Comments on "Killer whale (*Orcinus orca*) behavioral audiograms" [J. Acoust. Soc. Am. 141, 2387–2398 (2017)] (L)

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Branstetter and his colleagues present the audiograms of eight killer whales and provide a comprehensive review of previous killer whale audiograms. In their paper, they say that the present authors have reported a relationship between size and high-frequency hearing but that echolocating cetaceans might be a special case. The purpose of these comments is to clarify that the relationship of a species' high-frequency hearing is not to its size (mass) but to its "functional interaural distance" (a measure of the availability of sound-localization cues). Moreover, it has previously been noted that echolocating animals, cetaceans as well as bats, have extended their high-frequency hearing somewhat beyond the frequencies used by comparable non-echolocators for passive localization.

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The recent paper by Branstetter and his colleagues (2017) presents additional information on the behavioral audiogram of killer whales (*Orcinus orca*) as well as a helpful summary of previous killer whale audiograms. They note that we have found a relationship between animal size and high-frequency hearing to which echolocating Odontocetes (i.e., killer whales, porpoises, and dolphins) may be a special case. We agree that echolocating mammals, bats as well as cetaceans, are special cases, but not as special as they might at first seem. Our view is that mammals evolved high-frequency hearing for passive sound localization, enabling them to use the binaural intensity-difference cue and pinnae cues (although cetaceans, lacking pinnae, do not use the latter cue). These cues require that an animal's head and pinnae be sufficiently large to modify sounds. Although we begin with head measurements of mammals, these must be converted into *functional interaural distance*—the *time* required for sound to travel from one ear to the other. This time measure estimates the magnitude of the binaural time cues available to that species. Because the magnitude of locus cues is dependent on an animal's functional interaural distance, the shorter its functional interaural distance, the higher a species must hear to use the binaural intensity and pinna cues to localize sound. Despite their physically large size, Odontocetes have small *functional* interaural distances and would be expected to have better high-frequency hearing than simple head size or body weight might indicate.

In terrestrial mammals, functional interaural distance is the time it takes for sound to travel around the head from one ear to the other at the speed of sound in air. In mammals that hear underwater, it is the time it takes for sound to travel through the head from one cochlea to the other at the speed of sound in water—a speed more than four times faster than in air. Consequently, mammals that hear underwater, such as seals and cetaceans, have *physically large* heads, but they have *functionally small* interaural distances, thereby predicting good high-frequency hearing. Indeed, cetaceans provided key support for the hypothesis that mammals evolved high-frequency hearing for sound localization when the idea was first proposed (Masterton *et al.*, 1969). Although the sound transmission pathway in cetaceans appears to be through the lower jaw (e.g., Popov *et al.*, 2016), we use intercochlear distance to calculate the functional interaural distance because it estimates the upper limit of their high-frequency hearing required for passive sound localization—high-frequency hearing beyond that point can be attributed to the use of echolocation.

As previously noted, functional interaural distance gives an estimate of the interaural time delay available to an animal. It also provides an indication of the available binaural intensity difference of a sound at the two ears because the smaller the functional interaural distance, the higher an animal must hear for its head to generate an interaural intensity difference. Thus, the smaller an animal's functional head size, the higher it must hear in order to use high-frequency locus cues, and these become more important.

Figure 1 illustrates the relationship between functional interaural distance and highest frequency audible at 60 dB sound pressure level (SPL) re 20 μPa. The underwater audiograms (3 cetaceans and 3 seals) are identified by name. These species have been included in this figure for many years (e.g., Heffner and Heffner, 1980). Note that Fig. 1 contains two points for the killer whale: an earlier audiogram by Hall and Johnson (1972), and the recent audiogram by Branstetter *et al.* (2017), which includes data from Szymanski *et al.* (1999). As can been seen, the high-frequency limit for the killer whales changed from 32 kHz (the "1972" point), below the regression line, to 100 kHz (the "2017" point), above the regression line. The value found by Branstetter *et al.* is more consistent with our results for other echolocators which hear higher than

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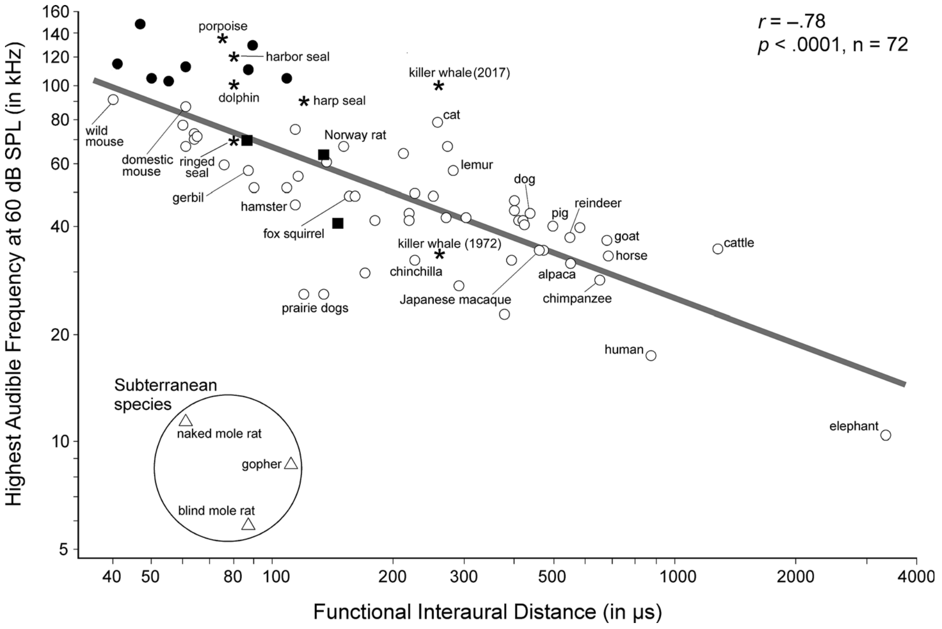

FIG. 1. Relation between the highest frequency audible at 60 dB SPL (re 20 μPa) and functional interaural distance, measured as the maximum time required for a sound to travel from one ear to the other (around the head from the opening of one auditory meatus to the other in air and through the head from one cochlea to the other underwater). Stars indicate seals and cetaceans tested underwater, filled circles indicate bats that use laryngeal echolocation, filled squares indicate bats that do not echolocate and the Egyptian fruit bat that uses clicks, open circles are terrestrial mammals, and open triangles are subterranean rodents. (Subterranean rodents do not localize sound and are not included in the regression analysis.) For references to individual species, see Heffner *et al.*, 2013, 2014; Koay *et al.*, 1998.

predicted based on non-echolocating mammals. Specifically, we previously reported that echolocating bats hear on average 0.7 octaves higher than an average non-echolocator having the same interaural distance (Heffner *et al.*, 2013). At that time, we noted that the same seemed to apply to echolocating cetaceans. Although the killer whale originally appeared to be an exception because it was below the regression line, the audiograms of Branstetter *et al.* and Szymanski *et al.* show that it is not.

When comparing air and underwater audiograms, there are two factors to be considered. The first is to correct for the different reference levels as the SPL in air is referenced to 20 μPa, whereas the SPL for underwater measurements is referenced to 1 μPa. To do this adjustment, one subtracts 26 dB from the underwater thresholds. The second is to equate the audiograms in terms of watts, which takes into account the different densities of the media. For this, one subtracts an additional 35.5 dB from the underwater threshold (e.g., Wodinsky and Tavolga, 1964).

In obtaining the highest frequency audible at 60 dB SPL for underwater audiograms, we have only corrected for the difference in reference levels and thus only subtract 26 dB from the underwater thresholds. The main problem with subtracting an additional 35.5 dB is that it reduces the number of underwater audiograms that can be compared because few studies have tested at such high sound pressure levels. (Indeed Branstetter *et al.* encountered this problem and used the 100-dB re 1 μPa definition of high-frequency cutoff, instead of the 121.5-dB re 1 μPa level that the full correction would call for.) It should be noted, however, that thresholds increase rapidly as the upper frequency limit is approached. The upper limit for the killer whale that we use, taken from the model data plotted in Fig. 3 of Branstetter *et al.* would increase from 100 to 130 kHz if we were to include the correction for the density of the media—an increase of about 1/3 octave. Nevertheless, regardless of how air and underwater audiograms are equated, we expected that cetaceans and seals would have good high-frequency hearing for passive sound localization, with the use of echolocation increasing it for cetaceans, as it does for bats. Just how much cetaceans hear beyond that required for passive sound localization may be estimated by comparing their hearing with the underwater hearing of seals, which do not echolocate.

The correlations between functional interaural distance, body weight (mass), and high-frequency hearing for the animals in Fig. 1 are shown in Table I. Although both functional interaural distance and body weight are reliably correlated with high-frequency hearing, functional interaural distance accounts for far more of the variance ($r^2 = 0.61$, $p < 0.0001$) than does body weight ($r^2 = 0.14$, $p = 0.0006$). Moreover, when a multiple regression analysis is conducted, functional interaural distance remains a strong predictive factor ($r^2 = 0.53$, $p < 0.0001$), but body weight weakens further ($r^2 = 0.08$, $p = 0.0155$. In summary, mammalian high-frequency hearing is robustly

TABLE I. Simple linear and multiple correlations between the log values of Functional interaural distance, Highest frequency audible at 60 dB SPL, and Body weight (mass) for the 72 mammals shown in Fig. 1 (excluding subterranean mammals).

Parameters	Correlation and probability
Simple linear correlations	
Functional interaural distance × High-frequency hearing:	$r = -0.779$, $p < 0.0001$
Body weight × High-frequency hearing:	$r = -0.380$, $p = 0.0006$
Functional interaural distance × Body weight:	$r = +0.748$, $p < 0.0001$
Multiple correlations	
Functional interaural distance × High-frequency hearing,	
Controlling for Body weight:	$r = -0.727$, $p < 0.0001$
Body weight × High-frequency hearing,	
Controlling for Functional interaural distance:	$r = +0.286$, $p = 0.0155$

predicted by *functional* interaural distance and only weakly predicted by body weight.

With regard to cetaceans, Branstetter *et al.* found a correlation between body mass and high-frequency hearing of $r^2 = 0.98$. However, this was based on only four species, which is a very small number to draw any definitive conclusions and does not permit multiple regression analysis. Although data were available for three additional species of cetaceans, they were not included because the studies each tested only one animal. Nevertheless, it would have been of interest to calculate the correlation with all seven species.

In remarking on the correlation between body mass and high-frequency hearing, Branstetter *et al.* note that size is also correlated with an animal's vocal anatomy and that auditory morphology may be scaled with body mass thus placing constraints on high-frequency hearing. With regard to vocal anatomy, we note that no one so far has attempted to correlate the frequency range of an animal's vocalizations with its high-frequency hearing. Moreover, our informal observations suggest that it would more likely be correlated with the frequency of best hearing—for example, humans need only hear up to 4 kHz to understand speech via the telephone, but require hearing above 4 kHz to use pinnae localization cues (e.g., Belendiuk and Butler, 1975). Regarding scaling, the idea that the size of the auditory apparatus and its consequent frequency response is passively determined by the size of an animal seems contrary to evolutionary principles. Specifically, the hearing abilities of animals are determined by what is useful for their success in their environment and the morphology of the ear evolves to match. As a result, there are small animals that have good low-frequency hearing (e.g., gerbils and least weasels) and other small animals that do not hear high frequencies (e.g., subterranean rodents). Thus, in correlating auditory morphology with behavioral hearing parameters, we would generally expect a good match, not because morphology determines hearing, but because the selective pressures on hearing determine the morphology needed to make that hearing possible. In short, we know of no evidence for constraints on high-frequency hearing in mammals; were it useful for a large mammal to hear high frequencies, it would seem possible for it to evolve a mechanism to permit that ability just as cetaceans have done.

It was the correlation between functional interaural distance and high-frequency hearing that led us to the hypothesis that selective pressure for passive sound localization resulted in mammals evolving the ability to hear above 10 kHz. Although correlations do not prove cause and effect, they do lead to predictions that can be tested. Indeed, testing began immediately after the hypothesis was proposed.

One of the first questions was whether the relationship between functional interaural distance and high-frequency hearing found in terrestrial mammals also applied to the underwater audiograms of seals and cetaceans—it did. This was the first discovery that severed the link between simple body weight and high-frequency hearing (Masterton *et al.*, 1969).

Another question was whether the relationship applied to the extremes of large and small mammals. The finding that it applied to elephants as well as to 12-g wild house mice indicated that it did apply to the extremes of size (Heffner and Heffner, 1980; Heffner and Masterton, 1980).

Another line of inquiry was whether mammals actually use high-frequency hearing for sound localization. The results indicated that most mammals require high frequencies for using both the binaural intensity-difference cue and pinna locus cues. Some small species, such as mice and rats, do not use the binaural time cue and rely exclusively on the binaural intensity and pinnae cues for localization. On the other hand, some hoofed mammals do not use the binaural intensity cue, but still require high-frequency hearing for using pinnae cues (Heffner *et al.*, 2014; 2015).

Finally, the theory that high-frequency hearing evolved to enable mammals to localize sound was made clear by the discovery that mammals that do not localize sound also do not have good high-frequency hearing. Specifically, subterranean rodents (blind mole rats, naked mole rats, and pocket gophers, see Fig. 1), can neither hear high frequencies nor localize brief sounds (e.g., Heffner and Heffner, 1993). This finding supports the theory that high-frequency hearing in mammals is related to sound localization while also providing examples of very small mammals that lack good high-frequency hearing.

In summary, we wish to emphasize that cetaceans are not exceptions, but, in fact, support the theory that high-frequency hearing evolved for passive sound localization. Moreover, as we have previously noted, echolocating bats and cetaceans have extended their high frequency hearing to accommodate echolocation.

We have here presented the evidence that was available to us when we wrote our previous articles. As more seal and cetacean audiograms have appeared, it would be of interest to see how they fit the analysis when their functional interaural distances become known. (For a recent summary of high-frequency hearing and sound localization, see Heffner and Heffner, 2016.)

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