LETTER TO THE EDITOR

Explaining High-Frequency Hearing

Kirk and Gosselin-Ildari (2009) have documented a reliable correlation between the volume of the cochlear labyrinth and high-frequency hearing limit among those Primates for which data are available. Specifically, the correlation shows that primates with small cochleas have better high-frequency hearing than those with larger cochleas. In discussing the implications of their finding, they provide a quote from one of our articles (Heffner, 2004) that they claim states that the size of the cochlea and the length of the basilar membrane are not functionally related to high-frequency hearing limit. However, that is a mistaken interpretation. The paragraph from which the quote is taken is making the point that the relationship between *functional* head size and high-frequency hearing limit is not explained by the size of the middle and inner ear. Functional head size is defined as the maximum time it takes for a sound to travel in air or water from one ear to the other. This measure indicates how high a mammal must hear to use the two high-frequency cues for sound localization—the binaural frequency-intensity spectral cues and pinna cues. The smaller the functional head size, the higher a mammal must hear for its head and pinnae to generate the high-frequency cues needed to locate the source of a sound.

Because both functional head size and the dimensions of the ear tend to increase with the size of the animal, it is necessary to perform a partial correlational analysis to determine how much of the variance in high-frequency hearing is accounted for by each factor. Restricting our analysis to those mammals that localize sound, there are 21 species for which we have data on functional interaural distance, basilar membrane length, and high-frequency hearing limit (Table 1). For these species, controlling for the length of the basilar membrane causes the correlation between functional head size and high-frequency hearing, $r = -0.870$ ($P < 0.0001$), to fall only slightly to $r = -0.814$ ($P < 0.0001$). However, the correlation between high-frequency hearing and the length of the basilar membrane, $r = -0.578$ ($P = 0.006$), falls to chance, $r = +0.269$ ($P = 0.257$), when controlling for functional head size. This is why we say that the relationship between functional head size and high-frequency hearing is not explained by the size of the inner ear.

Kirk and Gosselin-Ildari have found that among the 10 primates for which data are available, the size of the cochlea is a good predictor of high-frequency hearing; indeed, in this sample, it is a slightly better predictor of high-frequency hearing ($r = -0.780$) than functional head size ($r = -0.660$). Thus, we agree that when looking at fossil primates of similar size to those in the sample, the size of the cochlea may give a good estimate of their high-frequency hearing. However, the correlation between the size of the cochlea and high-frequency hearing among a broader sample of mammals is low enough that, contrary to a natural inclination to equate anatomy with behavior, it remains risky to do so.

Note that we do not include mammals that do not localize sound (subterranean rodents) in the correlations with high-frequency hearing. This is because we explain high-frequency hearing as evolving in mammals under selective pressure to localize sound. Thus, we expect that any mammal that does not localize sound will not hear high frequencies, and subterranean rodents do not—thus serving as exceptions that prove the rule. However, the poor high-frequency hearing in these species poses a problem for the view that high-frequency hearing is determined by the size of the cochlea as their cochleas are relatively small yet their high-frequency hearing is extremely limited compared with other species with similar-sized cochleas (see Table 2 in Kirk and Gosselin-Ildari). For a presentation of our views on the evolution of high-frequency hearing, see Heffner and Heffner (2008).

Finally, we should note that the explanation of the variation in high-frequency hearing offered by Kirk and Gosselin-Ildari addresses proximate mechanisms underlying hearing, that is, how mammals hear high frequencies. Such explanations are complementary to ultimate explanations that look for selective pressures acting on hearing, that is, why mammals hear high frequencies (Mayr, 1961). Failing to recognize the difference between proximate and ultimate explanations in biology and their complementary nature has been the source of many needless conflicts (Mayr, 1961). It is important to recognize that both types of explanations are important for a full understanding of any biological function.

Rickye S. Heffner and Henry E. Heffner
Department of Psychology
University of Toledo
Toledo, Ohio
email: Rickye.Heffner@utoledo.edu

TABLE 1. High-frequency hearing limit (kHz), functional interaural distance (μs), and basilar membrane length (mm) of 21 species of mammals

Species	High-frequency Hearing Limit (kHz)[a]	Functional Interaural Distance (μs)[b]	Basilar Membrane Length (mm)
Virginia Opossum (*Didelphis virginiana*)	68[c]	273	12.3[d]
Opossum (*Monodelphis domestica*)	76[e]	114	6.4[f]
Tree Shrew (*Tupaia glis*)	61[g]	136	14.3[h]
Greater Horseshoe Bat (*Rhinolophus ferrumequinum*)	103[i]	55	16.1[j]
Little Brown Bat (*Myotis lucifugus*)	115[k]	41	6.9[l]
Squirrel Monkey (*Saimiri sciureus*)	43[m]	302	22[n]
Pigtail Macaque (*Macaca nemestrina*)	34.5[o]	470	25.6[p]
Human (*Homo sapiens*)	17.6[q]	875	33.5[l,r]
Rabbit (*Oryctolagus cuniculus*)	49[s]	250	15.6[d]
Kangaroo Rat (*Dipodomys merriami*)	52[s]	90	11[n,t]
Gerbil (*Meriones unguiculatus*)	58[u]	87	11.9[d,v]
Lab Rat (*Rattus norvegicus*)	68[w]	150	9.5[d,x]
House Mouse (wild; *Mus musculus*)	92[s]	40	6.0[x]
House Mouse (laboratory; *Mus musculus*)	88[y]	61	6.5[x]
Hamster (*Mesocricetus auritus*)	46.5[z]	114	7.3[d]
Guinea Pig (*Cavia porcellus*)	49[aa]	160	19.5[d,bb]
Chinchilla (*Chinchilla lanigera*)	32.5[cc]	225	18.5[dd]
Cat (*Felis domesticus*)	79[ee]	258	23.3[d,r]
Indian Elephant (*Elephas maximus*)	10.5[ff]	3350	59[gg]
Cattle (*Bos taurus*)	35[hh]	1281	38[gg]
Porpoise (in water; *Tursiops truncates*)	136[ii]	75	40.7[jj]

[a]Highest audible frequency at 60-dB SPL.
[b]Time required for a sound to travel from one auditory meatus to the other or from one bulla to the other in the case of underwater animals.
[c]Ravizza et al., 1969.
[d]Bohne et al., 1977.
[e]Frost and Masterton, 1994.
[f]Muller et al., 1993.
[g]Heffner et al., 1969.
[h]Masterton, personal communication.
[i]Long and Schnitzler, 1975.
[j]Bruns and Schmieszek, 1980.
[k]Dalland, 1965.
[l]Bruns, 1985.
[m]Beecher, 1974; Green, 1975.
[n]Igarashi and Yoshinobu, 1965.
[o]Stebbins et al., 1966.
[p]Greenwood, 1990.
[q]Jackson et al., 1999; ISO standard 1961.
[r]Nadoll, 1988.
[s]Heffner and Masterton, 1980.
[t]Webster and Webster, 1977.
[u]Ryan, 1976.
[v]Plassmann et al., 1987.
[w]Heffner et al., 1994.
[x]Burda et al., 1988.
[y]Koay et al., 2002.
[z]Heffner et al., 2001.
[aa]Heffner et al., 1971.
[bb]Burda, 1984.
[cc]Heffner and Heffner, 1991.
[dd]Bohne and Carr, 1979.
[ee]Heffner and Heffner, 1985.
[ff]Heffner and Heffner, 1982.
[gg]Bekesy, 1953.
[hh]Heffner and Heffner, 1983.
[ii]Johnson, 1967.
[jj]Ketten, 1992.

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