pacos*). Their hearing at a level of 60 dB sound pressure level (SPL) (re 20 μPa) extended from 40 Hz to 32.8 kHz, a range of 9.7 octaves. They were most sensitive at 8 kHz, with an average threshold of –0.5 dB SPL. The minimum audible angle around the midline for 100-ms broadband noise was 23°, indicating relatively poor localization acuity and potentially supporting the finding that animals with broad areas of best vision have poorer sound localization acuity. The alpacas were able to localize low-frequency pure tones, indicating that they can use the binaural phase cue, but they were unable to localize pure tones above the frequency of phase ambiguity, thus indicating complete inability to use the binaural intensity-difference cue. In contrast, the alpacas relied on their high-frequency hearing for pinna cues; they could discriminate front–back sound sources using 3-kHz high-pass noise, but not 3-kHz low-pass noise. These results are compared to those of other hoofed mammals and to mammals more generally.

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I. INTRODUCTION

Comparative studies of hearing place human hearing in a broader evolutionary perspective. To that end, we now have behavioral auditory data for nearly 70 species of mammals, including some with unusual adaptations, such as aquatic mammals, echolocating and non-echolocating bats, and species that live exclusively underground (e.g., Heffner and Heffner, 2008). Yet, despite their world-wide ecological and economic importance, large hoofed mammals (in the broadest sense that includes elephants, that is, Paenungulata) are not often studied because they do not lend themselves to standard laboratory accommodations. Of the nine families of even-toed ungulates (Artiodactyla), only three have been sampled: Suidae (pigs), Cervidae (deer), and Bovidae (cattle, goats, and sheep) (Flydal *et al.*, 2001; Heffner and Heffner, 1983, 1989, 1990, 1992a, 2010; Wollack, 1963). Of the remaining families, Camelidae is of particular interest because it is the only family of large herbivores adapted to extremely arid environments. There are six living species, two large camels of the Old World (Dromedary and Bactrian) and four smaller species native to the New World (llamas, guanacos, vicunas, and alpacas), all six of which can interbreed and produce fertile offspring (Hoffman, 2003).

Recently, we have had the opportunity to broaden our sample of mammals by studying the hearing abilities of alpacas (*Vicugna pacos*), a domestic species important in South America and, more recently, in the United States (Saitone and Sexton, 2007). In addition to representing the niche of large desert herbivores in comparative analyses, their sound-localization ability may be of interest because all hoofed mammals tested so far, including pigs, cattle, goats, horses, and Indian elephants, differ from other mammals in that they are either completely unable to use the binaural intensity-difference cue to localize sound or else the frequency range over which they use it is severely restricted (Heffner and Heffner, 2003). The addition of alpacas to the sample of mammals would provide further information whether this characteristic is common to all hoofed mammals or if it varies depending on some other unsuspected factor.

We present here the pure-tone detection thresholds, left–right and front–back noise localization acuity, and the ability to localize pure tones (to assess the use of binaural locus cues) for three alpacas (*Vicugna pacos*) using standard behavioral procedures. These results are compared to what is known about the hearing and sound localization of other mammals, with particular attention to hoofed mammals. Possible selective pressures acting on these abilities are considered.

II. METHODS

The alpacas were tested with a conditioned suppression/avoidance procedure in which an animal continuously licked a spout to receive a steady flow of water. It was then trained to break contact with the spout whenever it detected a signal indicating upcoming shock (Heffner and Heffner, 1995). Detection thresholds were determined by successively reducing the amplitude of a signal until the animal could no longer detect it above chance, and sound localization thresholds were determined by reducing the angle of separation between two speakers centered on the midline. The ability to use the binaural time and intensity cues was assessed by examining the animals' ability to localize pure tone pips.

A. Subjects

Three young adult male *Vicugna pacos* (A, B, and C), 2–3 yr old, were used in this study. The animals were housed

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together and had free access to food. Water was used as the reward and was only available during the daily test sessions. The alpacas were weighed daily to monitor their deprivational state. The alpacas weighed 24.5–37 kg at the beginning of testing and 32–50 kg approximately 6 months later, at the end of testing, showing healthy growth. The use of animals in this study was approved by the University of Toledo Animal Care and Use Committee.

B. Behavioral apparatus

Testing was conducted in a carpeted, double-walled acoustic chamber (IAC model 1204; 2.55 × 2.75 × 2.05 m), the walls and ceiling of which were lined with egg-crate foam to reduce sound reflection. The equipment for stimulus generation and behavioral measurement was located outside the chamber and the alpacas were observed using closed-circuit television. During testing, an alpaca was confined in a rectangular wood-frame stall (112 × 53 × 69 cm). The top of the stall was well below an animal's head and shoulders. A reward spout, consisting of a shallow stainless steel oval spoon (10 × 7 × 1.8 cm, approximately 20 ml capacity) angled downward at approximately 60 deg toward the animal, was mounted 25 cm in front of the stall at a comfortable drinking height of 1 m above the chamber floor. This spout and stall configuration served to maintain the animal's head and body in a fixed position with no obstructions between the sound source and the animal's ears when it was drinking from the spout (Fig. 1).

Plastic tubing was connected to the spout and routed outside the sound chamber to an electrically operated water valve, flow meter (NEC F164), and finally to a 15–l water reservoir. A contact circuit, connected between the spout and a dampened floor mat (60 × 50 cm) on the chamber floor, was used to detect when an animal touched the spout and to trigger the water reward. Water was delivered in a steady flow of approximately 30–40 ml/min as long as an alpaca maintained contact with the spout.

A constant current shock generator (Grason-Statler 700) was connected between the reward spout and floor mat, and the shock was adjusted for each individual to the lowest level that produced a consistent avoidance response—either backing away slightly or lifting its mouth from the spout. A 25 -W light, mounted 0.3 m below the spout, was turned on and off concurrently with the shock to provide feedback for a successful avoidance and to indicate when it was safe to resume licking the spout.

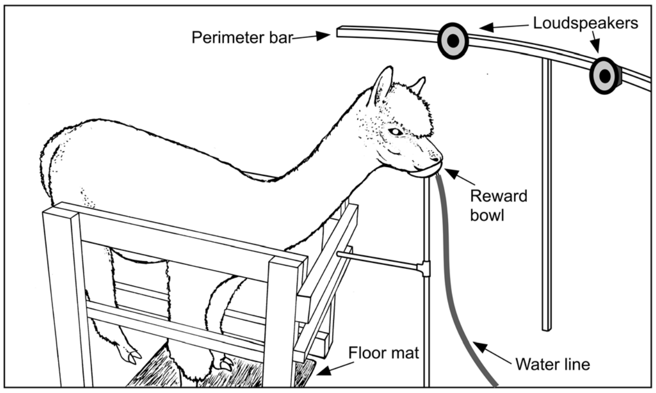

FIG. 1. Alpaca in the test stall. Drinking from the reward bowl kept the head fixed relative to the loudspeakers for both audiogram determination and sound localization. Speakers were placed on a perimeter bar of approximately 1 m radius centered on the animal's head at ear level.

C. Acoustical apparatus

1. Audiogram

Pure tones were generated (Zonic A & D 3525 signal generator), attenuated (Hewlett Packard 350D attenuator), and gated on and off (Coulbourn S84-04 rise-fall gate) with a 20-ms rise-decay for frequencies of 1 kHz and higher, 40-ms for frequencies from 125 to 500 Hz, and 100-ms for frequencies from 25 to 63 Hz. Tones of 125 Hz and higher were pulsed at 400 ms on and 100 ms off; the lower frequencies (25 to 63 Hz) were pulsed at 800 ms on and 400 ms off to compensate for the longer rise-fall times.

The electrical signals were then band-pass filtered (Krohn-Hite 3550, set 1/3 octave above and below the tone's frequency), amplified (Crown D-75), monitored with an oscilloscope (Tektronix TDS210), and routed to a loudspeaker in the test chamber: For frequencies from 25 to 2000 Hz, a 12-in. (30.4-cm) speaker was used whereas for frequencies of 4000 Hz and higher, either a ribbon tweeter (Panasonic EAS-10TH400C) or piezo tweeter (Motorola KSN 1005) was used. The loudspeaker was placed 1–1.5 m in front of an alpaca, directly facing the animal at ear height (about 1.15 m above floor level). Thresholds were obtained for all alpacas at octave steps from 32 Hz to 32 kHz, with additional thresholds at 25 Hz, 22.5 kHz, and 40 kHz.

Sound level measurements were taken by placing the microphone in the position normally occupied by an animal's head and ears while it drank from the spout, and pointing the microphone directly at the loudspeaker. For tones, the sound pressure level (SPL re 20 μPa) was measured daily with a 1/4-in. (0.64-cm) microphone (Brüel and Kjaer 4939, corrected for free-field with the protection grid on), preamplifier (Brüel and Kjaer 2669), and measuring amplifier (Brüel and Kjaer 2608). This measurement arrangement was calibrated frequently with a pistonphone (Brüel & Kjaer 4230). The output of the measuring amplifier was then routed to a spectrum analyzer (Zonic A & D 3525) to monitor the speaker output for harmonics or distortion. Care was also taken to produce a homogeneous sound field (within ± 1 dB) in the area occupied by the animal's head and ears when it was drinking from the spout.

2. Noise localization

Brief broadband noise bursts (100 ms duration, 0.1 ms rise-decay) were used for left−right minimum audible angle determination. The noise was generated (Zonic A & D 3525) and bandpass filtered from 50 Hz–50 kHz (Krohn-Hite 3202). The electrical signal going to the speakers was monitored with an oscilloscope (Tektronix TDS 210), and switched between three pairs of loudspeakers placed symmetrically to the left and right of midline. This arrangement allowed testing at three different angles of separation before physically moving the speakers to different locations, usually for the second half of a test session. The loudspeaker was a dual speaker configuration (3-in. woofer plus piezo tweeter) that produced a relatively flat noise spectrum from approximately 300 Hz to 25 kHz, with frequencies 25–40 kHz remaining well above background (Fig. 2). All noise bursts were set at 50 dB hearing level and randomly attenuated (0–3.5 dB in half-dB increments; Coulbourn S85–08 programmable attenuator) to reduce the likelihood of extraneous cues. Finally, pairs of speakers matched on the basis of their spectra were frequently interchanged, and one pair of loudspeakers was always placed at an angular separation that was below threshold to quickly reveal any artifact that might arise within a test session. Noise bursts were measured and their level equated daily for each speaker pair.

For front−back discriminations, the filter was set to either 3-kHz high-pass (48 dB/octave rolloff) or 2-kHz low-pass (48 dB/octave rolloff), and the intensity was equated at 50 dB above detection threshold. A ribbon tweeter (Panasonic EAS10TH100A) was used for the 3-kHz high pass noise, and a 3-in. speaker (Tang Band W3-319SF) was used for the 2-kHz low-pass noise. Both noise bands were presented at 50-dB above threshold and the same procedures were followed as for minimum audible angle. For noise spectra, see Fig. 2.

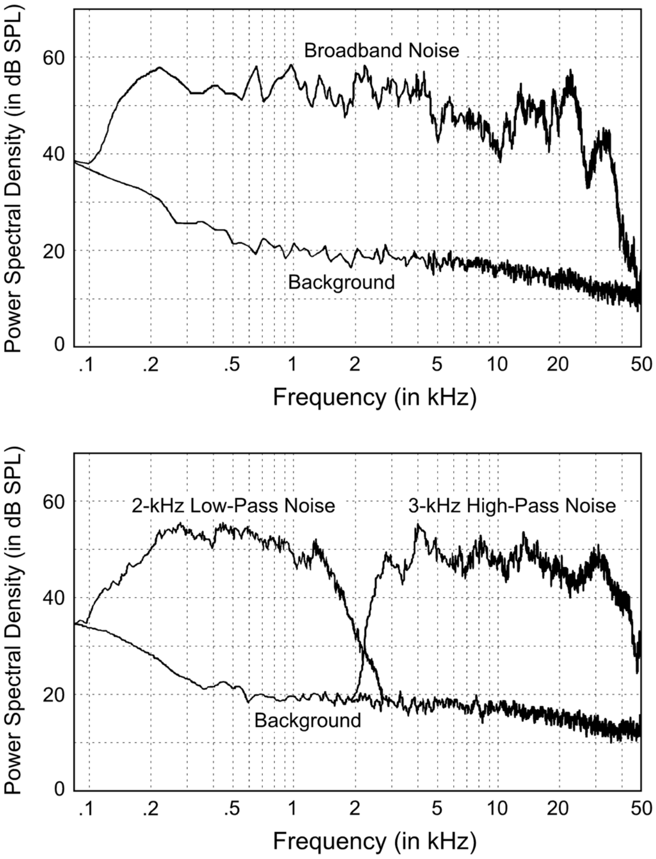

FIG. 2. Noise spectra used for determining minimum audible angle. The broadband noise was used to determine left−right minimum audible angle around 0° azimuth. The 3-kHz high-pass and 2-kHz low-pass signals were used for front/back discriminations around the interaural line, centered 90° to the right of the animal. All noise stimuli were presented at about 50 dB hearing level. Note that although background level was measured at 46 dB SPL, this intensity is a combination of background acoustics and electrical noise from the measuring instruments.

3. Tone localization

Pure tones used in localization tests were generated and measured using the same equipment used to present pure tones in the audiogram, with the exception that the signal was split between two lines after emerging from the filter and sent to separate channels of a stereo amplifier (Crown D75). Testing was carried out at all frequencies within the alpaca hearing range that could be produced at a 50 dB hearing level without distortion. For consistency of comparison with different species tested previously, the loudspeakers were placed at a fixed angle of 30° to the left and right of midline (60° total separation). Rise-decay times of 50 ms were used for all frequencies to prevent onset and offset transients. Each trial consisted of two 150-ms tone pulses (50 ms rise, 50 ms full amplitude, 50 ms fall) separated by 1.2 s; intertrial intervals were 1.5 s. A pair of woofers (Infinity RS 2000) was used for frequencies of 2 kHz and below, whereas frequencies above 2 kHz were produced using either ribbon tweeters (Panasonic EAS10TH400C) or piezo speakers (Motorola KSN 1005). The acoustic signals were checked for overtones using a spectrum analyzer (Zonic A & D 3525) and the loudspeakers were matched for intensity before each session. To prevent any slight imbalance in intensity from serving as a cue, the intensity of the tones was randomly attenuated on each trial over a 3.5-dB range (Coulbourn S85-08 programmable attenuator).

Additional tests were carried out with a 4-kHz tone that was sinusoidally amplitude modulated (Krohn-Hite 2400 AM/FM phase lock generator, 100% modulation depth) at a rate of 250 or 500 Hz. This signal permitted an ongoing time difference cue to be extracted from the envelope of a high-frequency carrier tone.

D. Behavioral procedure

1. Audiogram

A thirsty alpaca (approximately 23-h water restricted) was initially trained to drink steadily from the reward spout. Requiring the animal to maintain contact with the spout served to orient it toward the loudspeaker and served to activate the water valve to dispense a steady flow of water (approximately 30–40 ml/min), adjusted for each individual. For the audiogram, a train of tone pulses was presented at random intervals, followed immediately by an electric shock (300 ms duration, 4–8 mA), delivered between the spout and floor mat. Both the positive and negative contingencies are necessary to maintain high rates of correct detections and to eliminate false reporting. An alpaca learned to avoid the shock by breaking contact with the spout whenever it heard the tones and returned to the spout after the shock had been delivered (as indicated by the offset of the shock-indicator light). The shock level was considered mild because the alpacas did not develop a fear of the spout and returned to it readily after receiving a shock. Test sessions were divided into 2.5-s trials, separated by 1.5-s intertrial intervals.

Approximately 22% of the trial periods contained a pulsing tone (warning trial), whereas no sound was presented in the remaining trial periods (safe trial). Each 2.5-s trial had an equal probability of containing a warning trial (for a discussion of trial sequences, see Heffner *et al.*, 2006).

The contact circuit was used to detect whether the alpaca was in contact with the spout during the last 150 ms of each trial. If the alpaca broke contact for more than half of the 150-ms response period, a detection response was recorded. This response was classified as a hit if the trial had been a warning trial and as a false alarm if the trial had been a safe trial. The hit and false alarm rates were then determined for each stimulus intensity, with a single intensity presented in a consecutive block of 5–10 warning trials (with approximately 20–40 associated safe trials). Finally, the hit rate was corrected for false alarms to produce a performance measure (Heffner and Heffner, 1995) according to the formula: Performance = Hit rate – (False alarm rate × Hit rate). This performance measure proportionately reduces the hit rate by the false alarm rate associated with each intensity (i.e., each block of trials) and it varies from 0 (no hits) to 1 (100% hit rate with no false alarms).

Auditory detection thresholds were determined by successively reducing the intensity of the tones (in blocks of 5–10 warning trials) until the alpaca no longer responded to the warning tone above chance (i.e., the hit and false alarm rates did not differ significantly; $p > 0.05$, binomial distribution). Note that at intensities that were readily audible (i.e., near perfect performance), fewer warning trials (5–6) were presented before proceeding to the next lower intensity, and intensity was decreased in larger steps of 10 dB. When detection rates began to fall as threshold approached (usually about 25 dB above eventual threshold), 5-dB decrements were used and block size was increased to 8–10 warning trials. Threshold was defined as the intensity at which the performance measure equaled 0.50, which was usually determined by linear interpolation. It should be noted that this is a traditional measure of psychophysical threshold that is not based on chance and thereby not dependent on the number of trials. Because a 50% detection threshold is always higher than a threshold defined by chance (usually 30% to 35% detection, corrected for false alarms), it is also a more conservative definition. Testing was considered complete for a particular frequency when the thresholds obtained in at least three different sessions were within 3 dB of each other. Once the entire hearing range had been tested, selected frequencies were rechecked to ensure reliability, including the high- and low-frequency limits, best sensitivity, and any discontinuities in the audiogram. As an added control test at the lower frequencies, thresholds were obtained for a human observer at 32, 63, and 125 Hz, using the same stimulus conditions as for the alpacas for comparison with the standard human audiogram.

2. Left–right noise localization

Minimum audible angles were determined by presenting a single 100-ms broadband noise burst at 60-dB SPL re 20μPa [50 dB hearing level (HL)] every 4 s. The safe trials consisted of sounds emitted from one of the speakers to the right of midline, and warning trials consisted of sounds emitted from the matched speaker at an equal angle to the left of midline. Safe and warning trial probabilities were the same as for the audiogram. Angles of separation between speakers were fixed at 180, 120, 90, 60, 45, 30, 20, and 15 deg. Angles were tested in blocks of 8–10 warning trials each, with smaller angles tested in multiple blocks of trials. Six angles were usually tested in every session, including at least one angle that was below threshold. Threshold was defined as the angle at which performance equaled 50% corrected detection.

3. Tone localization

Two alpacas were also tested for their ability to localize pure tone bursts separated by a fixed angle of 60°. The measure of interest for comparative purposes was asymptotic performance, defined as the mean of the best half of the test blocks, with 12–14 blocks of 8 trials given at each frequency. Tone duration was 150 ms (50 ms rise/decay, on full 50 ms); two pulses were presented on each trial with a 1.2-s interpulse interval. All tones were presented at 50 dB above threshold and randomly attenuated by as much as 3.5 dB. Additional testing was carried out using a 4-kHz tone sinusoidally amplitude modulated at 250 or 500 Hz (100% modulation).

4. Front–back localization

Alpaca A was also tested on its ability to discriminate high- and low-frequency noise bursts from sources located symmetrically in front of or behind the interaural line, at 120, 90, or 60 deg separation. Because the binaural difference cues would be the same within each pair of speakers, this discrimination relied on pinna cues. As this is a more difficult discrimination, a longer noise burst of 500 ms was used. Sounds behind the interaural line (e.g., at 120°) were safe and sounds in front of the interaural line (e.g., at 60°) were warning. Two noise bands, a 2-kHz low-pass noise and a 3-kHz high-pass noise, were presented. The intensity of the noise was 50 dB above threshold and randomized over a 3.5 dB range.

III. RESULTS

A. Audiogram

Alpacas' natural habitat is a dry environment and they adapted easily to water restriction. The initial acclimation to the apparatus, learning to respond to sound, and becoming reliable observers for low-level sounds required 28 daily sessions. All thresholds, including rechecking, were completed in the subsequent 39 sessions. In a typical session lasting approximately 40–60 min, an alpaca would drink up to 2 l of water (enough to maintain body weight) and accumulate up to 120 warning trials (and 480 associated safe trials). Thus a threshold for one frequency could be easily obtained per session. We observed that the alpacas always directed their pinnae frontally toward the speaker, especially when the amplitude of the signal was reduced.

Thresholds for the three alpacas are illustrated in Fig. 3. They show the characteristic U-shape of mammalian audiograms, with good agreement between individuals—less than 4 dB difference at most frequencies. Like other mammalian audiograms, the largest variations between individual thresholds (up to 9 dB) are seen near the upper and lower limits of hearing, where sensitivity changes rapidly with frequency. Beginning with an average threshold of 70.5 dB SPL at 25 Hz, sensitivity improved as frequency was increased to 8 kHz, except for a slight decrease in sensitivity at 2 kHz. Their best hearing was at 8 kHz, showing a mean threshold of −0.5 dB SPL. Thresholds remained at 25 dB SPL or better up to 22.5 kHz, and then rose rapidly to a mean threshold of 79 dB SPL at 40 kHz, the highest frequency tested. At an intensity of 60 dB SPL, the hearing range of alpacas extends from 40 Hz to 32.8 kHz, a range of 9.7 octaves.

As a further check, a human observer was tested at the lowest frequencies using the same acoustic equipment and procedures (except for a button switch to indicate responses and a flash of light that followed the pulsing tone stimuli, but with the shock off). The low-frequency thresholds for the human control were within 3 dB of previous thresholds for humans (ISO, 2005; Jackson *et al.*, 1999), indicating that there was nothing unusual about the low-frequency sound field.

B. Broadband noise localization thresholds (minimum audible angle)

The sound-localization performance of the three alpacas is illustrated in Fig. 4. All three were capable of 90% or better performance at large angles, showing good motivation and ability to perform the cognitive and motor requirements of the task. Performance began to decline gradually at 60° separation, then sharply below 30°. The 50% corrected detection threshold was reached at an average of 23° and the alpacas fell quickly to chance below 20°.

C. Localization of pure tones

The ability to use the binaural locus cues can be demonstrated by determining the ability of an animal to perform a left−right locus discrimination for pure tones, presented from loudspeakers located in front of the animal, at a fixed angle of separation. This is possible because low-frequency pure tones are localized using binaural time-difference cues whereas high frequencies are localized using binaural intensity-difference cues. Specifically, low-frequency pure tones that bend around the head with little or no attenuation can only be localized by comparing the time of arrival of the phase of each cycle of the tone at the two ears (the binaural phase difference cue being a subset of the binaural time cue). However, the phase-difference cue becomes ambiguous for pure tones at high frequencies, when successive cycles arrive too quickly for the nervous system to match the arrival of the same cycle at the two ears (Woodworth and Schlosberg, 1954). The exact "frequency of ambiguity" depends on an animal's head size and the angle of the sound source relative to its midline—it is higher for smaller heads and sound sources closer to midline. Pure tones above the frequency of ambiguity, then, must be localized using the binaural intensity difference cue (a subset of binaural frequency-intensity cue). Thus, the ability of an animal to use the two binaural cues can be measured by determining the ability to localize pure tones above and below the frequency of ambiguity.

For alpacas, with a head diameter of approximately 12 cm, the frequency of phase ambiguity for an angle of separation of 30° to the left and right of midline is 1.9 kHz. Thus, above 1.9 kHz alpacas would have to depend on interaural intensity differences to localize pure tones. Intensity differences are generated at wavelengths shorter than the head diameter (approximately 3 kHz for alpacas) and increase with higher frequencies (e.g., Christensen-Dalsgaard, 2005). As Fig. 5 shows, alpacas can localize low-frequency pure tones well (250 and 500 Hz), with performances comparable to their performance with broadband noise at 60° separation, thereby

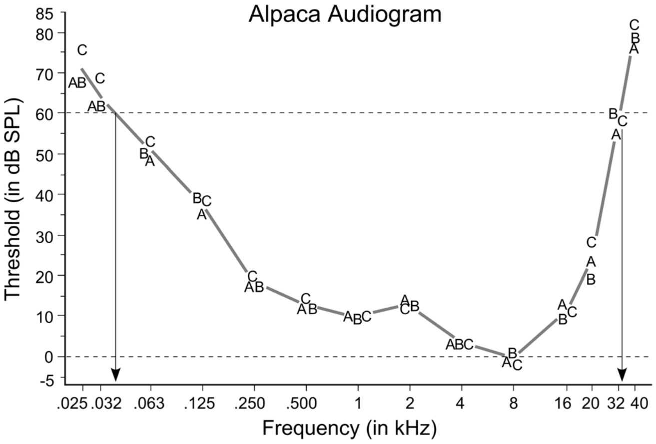

FIG. 3. Auditory detection thresholds for three alpacas. The solid line indicates the mean threshold. The highest and lowest frequencies audible at 60 dB SPL (indicated by arrows) provide a common measure with which to compare the hearing limits of alpacas with those of other species. Note good agreement between the three individuals and good sensitivity below 10 dB SPL over a broad range.

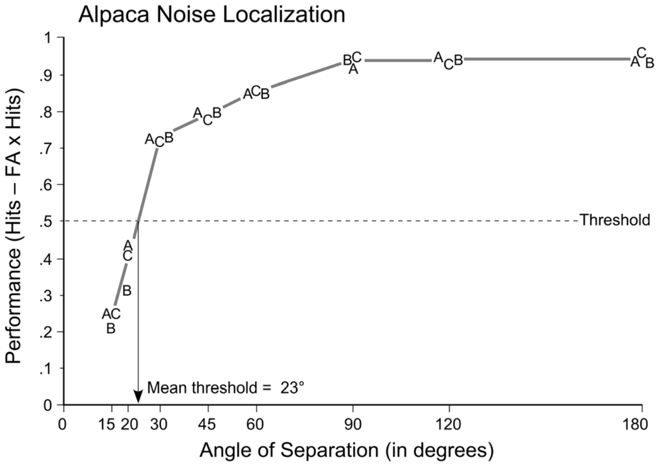

FIG. 4. Sound-localization performance of three alpacas. Note the good agreement between individuals, good performance at large angles, and the sharp decline in performance below 30°, falling to chance below 20°. The 50% corrected detection threshold (minimum audible angle) averaged 23° for the three animals.

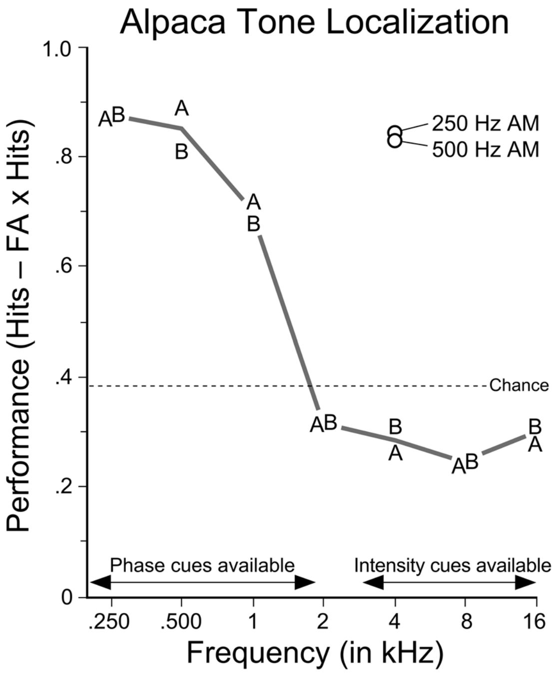

FIG. 5. Sound-localization performance at 60° separation for the two alpacas as a function of the frequency of a pure tone stimulus. The alpacas showed good performances at frequencies of 1 kHz and below, where binaural phase cues were available, but performances remained at chance for 2 kHz and higher, where only binaural intensity cues were available. However when amplitude modulation imposed an envelope on a high frequency tone of 4 kHz, the alpacas were easily able to localize that signal (as indicated by open circles).

showing that they can use the binaural time cue in the form of phase delays. Performance began to fall by 1 kHz, and for all pure tones of 2 kHz and higher, performance remained at chance. The inability to localize frequencies higher than the frequency of phase ambiguity indicates that alpacas cannot use the binaural intensity cue for sound localization.

The inability of alpacas to localize pure tones above the frequency of phase ambiguity raised the question of whether they could localize a high-frequency carrier tone if its envelope were amplitude modulated at a sufficiently low rate to permit the use of the binaural phase cue. The arrival of peaks and troughs in the envelope at each ear can be compared in the same manner as can peaks and troughs of a low-frequency pure tone, thereby permitting detection of an ongoing interaural delay. As can be seen in Fig. 5, although the alpacas could not localize a 4 kHz pure tone, they easily localized it when it was modulated at a rate of 250 or 500 Hz. Indeed, their performances were comparable to those with the 250- and 500-Hz pure tones. By failing to localize high frequencies, yet showing good localization of low-frequency tones or envelopes, the alpacas demonstrated that they are able to make use of binaural time cues, but not of binaural intensity cues, for sound localization.

D. Front–back localization

The inability to localize using the binaural intensity-difference cue might seem surprising in a species that hears frequencies up to 40 kHz. Detecting high frequencies nevertheless remains important because they also provide the basis for pinna cues used in sound localization (e.g., Butler, 1975, 1986). The ability to distinguish sound sources located symmetrically in front of and behind the interaural axis depends on pinna cues, because time delays are the same for these locations (e.g., Mills, 1972). Thus, testing the ability of an alpaca to distinguish sound sources symmetrically located in front of and behind the interaural line provided an opportunity to examine the ability to localize high frequencies using pinna cues even though high frequencies could not be localized using the binaural intensity cue.

Figure 6 illustrates the performance of alpaca A at three angles (±30°, ±45°, ±60°) centered symmetrically on the interaural axis on its right side. Although the alpaca was able to perform the front–back discrimination when the high-frequency noise burst was presented, it was never able to perform the discrimination with low-frequency noise bursts; these results from symmetrically placed speaker locations demonstrate that high frequency hearing is necessary for localization based on pinna cues in this species. For comparison, every test session included blocks of trials that were not symmetrical around the interaural axis (such as straight ahead at 0° and 120° to the right). Performance at these asymmetrical sound locations with both high- and low-pass noise bands ranged between 82% and 98%, demonstrating that the low-frequency noise burst was easily localized when interaural time differences were available.

These results indicate that alpacas are able to discriminate level differences monaurally, but not binaurally. They are able to perform a front–back discrimination when a high-frequency noise burst is presented, indicating that they are able to perform a sequential level analysis with one ear. On the other hand, they are not able to perform a left–right discrimination when high-frequency tones are presented, indicating that they are unable to perform a simultaneous level comparison between the two ears. In other words, alpacas are able to perform a level-by-frequency comparison of a sound with the memory of a previous sound, but are unable

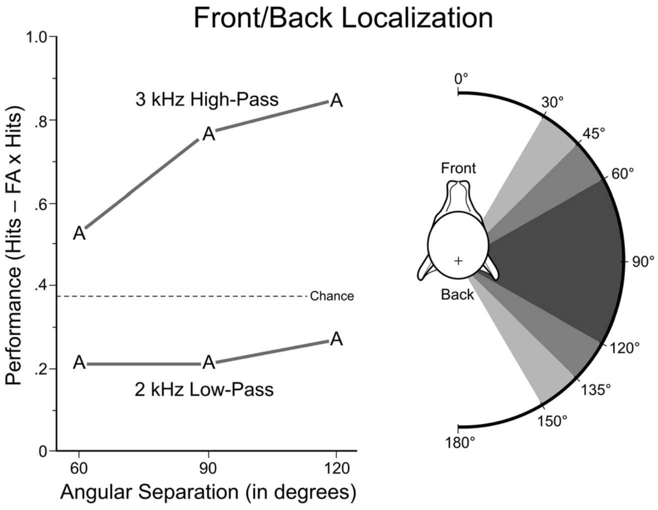

FIG. 6. Front/back sound-localization performance. The noise band containing only high frequencies above 3 kHz was easily localized, whereas the noise band containing only frequencies below 2 kHz was not localizable, even when the sources were separated by 120°. This illustrates the importance of high frequencies for localization using only pinna cues.

to make a similar analysis in which the comparison is between level differences in the two ears.

IV. DISCUSSION

A. Audiogram

The hearing of alpacas is typical of that of other artiodactyls that have been tested. They have good sensitivity to sound, including at the low frequencies, but their sensitivity is not unique. At their most sensitive, they hear better than pigs and horses but not as well as cattle, goats, and sheep, but the differences are less than 10 dB (Heffner and Heffner, 1983, 1990; Wollack, 1963). There is a remarkable similarity between alpacas and the two species of deer for which data are available—the New World white-tailed deer and the Old World reindeer (Fig. 7) (Flydal *et al.*, 2001; Heffner and Heffner, 2010). Between 1 and 16 kHz the hearing of these three species is virtually identical, including the reduced sensitivity at 2 kHz. Although it is not clear why alpacas show such resemblance to these two distantly related deer, it is not likely to be due to peculiarities of the test situation as each was tested in a different laboratory. The most and least sensitive artiodactyls (cattle and pig) are also included in Fig. 7 to illustrate the range of sensitivities observed in this order so far.

1. High-frequency hearing

In the late nineteenth century, Francis Galton noted that high-frequency hearing varied when he observed the reactions of animals to ultrasonic whistles, but a systematic basis for the variation among mammals was not discovered until nearly 100 years later. It was then recognized that head size was important when defined functionally as the travel time for sound from one ear to the other—around the head for animals that hear in air and through the head for underwater mammals. Animals with smaller functional head sizes tended to have better high-frequency hearing than animals with larger functional head sizes, a trend that was related not to a simple scaling effect but to the use of the cues for sound localization (Masterton *et al.*, 1969). There are three cues for sound localization, the difference in the time of arrival of a sound at the two ears, the difference in the intensity of a sound at the two ears, and the differences in the spectra of sounds originating from different locations caused by the orientation and convolutions of the pinnae. Whereas the magnitude of the binaural time cue is fixed by the functional distance between the ears, the magnitude of the binaural intensity and pinna cues depends on whether an animal hears frequencies high enough to be affected by its head and pinnae. Because the frequency at which the head and pinnae attenuate sound increases as head size decreases, the smaller an animal's head and pinnae, the higher it must hear to use the interaural intensity difference and pinna cues for sound localization.

As shown in Fig. 8, alpacas fit the relation between functional head size and high-frequency hearing ($r = -0.793$, $p < 0.0001$), which accommodates more than 60 species ranging in size from mice and bats to humans and elephants. However, the observation that alpacas apparently do not use the binaural intensity cue, indicated by their inability to localize pure tones of wavelengths too short to be localized using the binaural phase cue (see Sec. IV C below), suggests that the selective pressure for their high-frequency hearing is for localization using pinna cues. This is supported by their requirement for high frequencies when forced to rely on pinna cues for front/back discriminations. In this trait they join other species, specifically horses, pigs, and cattle that are also consistent with the relationship between functional head size and high-frequency hearing but do not use interaural intensity differences for localization (Heffner and Heffner, 1986a,b, 1989). Further, as demonstrated for humans by Robert Butler and his colleagues (e.g., Butler, 1975), pinna cues also make it possible to prevent front/back confusions, to localize in the vertical plane, and to localize sounds that are only audible in the ear nearest the sound source, none of which can be accomplished using the binaural time and intensity cues. Last, it may be noted that the inability of an animal to use the binaural intensity-difference cue does not necessarily mean that it is unable to localize high-frequency sounds; this is because most naturally occurring high-frequency sounds are fluctuating and complex sounds that can be localized based on an analysis of interaural differences of their temporal envelopes as long as the sound is audible in both ears.

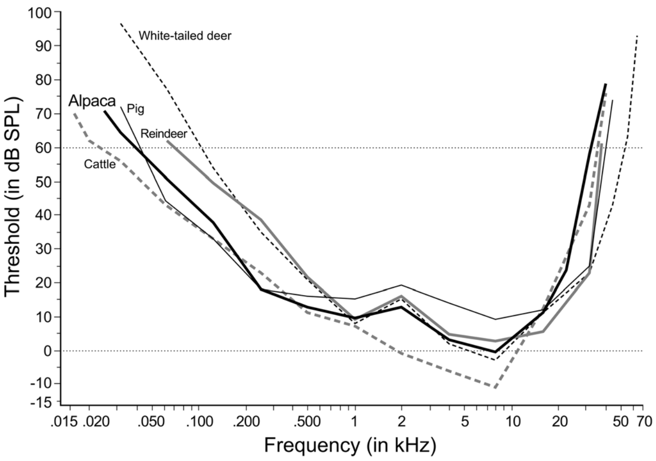

FIG. 7. Alpacas compared with other artiodactyls. The alpaca audiogram closely resembles that of white-tailed deer and reindeer in the midrange of their audiograms where their hearing is most sensitive. The similarity includes a noticeable decrease in sensitivity at 2 kHz. The audiograms of cattle and pigs are illustrated for comparison to show the range of sensitivities in artiodactyls. Alpaca auditory sensitivity (bold black line), pig (Heffner and Heffner, 1990), cattle (Heffner and Heffner, 1983), reindeer (Flydal *et al.*, 2001), and white-tailed deer (Heffner and Heffner, 2010).

B. Sound-localization acuity (minimum audible angle)

The minimum audible angle for brief noise bursts is 23° for alpacas. Although this indicates poorer localization acuity than that of many species, it is not unprecedented. Nevertheless, the wide variation in localization acuity revealed in Fig. 9 warrants an explanation. As can be seen in Fig. 9, most large hoofed mammals tested so far also have relatively poor localization acuity, including domestic horses, cattle, and goats (Heffner and Heffner, 1984, 1992a).

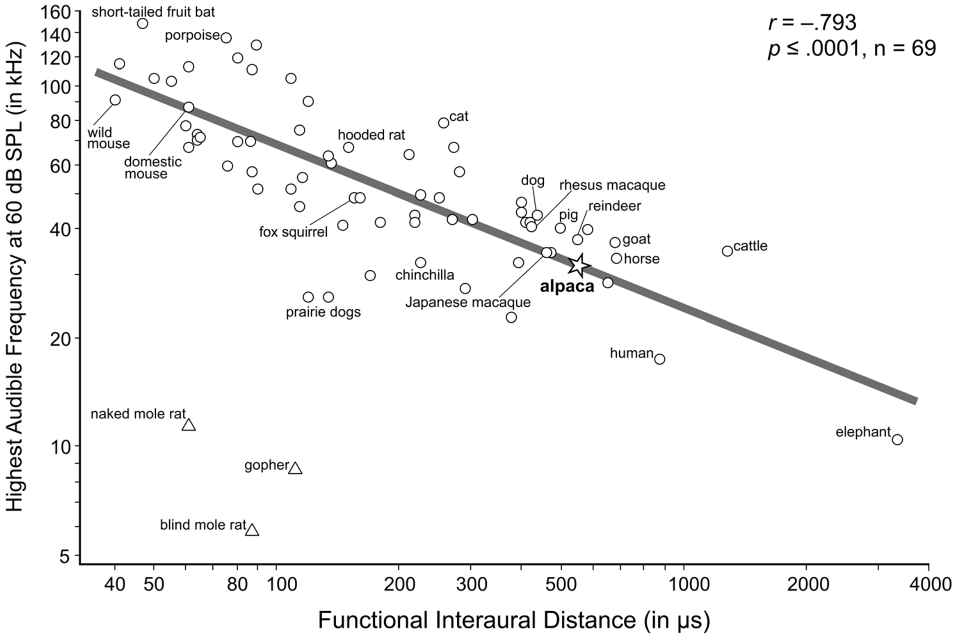

FIG. 8. High-frequency hearing among mammals is strongly correlated with their functional interaural distance (time delay between the two ears in μs). Species with small time delays are under greater selective pressure to hear high frequencies for sound localization. The high-frequency hearing limit of alpacas (indicated by the star) is consistent with this relationship. For a more extensive discussion of the basis for this relationship and for the exceptions, see Heffner and Heffner, 2008.

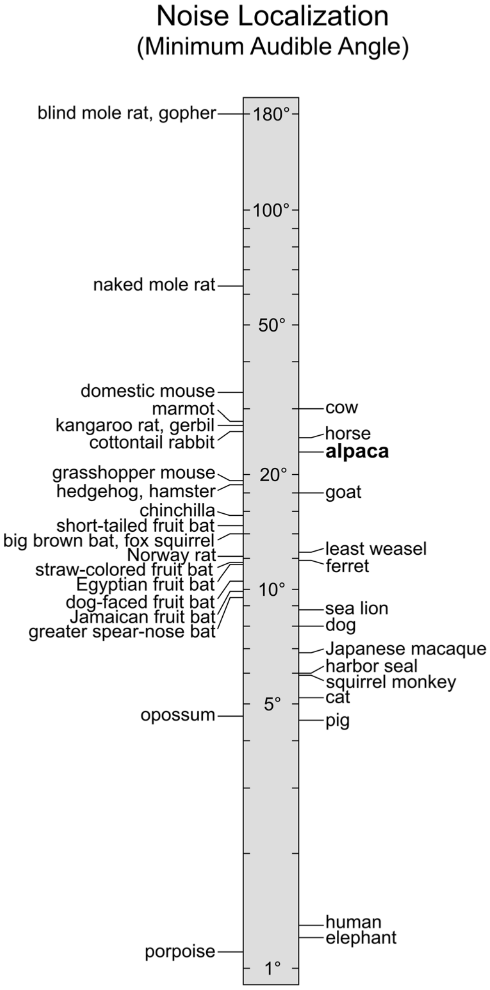

FIG. 9. Behaviorally determined sound-localization thresholds for mammals. Species with most acute localization in the azimuthal plane are located near the bottom of the scale and those with poor acuity are at the top; for convenience, hoofed mammals, carnivores, and primates are listed on the right, and rodents, bats, and other species on the left. For specific citations, see Heffner and Heffner, 2003, and Heffner *et al.*, 2007.

Yet domestic pigs are among the most acute localizers, indicating that poor acuity is not characteristic of all artiodactyls, hoofed mammals, or even of domesticated species (Heffner and Heffner, 1989). Accordingly, we have sought an explanation in the functions served by sound localization—specifically the use of hearing to direct an animal's vision to scrutinize a sound source.

It has long been recognized that the senses do not function in isolation but instead work together to provide information about biologically relevant objects and activity in the environment (Pumphrey, 1950). Thus it is not surprising that a visual ability should be correlated with sound localization and, very possibly, impose selective pressure on it. Specifically, when a species orients to scrutinize a sound source, it is the most acute vision that is oriented. Species with narrow fields of best vision (such as primates and pigs) seem to require more accurate information to pinpoint the location of sound sources for visual orienting than do species with broad fields of good vision (most hoofed mammals and many rodents), hence the strong correlation between sound-localization acuity and the width of the field of best vision ($r = 0.89$; Heffner *et al.*, 2008). Although there are yet no retinal data for alpacas on which to estimate the exact extent of their best vision, alpacas do have horizontal pupils and are likely to have broad fields of best vision, with the possible addition of a vertical streak in the temporal retina, similar to that of pigs and the larger Camelidae (Harman *et al.*, 2001). *If* this does prove to be the case, alpacas will support the strong relationship between sound localization and the width of the field of best vision (cf. Heffner and Heffner, 1992b; Heffner *et al.*, 2008).

C. Use of binaural locus cues

The localization of a high-frequency tone pip that is too brief to be scanned by head and pinna movements requires the ability to use the binaural intensity-difference cue, whereas localization of a brief low-frequency tone pip requires the use of the binaural phase-difference cue, a form of binaural time cue (e.g., Mills, 1960). Phase differences become ambiguous at higher frequencies when successive cycles arrive too quickly for the nervous system to match the arrival of the same cycle at the two ears. For alpacas (with their approximate head diameter of 12 cm), this estimated frequency of phase ambiguity with loudspeakers located ± 30 deg from the midline is 1.9 kHz. By testing the ability to localize brief pure tones throughout much of the hearing range, we were able to determine the alpacas' ability to use the two main binaural locus cues without the complication of fitting headphones on animals.

As shown in Fig. 5, the alpacas easily localized low-frequency pure tones (250 Hz to 1 kHz), demonstrating their ability to use the binaural phase cue to localize sound, but were unable to localize high-frequency pure tones (2–16 kHz), indicating that they could not use the binaural intensity-difference cue. Although they are able to localize high frequency sounds using the pinna cues, pinna cues work best with complex sounds (e.g., noise) and are of little help in localizing pure tones.

We have long been aware that there are some mammalian species that do not use one binaural locus cue or the other, bringing us to question what factors might be related to this phenomenon. From a physiological approach we might pursue the wide variation in the anatomical features and response types in the Superior Olives (both Medial and Lateral) to understand the mechanisms underlying the variation in the use of binaural locus cues. The Lateral Superior Olive is responsive to interaural differences in level, but it contains different cell types with different response characteristics. It is quite likely that the preponderance of the various cell types also varies among species, but very few species have been examined physiologically and none of those belong to the group that does not use interaural level differences for localization (Heffner, 1995; Heffner and Heffner, 1989). Hence, we cannot address the mechanisms that have been lost or gained in different lineages as sound localization has evolved in each.

Alternatively, we have searched for selective pressures that might have influenced the advantages and disadvantages of using each of the binaural locus cues. One possibility might be that species that have relinquished one of the binaural locus cues are less accurate localizers than those that use both cues, but this does not seem to be the case. As shown in Fig. 10, animals that do not use the binaural time cue (e.g., Norway rat, greater spear-nosed bat) and those that do not use the binaural intensity cue over at least part of the available range (e.g., pig, elephant) have better left−right localization acuity than some species that use both cues (e.g., chinchilla, gerbil, prairie dog). Similarly, there is overlap in the localization acuity of those animals that do not use binaural time with those that do not use binaural intensity. In short, relinquishing one or the other binaural locus cue does not seem to compromise localization acuity.

A second possibility is that the use of only one binaural locus cue is related to the head size of an animal. Specifically, an animal with a small interaural distance may give up use of the binaural time cue because the interaural time delay generated by its head is too small to be useful. On the other hand, a large functional head size would so greatly reduce the intensity of a sound as it traveled from one ear to the other that high frequencies would be audible only in the near ear and no binaural comparison would be possible. Indeed, as shown in Fig. 11, those animals that have given up the binaural time cues have small functional head sizes whereas those that have given up the binaural intensity cue have large functional head sizes. However, again there is overlap with species that use both binaural cues. As can be seen in Fig. 11, not all small animals have relinquished the use of the binaural time cue (e.g., gerbil, least weasel, Jamaican fruit bat) and there is at least one large animal that that uses the binaural intensity cue (humans).

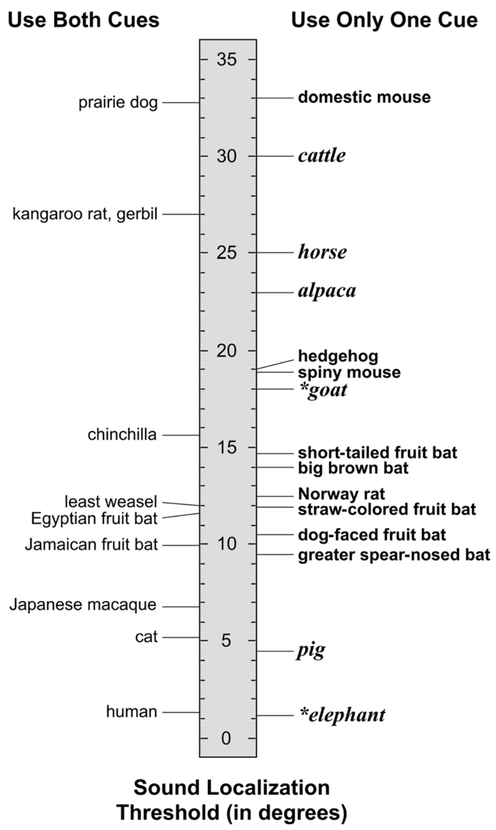

FIG. 10. Sound-localization acuity among species that use only one binaural locus cue compared to those that use both cues. There are both good and poor localizers in each group, indicating that use of only one cue does not necessarily compromise localization acuity and that the use of both binaural cues does not guarantee good acuity. Species that use only one binaural locus cue are shown on the right side of the scale, and those that use both cues are on the left side of the scale. Species, including alpacas, that use only time cues are listed in *italics*; those that use only intensity cues are listed in bold type; * indicates that elephants and goats use binaural intensity cues, but only in the lower-frequency part of the range for which is available (cf. Heffner and Heffner, 1982).

Given these considerations, we might be persuaded to direct our thinking less on why some species use only one of the cues, and consider why similarly large or small species, good and poor localizers alike, continue to use both cues when one cue appears quite adequate. It is reasonable to ask what distinguishes those species that use both binaural locus cues from those that find a single cue sufficient. It seems that the size and perhaps ecological niche of a species, and even

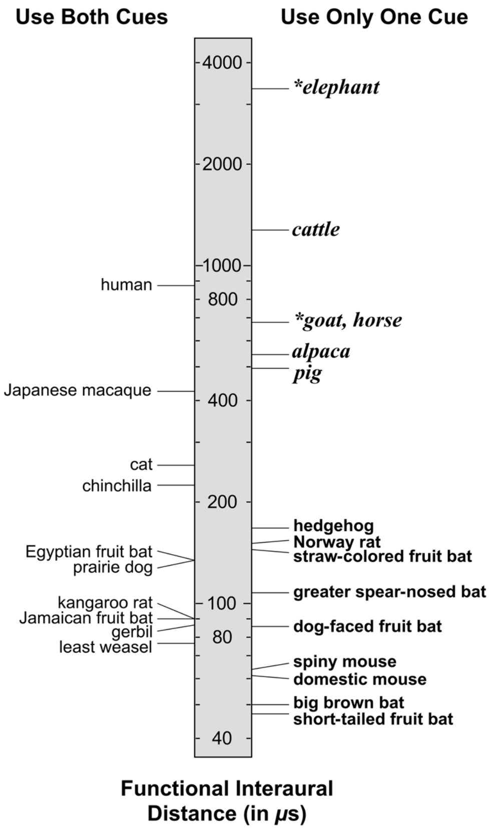

FIG. 11. Functional interaural distance among species that use only one binaural locus cue (right side of scale) compared to those that use both cues (left side of scale). Species, including alpacas, that use only time cues tend to be larger species and are listed in *italics*; those that use only intensity cues are among the smaller species and are listed in bold type; * indicates that elephants and goats can use binaural intensity cues, but only in the lower-frequency part of the range for which is available (cf. Heffner and Heffner, 1982). Note the overlap of both groups that use only one cue with the species on the left that use both cues.

its phyletic lineage, could influence whether and which locus cue might not be used, but with so many possible contributing factors, we simply have data on too few cases in each group to speculate. To address this question it would be helpful to have data on additional large and medium-sized species from other phyletic lineages and lifestyles, as the sample of large mammals remains small. Of particular interest would be large species that are not ungulates, such as very large felids, canids, and ursids, and some very small ungulates, such as the mouse deer. It would also seem prudent to begin gathering information on the size, shape, and mobility of the pinnae of species for which localization data are available.

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