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Hearing Ranges of Laboratory Animals

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Any attempt to assess the effects of sounds on animals must consider species differences in hearing abilities. Although the hearing ranges of most species overlap to a large degree, considerable variation occurs in high- and low-frequency hearing as well as in absolute sensitivity. As a result, a sound that is easily audible to one species may be less audible, or even inaudible, to another. The purpose of this review is to describe the variation in the hearing ranges of common laboratory animals.

In our interactions with animals, we often assume that their hearing abilities are, if not identical to ours, at least quite similar. For example, we easily hear the vocalizations of cats and dogs, and they, in turn, are easily trained to come to the sound of our calls. However, comparative studies have shown that the auditory sensitivity of different species can vary widely, especially with regard to the ability to hear high- and low-frequency sounds. The purpose of this review is to illustrate the differences in the hearing sensitivities of mammals and birds, about which much is known, as well as of amphibians and reptiles, about which little is known. Not addressed are the hearing abilities of fish and invertebrates (for brief descriptions of the hearing of these 2 groups, as well as that of vertebrates in general, see references 3 and 7).

The Audiogram

The basic test of hearing consists of determining the ability of an animal to hear pure tones at intervals throughout its hearing range. This testing is done by training an animal to respond to a tone and then reducing the tone's intensity until the animal fails to respond.[11,17] An animal's threshold for a tone typically is defined as the intensity that the animal detects half of the time (the 50% detection threshold), and the thresholds for frequencies spanning the hearing range collectively are referred to as an audiogram. Note that an audiogram is determined *behaviorally*; measures of neural responses to sound, such as the auditory brainstem response, often give estimates of hearing sensitivity that diverge from what an animal can actually hear.[8] Moreover, the animal must be trained to make a response to a sound—unconditioned responses tend to underestimate an animal's sensitivity because an animal may not always react to sounds that it can hear.

An example of an audiogram for humans is shown in Figure 1, with the intensity of a tone at threshold plotted against frequencies spanning the range of hearing. Note that intensity is plotted in decibels (dB) using a scale in which 0 dB is equal to a sound pressure level (SPL) of 20 $\mu N/m^2$, which is the average human threshold at a frequency of 1 kHz; thus, as in the Fahrenheit and Celsius temperature scales, SPL can have negative values. Note also that frequency is plotted on a log scale such that a change in frequency from 1 to 2 kHz is the same step size (1 octave) as from 16 kHz to 32 kHz.

The shape of the human audiogram (Figure 1) is characteristic of normal audiograms in other species. Beginning at the low frequencies, the audiogram shows a gradual improvement in sensitivity as frequency is increased until a point of best hearing is reached, which for humans is at about 2 to 4 kHz; above this point there is a gradual decrease in sensitivity that becomes more rapid as the upper limit of hearing is approached. Note that the human hearing range is often stated as '20 Hz to 20 kHz,' which is the nominal range for humans. However, we can hear lower frequencies if the intensity is sufficiently high, and only the young ear that has not been damaged by disease or loud sound can hear 20 kHz at any intensity. For comparative purposes, hearing range is usually given as the range of frequencies audible at a level of 60 dB SPL. Using this definition, the hearing range for humans is 31 Hz to 17.6 kHz.[16] Sounds that are too high for us to hear are labeled as 'ultrasonic,' whereas those that are too low are labeled as 'infrasonic.' Therefore, these terms are anthropocentrically defined and only indicate that humans cannot hear these sounds.

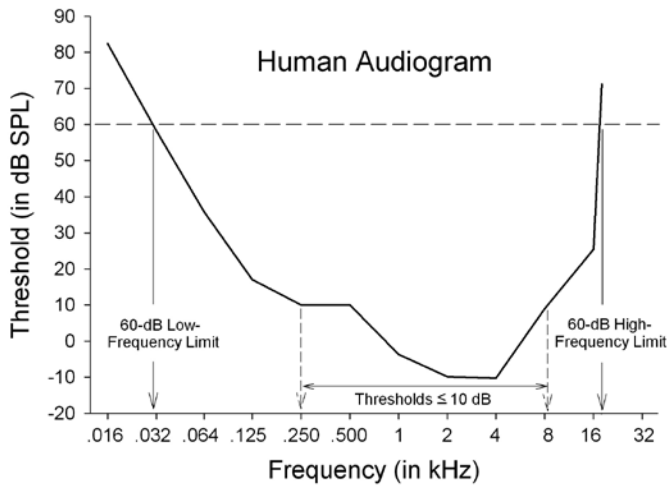

Figure 1. Audiogram showing the average human threshold for pure tones obtained in a sound field used to test other mammals. Low values on the *y* axis (dB) indicate greater hearing sensitivity. For comparative purposes, hearing range is usually specified as the range of frequencies audible at a level of 60-dB SPL; the range of frequencies audible at a level of 10 dB SPL specifies the frequencies to which an animal is very sensitive. Adapted with permission from reference 16.

In addition to the 60-dB hearing range, it may be useful for comparative purposes to know the range of frequencies at which an animal has good absolute sensitivity. For this measure, we have adopted the range of frequencies audible at a level of 10 dB, a level that is approximately 1 standard deviation above the median best sensitivity for mammals (excluding aquatic and subterranean species, whose hearing differs from that of other mammals). The 10-dB hearing range of humans is from 250 Hz to 8.1 kHz (Figure 1).

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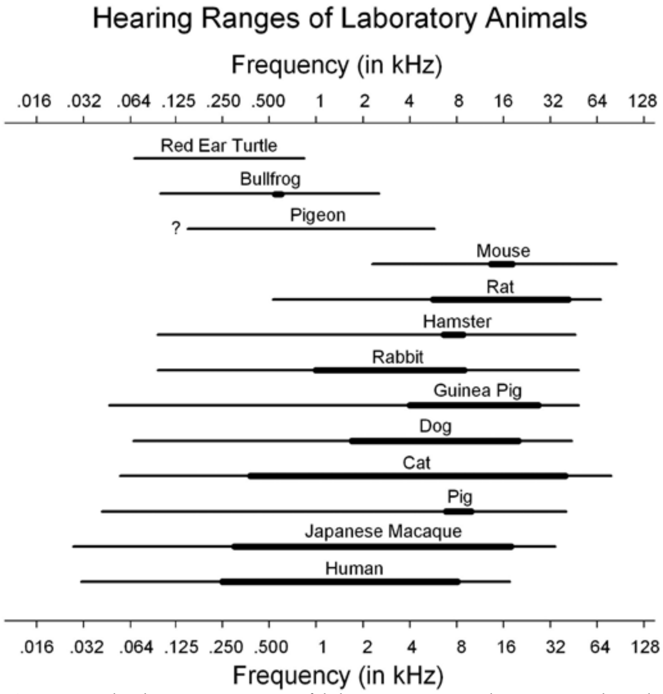

Figure 2. The hearing ranges of laboratory animals compared with those of humans. Thin lines indicate the range of frequencies that can be detected at 60 dB SPL; thick lines indicate the range that can be detected at 10 dB SPL. The low-frequency hearing of the pigeon has not been completely determined (as indicated by ?). Data obtained from references 5, 6, 10, 12–16 20, 22, and 23.

Hearing in Mammals

Behavioral audiograms are available for those mammals commonly used in laboratories, as well as for many exotic species.[7–9] The hearing ranges of 9 species of common laboratory mammals are compared with those of humans in Figure 2, which shows both the 60- and 10-dB hearing ranges for each species. Three points can be drawn from this figure.

First, all of the mammals shown here have better high-frequency hearing than do humans, with the 60-dB upper limits ranging from the 34.5-kHz upper limit of the Japanese macaque to the 85.5-kHz upper limit of the domestic house mouse, whose upper limit is more than 2 octaves higher than the 17.6-kHz upper limit of humans. The main reason for this variation is that small mammals need to hear higher frequencies than do larger mammals in order to make use of the high-frequency sound-localization cues provided by the attenuating effect of the head and pinnae on sound. As a result, mammals with small heads generally have better high-frequency hearing than do mammals with large heads. Thus, only 2 groups of mammals do not hear as high as humans: those with larger heads, such as the Indian elephant, and those that do not localize sound and therefore are not under selective pressure to hear high frequencies, such as subterranean rodents.[8]

Second, almost all of the mammals shown (Figure 2) have poorer low-frequency hearing than do humans, with the 60-dB lower limits ranging from 28 Hz for the Japanese macaque (whose lower limit slightly exceeds that of humans [31 Hz]) to 2.3 kHz for the domestic mouse. Thus low-frequency hearing varies over a range of more than 6 octaves. Only the Indian elephant, with a 60-dB low-frequency limit of 17 Hz, is known to have significantly better low-frequency hearing than humans. Although the reason for this variation is not well understood, it is possible that some animals have reduced their low-frequency hearing to prevent the low-frequency components of sounds from masking the high-frequency components they need for sound localization.[8]

Finally, the range of good hearing (that is, the frequencies audible at 10 dB) varies both in the size of the range as well as the frequencies that are encompassed. As shown in Figure 2, some animals, such as domestic cats, have a broad range of good hearing (6.6 octaves) whereas others, such as mice and hamsters, have a narrow range (0.4 octaves). Similarly, the range of good hearing can reach as low as 250 Hz (humans) and as high as 42 kHz (Norway rat). The range of good hearing is affected by the external ear or pinna, which can amplify or attenuate sound. Because the audiograms on which Figure 2 is based were conducted with the loudspeaker located in front of an animal, those animals with mobile pinnae were able to optimally position their pinnae for detecting sound. Just how much pinna position can affect thresholds is demonstrated by a study of reindeer, in which thresholds were shifted by as much as 21 dB depending on whether the reindeers' pinnae were pointing toward or away from the sound source.[4] Therefore animals with mobile pinnae, which includes most mammals, can increase or decrease the intensity of a sound reaching their ears simply by directing their pinnae toward or away from the source of the sound.

Hearing in Birds

Audiograms are available for a variety of species of birds, including the domestic pigeon, an animal often used in laboratory studies.[2,7] The most striking feature of bird hearing is the high-frequency limit, which falls between 6 to 12 kHz. Not only are the upper limits of birds well below those of most mammals, including humans, but birds also lack the systematic variation seen in mammalian high-frequency hearing. Low-frequency hearing does appear to vary among birds, but the incomplete assessment of the low-frequency hearing of many species of birds hinders determination of the degree or basis of this variation. Similarly, although the absolute sensitivity of birds does appear to vary, this variation has not been verified or explained.

The hearing range of the domestic pigeon is shown in Figure 2 in comparison with those of other laboratory animals. The pigeon has a 60-dB high-frequency hearing limit of 5.8 kHz, demonstrating that it, like other birds, lacks the good high-frequency hearing of mammals.[23] The pigeon's low-frequency hearing, in comparison, falls into the same range as mammals and, although pigeons do not appear to hear as low as humans, they may be sensitive to ultra-low-frequency pressure changes.[19] Finally, although some studies indicate that the absolute sensitivity of pigeons is within the range of mammals,[3] others have indicated that pigeons are somewhat less sensitive and unable to hear down to 10 dB SPL. In summary, pigeons are noticeably less sensitive to sound than humans.

Hearing in Reptiles and Amphibians

Although reptiles can be trained to respond to visual stimuli,[1] it has so far proven virtually impossible to train them to respond to sound. The red-ear turtle is the only reptile for which behavioral thresholds are available, and even it proved difficult to test.[22] The 60-dB range of hearing for the turtle (Figure 2) is 68 to 840 Hz (with lowest thresholds of about 40 dB SPL). In short, the little information available suggests that turtles are not only generally unresponsive to sound, they are also insensitive.

Among amphibians, only frogs and toads appear to be well adapted to hearing airborne sounds and, indeed, they make extensive use of vocalizations in locating mates.[21] Therefore, it is perhaps not surprising that the bullfrog, with a 60-dB hearing range of 100 Hz to 2.5 kHz, has better hearing than the turtle (Figure 2). However, the high-frequency hearing of bullfrogs is easily surpassed by that of birds and mammals.[7]

Conclusion

Although the hearing abilities of humans and laboratory animals overlap extensively, the differences make it necessary to consider what a particular species can hear before presuming that a sound is easily audible, or potentially annoying, to it. Because of our good low-frequency hearing, we humans are likely to overestimate the loudness of low-frequency sounds to other animals. For example, the sound of the air-handling system in an animal room may be noticeable to us but inaudible to the animals housed in it. In contrast, humans' complete inability to hear above 20 kHz means that we require special equipment to detect sounds that are easily audible to other animals, especially mice. However, the likelihood of high frequencies being a problem in the laboratory is reduced by the fact that they are highly directional and thus less likely to bend around objects to reach an animal in a cage. In addition, high frequencies are more easily attenuated by the mobile pinnae of most laboratory animals.

Finally, although mere knowledge of auditory sensitivity is insufficient to answer the question of whether an animal finds a particular sound psychologically annoying, two observations compel us to recognize the adaptability of animals to noisy environments. First, despite the number of acoustic pest repellers on the market, there is no convincing evidence that animals are deterred by loud sound. Despite the intensive search for sounds that repel animals, none has been found. Second, our personal observation is that animals are not deterred by intense sounds that humans find exceedingly annoying. Specifically, we have noticed that in our area of northwestern Ohio, groundhogs commonly make their burrows in the banks of elevated railroad beds within 1 to 2 m of tracks that carry over 90 heavily loaded freight trains each day—trains that emit so much noise that it forces all human conversation within 100 m to cease. Therefore, the benefits these animals gain from locating their burrows in these elevated beds (one of which is that this location places their burrows above flood level) appear to outweigh any adverse effects that exposure to such extreme noise might have.

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