

Letter to the Editor

## Response to Manley: An evolutionary perspective on middle ears

In his recent article on the evolution of middle ears, published in the May 2010 issue of *Hearing Research*, Manley states that we use “unscientific evolutionary terminology” giving the impression that evolution is, in his words, “purposeful”. We would like to respond to his statement, as well as to his subsequent assessment of our work on the evolution of mammalian high-frequency hearing.

Before proceeding, some errors in Manley’s paper should be corrected to avoid confusion. In “A cautionary note” (p. 7), Manley gives two quotes from our work to support his claim that we use inexact language; the attributions of these quotes are incorrect. The first is not from Masterton et al., but from [Heffner et al. \(2001\)](#). The second is from Masterton et al., but the correct date of the article is 1969.

Turning to the issue of evolutionary terminology, it is true that for over 40 years we have been using language that could be interpreted, if one were determined to do so, as indicating conscious motives. Indeed, such language is common in English descriptions of evolution, a prominent example being the title of Richard Dawkins’ book, “*The Selfish Gene*”, which, in spite of its title, does not mean that Dawkins is claiming that genes have conscious intent ([Dawkins, 1976](#)). This is because perfectly precise descriptions of evolutionary processes tend to be cumbersome, often getting in the way of understanding. However, to claim that our wording indicates intent, one must misconstrue our words. For example, the sentence quoted from [Masterton et al. \(1969, p. 975\)](#) that “. . . some mammals have lost their high-frequency sensitivity in order to gain low-frequency sensitivity . . .” [italics in [Manley, 2010](#)] is raising the possibility that there might be a trade-off between high- and low-frequency hearing, but does not specify the mechanism through which it might occur. To claim that this wording indicates intent on the part of mammals, one must ignore a subsequent sentence that “. . . high-frequency sensitivity may have been lost . . . through selective pressure for low-frequency sensitivity and against high-frequency sensitivity. . .” (italics in [Masterton et al., 1969](#)). In short, it is easy to draw conclusions contrary to an author’s meaning by taking words out of context, especially in scientific writing where complex arguments are constructed through a series of statements each building on and clarifying preceding points. Nevertheless, we are reluctant to change a style of writing that has been accepted by numerous reviewers and editors, even drawing the occasional compliment for its clarity.

With regard to our view that mammalian high-frequency hearing evolved for sound localization, Manley cites a correlation between body weight and high-frequency hearing ([Masterton et al., 1969](#)), noting that it is insufficient to prove anything. Of course. However, the correlation that led to our research on the evolution of high-frequency hearing used functional head size, not body weight as a correlate of high-frequency hearing and a difference of theoretical importance. And that correlation stimulated 40 years of research that led to the view that mammalian high-frequency hearing

evolved in conjunction with the pinnae that (using precise terminology) succeeded by enabling them to use pinnae locus cues that not only supplied additional cues for localizing in the horizontal plane, but also reduced front-back confusions and enabled them to localize in the vertical plane (for a recent summary of this work, see [Heffner and Heffner, 2008](#)).

We believe the real issue here is the conflation of two different levels of biological explanation ([Mayr, 1961](#)). At one level are how questions that ask how the ears or auditory system work to give animals the hearing abilities they have. Thus, for example, explaining an animal’s high-frequency hearing in terms of the anatomical features of the middle ear answers a how question and is referred to as a proximate explanation of hearing ability. At the other level are why questions that ask why an animal has the hearing abilities it has. Discovering the selective pressures that led to the evolution of mammalian high-frequency hearing answers a why question and is referred to as an ultimate explanation. It is important to keep in mind that the two types of explanations do not compete with each other, but are complementary, a fact sometimes overlooked. As Ernst Mayr wrote in 1961, “. . . many heated arguments about the “cause” of a certain biological phenomenon could have been avoided if the two opponents had realized that one of them was concerned with proximate and the other with ultimate causes”. We believe this is the case here; Manley is seeking answers to how questions whereas we are seeking answers to why questions. The answers to the two types of questions will be different, both can be correct, and both are required for a complete understanding.

### References

Dawkins, R., 1976. *The Selfish Gene*.



transitional organisms. That the results generally seen in eutherian (placental and marsupial) mammals – high upper frequency limits – were not inevitable can be seen by a glance at the low upper frequency limits in the monotreme mammals Platypus and Echidna that almost certainly have not “lost” a high-frequency capability. (e.g., Meng and Wyss, 1995).

# The Evolution of High-Frequency Hearing in All Mammals

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Manley's 2010 response to our Letter to the Editor (2010) states that our analysis does not explain high-frequency hearing in cetaceans nor the apparent lack of high-frequency hearing in monotremes. We disagree.

## **Manley misunderstands our correlation**

Many years ago, we found a correlation between the high-frequency hearing and the availability of the binaural time difference cues (Masterton et al., 1969). Manley incorrectly states that our correlation is between high-frequency hearing and "head width". It is not. The correlation we use is between high-frequency hearing and the maximum size of the binaural time difference cue that an animal can experience, which we refer to as "functional" interaural distance.

For terrestrial mammals, functional interaural distance is determined by dividing the distance around the head from the opening of one ear canal to the other by the speed of sound in air.

For marine mammals, water borne sound takes a different path requiring a different measure. Functional interaural distance is determined by dividing the distance between the bullae, measured *through* the head, by the *speed of sound in water* (which is much faster than in air)

