The behavioral audiogram of whitetail deer (*Odocoileus virginianus*)

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Abstract: The behavioral audiograms of two female white-tailed deer (*Odocoileus virginianus*) were determined using a conditioned-suppression avoidance procedure. At a level of 60 dB sound pressure level, their hearing range extends from 115 Hz to 54 kHz with a best sensitivity of −3 dB at 8 kHz; increasing the intensity of the sound extends their hearing range from 32 Hz (at 96.5 dB) to 64 kHz (at 93 dB). Compared with humans, white-tailed deer have better high-frequency but poorer low-frequency hearing.

PACS numbers: 43.80.Lb, 43.66.Gf, 43.66.Cb [CM]
Date Received: November 10, 2009 **Date Accepted:** December 10, 2009

1. Introduction

White-tailed deer have perhaps the largest economic impact of any wild animal in North America. On the one hand, billions of dollars are spent each year on equipment and travel related to deer hunting (e.g., Conover, 1997). On the other hand, deer spread Lyme disease, causing millions of dollars of damage to both the agriculture and timber industries, and over a billion dollars of damage to vehicles that collide with them each year (Conover, 1997; Schwabe and Schuhmann, 2002). Indeed, more than 100 people are killed each year in deer-vehicle collisions, with many more seriously injured, making deer the most deadly wild animals in North America (Bailey, 2001). As a result, there is much interest in the behavior of white-tailed deer, particularly in their sensory abilities (e.g., Gerlach *et al.*, 1994).

Because deer are naturally afraid of humans and do not readily tolerate our presence, it is difficult to conduct behavioral tests on them. As a result, the only measure of their hearing currently available is their auditory brainstem response (D'Angelo *et al.*, 2007). This measurement indicates that the hearing range of deer extends from 250 Hz to 30 kHz, with a best sensitivity of only 42 dB at 4 and 8 kHz. However, the auditory brainstem response does not give an accurate measure of an animal's absolute sensitivity nor does it necessarily indicate the relative sensitivity of an animal to different frequencies (Heffner and Heffner, 2003). Such information can only be obtained from a behavioral audiogram.

We present here the absolute pure-tone thresholds obtained for two domestically raised whitetail deer using standard animal psychophysical procedures. These results will be of interest to those who wish to attract, repel, or conceal their presence from deer.

2. Method

The animals used in this experiment were two whitetail does (*Odocoileus virginianus*) 1–2 years of age that had been born and raised domestically. The animals were weighed daily during testing to help monitor their health.

The deer were tested using a conditioned-suppression avoidance procedure in which a thirsty animal was trained to maintain mouth contact with a small stainless steel water bowl in order to receive a steady trickle of water. The bowl, which was mounted on a post 0.5 m above the floor, was carefully positioned so that the animals made little or no drinking noise. Pure tones were then presented at random intervals followed by a mild electric shock delivered between the

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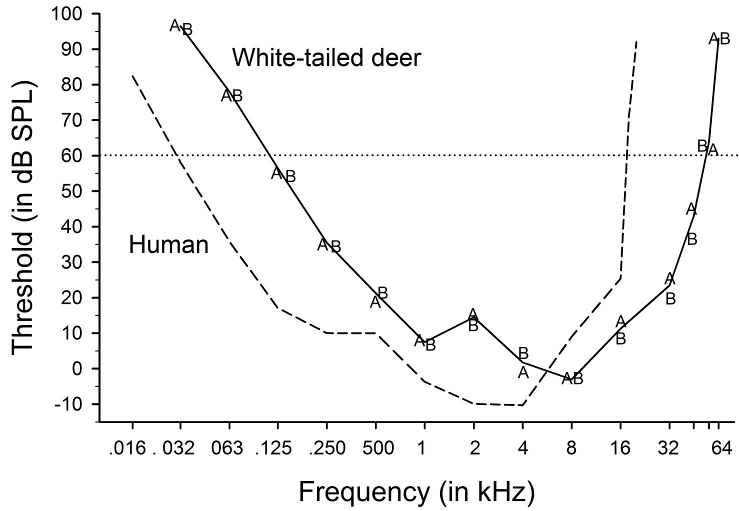

Fig. 1. Absolute thresholds of two white-tailed deer (A and B). The solid line indicates the average thresholds of the deer. The dashed line is a human audiogram obtained in comparable free-field conditions (Jackson *et al.*, 1999). The horizontal dotted line indicates the 60 dB sound pressure level, which is the level commonly used when comparing the hearing ranges of different species.

bowl and the floor. An animal avoided the shock by breaking contact with the bowl whenever it heard a tone, thereby also indicating that it had detected the tone. Thus, the task resembles the natural situation in which an animal at a water hole pauses when it senses danger. That the shock level used was "mild" was indicated by the fact that the deer never developed a fear of the water bowl and returned to it as soon as the sound was turned off (for details of this procedure, see Heffner and Heffner, 1995).

Thresholds were determined by reducing the intensity of a tone in 5 dB steps until an animal could no longer detect it above chance level. Threshold was defined as the intensity at which an animal could detect a sound 50% of the time (corrected for false positives), which was usually calculated by interpolation (Heffner and Heffner, 1995).

To produce the tones, sine waves were generated with an oscillator or a digital signal generator, gated with a rise-fall gate set to at least 10 ms to eliminate onset and offset artifacts, pulsed (400 ms on, 100 ms off), filtered ($\pm 1/3$ octave settings), monitored with an oscilloscope, amplified, and sent to a loudspeaker: either a subwoofer (32–63 Hz), woofer (125–4 kHz), piezoelectric tweeter (8–32 kHz), or leaf tweeter (45, 56, and 64 kHz). Most testing was conducted with the speaker placed in front of the animal at a distance of 1 m. However, because the animals sometimes did not point their pinnae forward, a second speaker was placed off to one side or behind an animal at a distance of 1.5 m or more with the exact location depending on the direction in which an animal tended to point its pinna. The procedure for calibrating the sound has been described elsewhere (Jackson *et al.*, 1997) and the sound pressure level (SPL) used was referenced to 20 $\mu N/m^2$. Testing was conducted in a single-wall sound-proof chamber, the walls and ceiling of which were lined with acoustic foam.

3. Results

The deer learned to enter the sound chamber, drink from the water bowl, and break contact with the bowl whenever a suprathreshold stimulus was presented. Although the animals usually pointed their pinnae straight ahead at the loudspeaker located in front of them, they sometimes rotated their pinnae to the side or back as though they were checking for sounds coming from those directions. When this occurred, the tone trials were delayed until their pinnae were again directed toward the loudspeaker. However, for frequencies of 8 kHz and higher, a second loudspeaker was placed in the location toward which they oriented their pinna. This procedure resulted in stable thresholds that represent the animals' optimal sensitivity.

The audiograms of the two deer, shown in Fig. 1, have the characteristic shape of mammalian audiograms. Beginning at the low frequencies, the deer were able to hear 32 Hz at an average threshold of 96.5 dB with sensitivity improving as frequency was increased. The animals showed a broad range of good sensitivity extending from 500 Hz to 32 kHz with a best threshold of −3 dB at 8 kHz. Above 32 kHz, sensitivity decreased rapidly to an average threshold of 93 dB at 64 kHz. Overall, at an intensity of 60 dB SPL, the deer were able to hear from 115 Hz to 54 kHz.

4. Discussion

There are two points to note about this deer audiogram. First, because sounds were only presented when at least one, if not both, of an animal's pinnae were pointed toward a loudspeaker, they represent the animals' optimal sensitivity. As has been demonstrated in reindeer, the pinnae of deer are directional for high frequencies and sensitivity may be reduced by 20 dB or more when the pinnae are pointed away from the sound source (Flydal *et al.*, 2001). Second, although we only tested females, these results are expected to apply to male deer as well, as the auditory sensitivity of mammals has not been observed to differ between the sexes (Heffner and Heffner, 2003).

Because of the extensive interactions between humans and white-tailed deer, it is of interest to compare their audiogram with that of humans. As can be seen in Fig. 1, the deer audiogram is similar in shape to that of humans and, indeed, looks like the human audiogram shifted approximately two octaves toward the higher frequencies. Some of the differences between the human and deer audiogram are well understood. In particular, the better high-frequency hearing of deer is explained by the observation that mammals rely on high-frequency cues to localize sound, high frequencies being particularly important for localization in the vertical plane and for preventing front-back confusions (Heffner and Heffner, 2008). However, because the directionality of high frequencies depends on the size of an animal's head and pinnae, the smaller the animal, the higher it must hear in order to use the high-frequency locus cues. Thus, deer hear higher than humans because they are smaller. However, less is known about the variation in mammalian low-frequency hearing and there is currently no explanation for the difference in the low-frequency sensitivity of humans and deer (Heffner and Heffner, 2003). (The audiograms of other mammals are available at http://psychology.utoledo.edu/showpage.asp?name=mammal_hearing for comparison with deer.)

Finally, the audiogram provided here can be used to obtain a preliminary estimate of the audibility of a sound to deer. That is, sounds whose spectra fall within the bounds of the audiogram will be audible to deer if they reach a deer's ear at a sufficient sound pressure level. Sounds that fall above or below the frequency range of deer will not be audible to them regardless of the intensity. However, care must be taken in using these data to estimate the relative loudness of sound to deer. This is because the audiogram measures the sensitivity to pure tones, whereas most sounds of interest are complex sounds containing multiple frequencies, and it has been shown that the perceived loudness of such sounds is not easily estimated from measures of pure-tone sensitivity (e.g., Hellman and Zwicker, 1987).

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