



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—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) increased the reproductive success of mammals 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.

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Letter to the Editor

The origin and evolution of high-frequency hearing in (most) mammals

I am delighted to have the opportunity to clarify issues raised in my paper on the evolution of middle ears (Manley, 2010) as described in Heffner and Heffner's (2010) letter to the editor. First: my apologies to readers who may have been misled by the database errors in my citations which, fortunately, do not change my arguments.

It is interesting that Heffner and Heffner use Dawkins' (1976) book title to justify the use of implied conscious motives when discussing evolution. Apart from the question as to the interpretation of the title, it should be noted that Dawkins held the "Charles Simonyi Chair of Public Understanding of Science" at Oxford and his books are a fulfillment of the obligations implied by that title – mostly written for the general public. Nonetheless Dawkins' use of language is carefully thought out, including the use of eye-catching titles. This in no way reduces our obligations towards language use in the scientific literature.

My text was not intended in any way diminish the importance of the results of the Heffners' and colleagues' "forty years of research" (Heffner and Heffner, 2010). Their work led to the important observation that it is not so much body weight (Masterton et al., 1969) but head width (Heffner and Heffner, 2008) that correlates with sound localization cues.

Let me first clarify one point: There is no question that the earliest mammals were small animals with very short and uncoiled cochleae (e.g., length of basilar membrane ~3 mm, Luo et al., 2010; Manley, 2010; Vater et al., 2004). At some time during the transition from mammal-like amniotes to true mammals, changes in the configuration of the skull (including an increase in brain size and the development of a secondary palate) must have reduced the ancestral coupling between the middle ears (Manley, 2010). Our recent data in lizards (Christensen-Dalsgaard and Manley, 2005, 2008) demonstrated that such coupling can supply very strong sound localization information even at the level of the eardrums and of course at the auditory nerve. This was the condition in mammalian ancestors. The loss of such a coupling must have been a powerful selective pressure increasing the survival and reproductive abilities of those ancestral mammals that were better able to use alternative cues – and these cues must have required much more neural processing (Christensen-Dalsgaard and Carr, 2008; Manley, 2010). The use of such cues presumably led to a further increase in brain size and this again led to the effectively complete acoustical isolation of the two ears as seen in modern mammals. Any genetic tendency to increase upper frequency limits which, in the direct ancestors

of mammals and in the earliest mammals were almost certainly quite low (Vater et al., 2004), would have been of great selective advantage, as would any tendency to the development of pinnae. From such beginnings, the upper frequency limits rose in some mammalian lineages to high extremes. Since both (a) the cues available for sound localization from head shadowing and (b) the physics of sound reception by the middle ear (and of course of sound emissions in vocalizations) change with head size, it is not unexpected that very nice correlations exist between head size and high-frequency hearing (Heffner and Heffner, 2008). The exceptions (e.g., cetaceans such as dolphins that in spite of having large heads have extremely high upper frequency limits) only strengthen the understanding of mechanisms (these cetaceans have a very different, "aquatic" middle ear that circumvents the correlation between head size and eardrum dimensions in "air" middle ears).

Heffner and Heffner (2010) write: "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.we are seeking answers to *why* questions." On this point, I suggest that Heffner and Heffner have reached an incorrect answer to this "why" question. Evolutionary changes are often complex and selective pressures seldom act on a single feature. For example, the *de novo* development of a three-ossicle middle ear that ultimately made high-frequency hearing possible was the direct result of selective pressures changing the jaw structure related to changes in diet and mastication. Any improvements in high-frequency audition and sound localization that resulted from these changes were a lucky accident (sometimes also called "pre-adaptation") and not causal. It was highly fortuitous for the very small early mammals that the loss of the pressure-gradient middle ear could be compensated for by cues only made possible by the improving high-frequency capabilities of the (simultaneously-developed) new mammal-type middle ear. The latter undoubtedly preceded and drove the evolution of the elongation and coiling of the mammalian cochlea that made an extended hearing range possible. Thus the questions of the *how* and the *why* these changes occurred are in fact inseparably linked. In this case, the question as to *how* and *why* mammals developed high-frequency hearing can only be answered by an understanding of the (only apparently unrelated) changes that occurred in animal size, in the skull, jaw (feeding patterns) and buccal-middle-ear spaces of

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).

Thus great caution needs to be exercised regarding “why” questions, since they imply a causality in the course of evolutionary history and this methodology bears a high risk of misleading conclusions. Such post hoc explanations of distant historical events can generate compelling just-so stories (as emphasized by Stephen Jay Gould, e.g., Gould, 1977). As an additional example, the usual answer to the question as to why the tetrapod limb evolved from a fish fin would be a story about the limb being evolved in connection with locomotion on land. Such a story must now be regarded as incorrect – instead, the tetrapod limb evolved in aquatic forms with very similar life styles as their finned relatives (Clack, 2002).

Heffner and Heffner (2010) imply that being mainly interested in the “why” questions in some way justifies the use of different terminologies. I suggest that how and why questions are inseparable and only adequately answerable via the integration of detailed studies of early mammals on the one hand and comparative studies of modern land vertebrates on the other.

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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) as this is the path that water-borne sound takes when traveling from one bulla to the other. Thus cetaceans actually have a small functional interaural distance and Manley is incorrect when he says that cetaceans with their large heads are an exception to our correlation. Indeed, cetaceans have been included in this correlation and scatterplots since the relationship was first described (Masterton et al., 1969).

Monotremes

Manley states that good high-frequency hearing was not inevitable in mammals as the platypus and echidna do not appear to have evolved good high-frequency hearing.

That is not a problem for our theory as we argue that mammals evolved high-frequency hearing for sound localization which they use to guide their gaze to the source of a sound (e.g., Heffner and Heffner, 1992; 2018). So if monotremes do not hear high frequencies (i.e., above 10 kHz), then we predict that they have poor sound localization acuity—indeed, subterranean rodents that do not localize sound also do not have good high-frequency hearing. This is an empirical question that can be answered by obtaining monotreme's behavioral audiogram, sound localization acuity, and the width of their field of best vision.

Just-So Stories

Manley cites S. J. Gould for labeling evolutionary explanations as “just-so stories” implying that they are untestable. On the contrary, we have been testing our theory for many years by demonstrating that it applies to large mammals, small mammals, marine mammals, and echolocating mammals. It also applies to subterranean rodents as they do not localize sound and have subsequently lost the ability to hear high frequencies. For a recent summary, see Heffner and Heffner, 2018.

How and Why Questions

Manley states that how and why questions are inseparable. We agree that a complete understanding requires explanations at both levels. However, it is possible to answer Why questions without knowledge of the

mechanism. A classic example is Darwin's theory of natural selection as the explanation of adaptation and speciation (Darwin, 1859). Darwin was correct, although it wasn't until nearly 100 years later that the mechanism, genetics, was sufficiently understood to explain the How. In short, the study of the selective pressures on high-frequency hearing can proceed without knowledge of the physiological mechanisms involved.

Conclusion

The primary source of selective pressure on mammalian high-frequency hearing is the need to localize the source of a sound to direct the gaze to it.

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