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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 "unscienti c 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 rst 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 Sel sh Genë, 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 lowfrequency 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 scienti c writing where complex arguments are constructed ththem 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 con ation 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 arrsvorss/a where questioneand 2010 feared to as an ghultissated explanafiein1.911939/interreare to Receip 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 in1961, ". many heated arguments about the "cause" of a certain biological phenomenon could have been avoided if the two opponents



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- Manley, G.A., 2010. An evolutionary perspective on middle ears. Hear. Res. 263, 3 –8. Masterton, B., Heffner, H., Ravizza, R., 1969. The evolution of human hearing. J. Acoust. Soc. Am. 45, 966–985.

Mayr, E., 1961. Cause and effect in biology: kinds of causes, predictability, and teleology are viewed by a practicing biologist. Science 134, 1501 –1506.

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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 HighFrequency Hearing in AMammals Henry E. Heffner and Rickye S. Heffner Written March 12, 2019

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

Manley misunderstands our correlation

Many years ago, we found a correlation between the highrequency hearing and the availability of the binaural time difference cues (Masterton et al., 1969). Manleincorrectly states that ourcorrelation is between highfrequency hearing ancheadwidth". It is not. The correlation we use isbetween highfrequency hearing and thearimumsize of the binaural time difference cute at an animal can experience, which we refer to as "functional" interaural distance.

For terrestrial mammals, functional inter aural distance is determined by dividing the distance around the head from the beening 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. Enctional interaural distance is determined by dividing the distance between the bullae, measure thorough the head, by the speed of sound in wate which is much faster than in air)

Darwin Wasalso Criticized for His Language

Henry E. Heffner and Rickye S. Heffner

: U L WJWMeH1Q, 2021

Jeff Manley objects to our use of language that, in his view, implies conscious motives on the part of evolution. He also rejects our noting that Richard Dawkin use of such language as Dawkins is writing for the general public whereas we are writifog a scientificaudience

Charles Darwin faced the same criticism. Here is how heesponded

³6HYHUDO ZULWHUV KDYH objected to the term Natural **Se**tion. Some « KDYH REMHFWHG WKDW

implies conscious choice in the animals which become modified; and it has even been urged that, as plants have no volition, natural selection is not applicable to them! In the literal sense of the wordho doubt, natural selection is a false term; but who ever objected to chemists speaking of the elective affinities of the various elements? and yet an acid cannot strictly be said to elect the base with which it in preference combines. It has been said that I speak of natural selection as

an active power or Deity; but who objects to an author speaking of the attraction of gravity as ruling the movements of the planets? Every one knows what is meant and is

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